BAT CONSERVATION
INTERNATIONAL

Bat Conservation and Management Workshop

COURSE BOOK

Carter Caves State Resort Park, KY 2011

Field Sites:
Carter Caves State Resort Park, Olive Hill KY

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Table of Contents

The World of Bats

By: Merlin D. Tuttle

Excerpted and updated with permission from *America's Neighborhood Bats*
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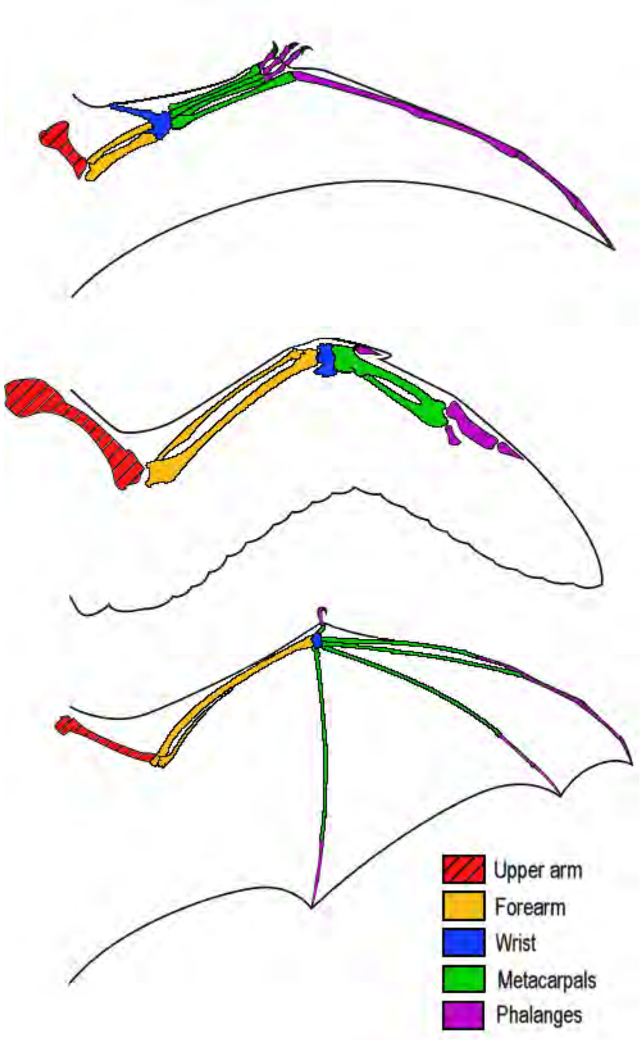
ORIGINS AND RELATIVES

Bat fossils have been found that date back approximately 50 million years, but, surprisingly, the bats of that ancient period very closely resembled those we know today. Thus, bats have been around for a very long time. Before humans began to affect their numbers, bats were extremely abundant. In some places they probably dominated the night skies just as passenger pigeons filled the daytime skies of the eastern United States prior to the nineteenth century. In the evolution of nature's system of checks and balances, bats long have played essential roles; their loss today could compromise the health and stability of our environment.

Bats are mammals, but such unique ones that scientists have placed them in a group of their own, the Chiroptera, which means hand-wing. All living bat species fit into one of two major groups, the Microchiroptera or the Megachiroptera. Members of the latter group are commonly referred to as flying foxes because of their fox-like faces. They are found only in the Old World tropics, while the Microchiroptera, which are highly varied in appearance, occur worldwide.

Like humans, bats give birth to poorly developed young and nurse them from a pair of pectoral breasts. In fact, Linnaeus, the father of modern taxonomy, was so impressed by the similarities between bats and primates (lemurs, monkeys, apes, and humans) that he originally put them into the same taxonomic group. Today's scientists generally agree that primates and bats share a common shrew-like ancestor, but belong to separate groups.

A heated debate was recently triggered by the discovery that flying foxes, primates, and flying lemurs share a unique brain organization. (Flying lemurs, apparently close relatives of the true lemurs of Madagascar, are a poorly known group of cat-size gliding mammals that live in the Indonesian region and, like bats, are in a separate group of their own, the Dermoptera.) Did both the Micro- and Megachiroptera come from a single, shrew-like, gliding ancestor, or did the flying foxes evolve separately from primates? If the latter notion is correct, are their unique brain characteristics sufficient reason for reclassifying flying lemurs and flying foxes as primates? The issue remains unresolved, but most scientists agree that bats are far more closely related to primates than to the rodents with which they often are linked in the public mind.



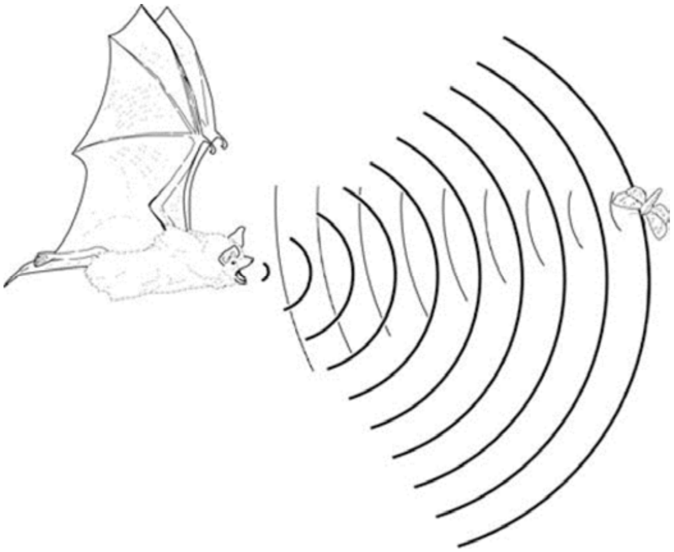
DIVERSITY AND DISTRIBUTION

Over one thousand kinds of bats amount to nearly a quarter of all mammal species, and they are found everywhere except in the most extreme desert and polar regions. Over forty species live in the United States and Canada, but the majority inhabit tropical forests where, in total number of species, they sometimes outnumber all other mammals combined.

Bats come in an amazing variety of sizes and appearances. The world's smallest mammal, the bumblebee bat of Thailand, weighs less than a penny, but some flying foxes of the Old World tropics have wingspans of up to 6 feet. The big-eyed, winsome expressions of flying foxes often surprise people who would never have thought that a bat could be attractive. Some bats have long angora-like fur, ranging in color from bright red or yellow to jet-black or white. One species is furless, and another even has pink wings and ears. A few are so brightly patterned that they are known as butterfly bats. Others have enormous ears, nose leaves, and intricate facial features that may seem bizarre at first, but become more fascinating than strange when their sophisticated role in navigation is explained.

NAVIGATION AND MIGRATION

Like dolphins, most bats communicate and navigate with high-frequency sounds. Using sound alone, bats can "see" everything but color, and in total darkness they can detect obstacles as fine as a human hair. The sophistication of their unique echolocation systems surpasses current scientific understanding and on a watt-by-watt, ounce-per-ounce basis has been estimated to be literally billions of times more efficient than any similar system developed by humans. In addition, bats are not blind and many have excellent vision.



In temperate regions, cold winters force bats to migrate or hibernate. Most travel less than 300 miles to find a suitable cave or abandoned mine, where they remain for up to six months or more, surviving solely on stored fat reserves. However, several species are long-distance migrators, traveling from as far north as Canada to the Gulf-states or Mexico for the winter. A few species can survive short-term exposure to sub-freezing temperatures, enabling them to over-winter in cliff faces or in the outer walls of buildings.

Typically, bats are very loyal to their birthplaces and hibernating sites, but how they find their way over the long distances that often exist between their hibernating and summer caves remains largely a mystery. It appears that some orient visually, using mountain ranges and other landmarks to guide them, but a few are known to have found their way even when blinded. Information about how to find obscure sites, such as small cave entrances, apparently is passed on from generation to generation.

COURTSHIP, REPRODUCTION, AND LONGEVITY

Most bats that live in temperate regions, such as the United States and Canada, mate in the fall just before entering hibernation. Some sing, do wing displays, and perhaps more to attract mates, but little is known about the details. Ovulation and fertilization (through sperm that have been dormant in the female reproductive tract since the previous fall) occur in the spring as females emerge from hibernation. Pregnant females then move from hibernating sites (hibernacula) to warmer roosts, where they form nursery colonies. Birth occurs approximately a month and a half to two months later. The young grow rapidly, often learning to fly within three weeks. While they are being reared, males and non-reproductive females often segregate into separate groups called bachelor colonies.

Some tropical bats engage in elaborate courtship displays. For example, male epauletted bats sing and flash large fluffs of white shoulder fur to attract mates, while male crested bats perform a spectacular display by expanding long hairs on top of the head, similar to a peacock spreading its tail. At least a few tropical species are monogamous, sharing hunting and family duties. Vampire bats even adopt orphans, unusual for any wild animal.

Bats are, for their size, the slowest reproducing mammals on earth. On average, mother bats rear only one young per year, and some do not give birth until they are two or more years old. Exceptionally long-lived, a few survive for more than 34 years.

FEEDING AND ROOSTING BEHAVIOR

Although 70 percent of bats eat insects, many tropical species feed exclusively on fruit or nectar. A few are carnivorous, hunting small vertebrates, such as fish, frogs, mice, and birds. Despite their notoriety, vampire bats make up only a small portion of all bats (there are only three species), and they live only in Latin America. With the exception of three species of nectar-feeding bats that live along the Mexican border of Arizona and Texas, all bats in the United States and Canada are insectivorous.

Bats can be found living in almost any conceivable shelter, though they are best known for living in caves. Many species that now live mostly in buildings do so, at least in part, because they have few alternatives. Tropical species occupy a wider range of roost sites than temperate species. For example, some make tent-like roosts by biting through the midribs of large leaves, and several species have suction discs on their wings and feet that enable them to live in the slick-walled cavities formed by unfurling leaves, such as those of the banana plant. Others live in animal burrows, flowers, termite nests, and even in large tropical spider webs. Despite the wide variety of roosts used by bats, many species have adapted to living in roosts of only one or a few types and cannot survive anywhere else.

ECOLOGICAL AND ECONOMIC VALUE

Worldwide, bats play essential roles in keeping populations of night-flying insects in balance. Just one bat can catch hundreds of insects in an hour, and large colonies catch tons of insects nightly, including beetle and moth species that cost American farmers and foresters billions of dollars annually, not to mention mosquitoes in our backyards. The 20 million free-tailed bats from Bracken Cave in Central Texas, eat more than 200 tons of insects in a single mid-summer night!

Throughout the tropics the seed dispersal and pollination activities of fruit- and nectar-eating bats are vital to the survival of rain forests, with some bats acting as “keystone” species in the lives of plants crucial to entire ecosystems. Many plants bloom at night, using unique odors and special flower shapes to attract bats. The famous baobab tree of the eastern African savannas is a good example. Only bats approach from below in a manner likely to contact the flower’s reproductive organs and achieve pollination. Of course they do so because the plant rewards them handsomely with nectar. This tree is so important to the survival of other kinds of wildlife that it is often referred to as the “Tree of Life.”

Wild varieties of many of the world’s most economically valuable crop plants also rely on bats for survival. Some of the better-known commercial products are fruits such as bananas, breadfruit, avocados, dates, figs, peaches, and mangoes. Others include cloves, cashews, carob, balsa wood, kapok (filler for life preservers), and even tequila. Most of the plants from which these products come are now commercially cultivated, but the maintenance of wild ancestral stocks is critically important. They are the only source of genetic material for developing disease-resistant strains, rejuvenating commercial varieties, and for producing new, more productive plants in the future.

We already know that more than 300 plant species in the Old World tropics alone rely on the pollinating and seed dispersal services of bats, and additional bat-plant relationships are constantly being discovered. These plants provide more than 450 economically important products, valued in the hundreds of millions of dollars annually. Just one, the durian fruit of Southeast Asia, sells for $120 million each year and relies almost exclusively on flying foxes for pollination. Other products from these 300-plus plants include 110 for food and drinks, 72 for medicines, 66 for timber and wood derivatives, 34 for ornamentals, 29 for fiber and cordage, 25 for dyes, 19 for tannins, 11 for animal fodder, and 8 for fuel. Numerous additional bat-dependent plants of the New World tropics are of similarly great importance.

The value of tropical bats in reforestation alone is enormous. Seeds dropped by bats can account for up to 95 percent of forest re-growth on cleared land. Performing this essential role puts these bats among the most important seed-dispersing animals of both the Old and New World tropics.

Studies of bats have contributed to the development of navigational aids for the blind, birth control and artificial insemination techniques, vaccine production, and drug testing, as well as to a better understanding of low-temperature surgical procedures. Unfortunately, however, careless exploitation of bats has sometimes decimated local populations, and careful management planning is required.

Bats of the United States and Canada

(47 Species)

FAMILY MORMOOPIDAE

Mormoops

Mormoops megalophylla – ghost-faced bat (Peter's ghost-faced bat)

FAMILY PHYLLOSTOMIDAE

Artibeus

Artibeus jamaicensis – Jamaican fruit-eating bat

Choeronycteris

Choeronycteris mexicana – Mexican long-tongued bat

Leptonycteris

Leptonycteris nivalis – greater long-nosed bat
Leptonycteris yerbabuenae (*sanborni*, *curasoae*-in part) – northern long-nosed bat (lesser long-nosed bat)

Macrotus

Macrotus californicus – California leaf-nosed bat

FAMILY VESPERTILIONIDAE

Antrozous

Antrozous pallidus – pallid bat

Corynorhinus (formerly, Plecotus)

Corynorhinus rafinesquii – Rafinesque's big-eared bat
Corynorhinus townsendii – Townsend's big-eared bat

Eptesicus

Eptesicus fuscus – big brown bat

Euderma

Euderma maculatum – spotted bat

Idionycteris

Idionycteris phyllotis – Allen's big-eared (lappet-browed) bat

Lasionycteris

Lasionycteris noctivagans – silver-haired bat

Lasiurus

Lasiurus blossevillii – western red bat
Lasiurus borealis – (eastern) red bat
Lasiurus cinereus – hoary bat
Lasiurus ega – southern yellow bat
Lasiurus intermedius – northern yellow bat
Lasiurus seminolus – Seminole bat
Lasiurus xanthinus – western yellow bat

Myotis

Myotis auriculus – southwestern myotis
Myotis austroriparius – southeastern myotis
Myotis californicus – California myotis
Myotis ciliolabrum – western small-footed myotis
Myotis evotis – long-eared myotis
Myotis grisescens – gray myotis
Myotis keenii – Keen's myotis
Myotis leibii – eastern small-footed myotis
Myotis lucifugus – little brown myotis
Myotis melanorhinus – dark-nosed small-footed bat
Myotis occultus – Arizona myotis
Myotis septentrionalis – northern (long-eared) myotis
Myotis sodalis – Indiana myotis
Myotis thysanodes – fringed myotis
Myotis velifer – cave myotis
Myotis volans – long-legged myotis
Myotis yumanensis – Yuma myotis

Nycticeius

Nycticeius humeralis – evening bat

Pipistrellus

Parastrellus (=Pipistrellus) hesperus – canyon bat (formerly, western pipistrelle)
Perimyotis (=Pipistrellus) subflavus – tri-colored bat (formerly, eastern pipistrelle)

FAMILY MOLOSSIDAE

Eumops

Eumops floridanus – Florida bonneted bat (formerly, Wagner's mastiff bat, *Eumops glaucinus*)
Eumops perotis – western bonneted bat (mastiff bat)
Eumops underwoodi – Underwood's bonneted bat (Underwood's mastiff bat)

Molossus

Molossus molossus – Pallas's mastiff bat

Nyctinomops

Nyctinomops femorosaccus – pocketed free-tailed bat
Nyctinomops macrotis – big free-tailed bat

Tadarida

Tadarida brasiliensis – Brazilian (Mexican) free-tailed bat

Simons, N.B. (In press.) Chiroptera. In: D.E. Wilson and D.M. Reeder (Eds.). *Mammal Species of the World: A Taxonomic and Geographic Reference* (Smithsonian Series in Comparative Evolutionary Biology) 3rd Edition. Smithsonian Inst. Press, Washington DC.

Status of Bats in the United States

by: Michael J. Harvey

American Caves, Vol. 10, No. 1: Pages 10-13, Spring/Summer 1997.

Of the forty-five U.S. bat species, six wholly or partially (i.e., certain subspecies) are considered endangered (in danger of extinction throughout all or a significant portion of their range) by the US. Fish and Wildlife Service as well as most state wildlife agencies. Five of the six are cave dwellers. Twenty additional entire species or subspecies, mostly cave bat species, are considered to be of special concern. Several of the remaining species, especially cave bats, also appear to be declining in numbers. Because of concern for the welfare of endangered, as well as other bat species, the necessity for protection and management of these species and their most critical habitat is evident. Before management recommendations could be formulated, studies had to be conducted to obtain pertinent data concerning distribution, status, and ecology of these species. Studies were initiated by several state and federal agencies. Primary objectives were to determine distribution and status of endangered and special concern species, to obtain information concerning various aspects of their ecology, and to formulate management recommendations. Gathering data about other non-endangered bat species was an additional objective. Techniques used included searching caves previously known to be inhabited by bats and attempting to locate additional bat caves. In addition to identifying important bat caves, sampling for the presence of bats was done by mist-netting or by using bat traps at numerous locations.

Mist nets are large (up to 3 x 18 m; 10 x 60 ft) nets made of very fine thread, which are used to capture flying bats. Bat traps consist of two frames a few inches apart over which are strung very thin vertical wires, one inch (2.5 centimeters) apart. Bats flying into a trap detect and avoid the first set of wires, then hit the second set of wires and fall into a collecting bag. Observations of bat activity were made using night vision (or starlight) scopes and with ultrasonic bat detectors, devices that render ultrasonic bat cries audible to human ears. On some occasions, bats were fitted with small vials containing a chemical light substance (Cyalume) to study flight behavior and to determine foraging habitat and movements. Some bats were also studied by fitting them with tiny radio transmitters and tracking their movements with directional antennae and radio receivers. To study migration and movement patterns, numerous bats were banded with colored, celluloid, numbered, wing bands or with numbered metal bands provided by the U.S. Fish and Wildlife Service. Temperature and humidity at roost sites were also obtained. Other data gathered included information on sex ratios, reproduction, swarming, longevity, food habits, mortality, effects of cave gates and fences, and various other behavioral and ecological data. Long-term monitoring programs were initiated to determine population trends over time and to ascertain the effectiveness of management measures already initiated. The U.S. Fish and Wildlife Service has had Recovery Plans prepared for endangered bats by Recovery Teams comprised of bat experts.

Certain protective management measures have already been taken, as recommended in the Recovery Plans. These include gating or fencing important bat caves and placing of warning signs at other caves to minimize human disturbance to bat colonies. Signs placed at selected cave entrance tell what endangered bat species inhabit the cave, the season when they are present, information concerning bats' beneficial nature, and adverse effects of disturbing bat colonies. Signs also point out that entering these caves during restricted times is a violation of the Federal Endangered Species Act, punishable by fines of up to $50,000 for each violation. Several state and federal agencies and organizations are now actively involved in bat conservation. These include state wildlife agencies, U.S. Fish and Wildlife Service, U.S. Forest Service, National Park Service, Bureau of Land Management, U.S. Army Corps of Engineers, Tennessee Valley Authority, state parks, natural heritage commissions, Nature Conservancy, National Speleological Society, Cave Research Foundation, Bat Conservation International, and the American Cave Conservation Association. Members of several other organizations and numerous private landowners and other individuals are also involved. All are to be commended for their efforts. Information concerning the location of additional important bat caves is needed as part of the continuing bat conservation effort. Individuals with knowledge of caves containing bat colonies should contact appropriate wildlife agency personnel.

ENDANGERED CAVE BATS

Leptonycteris curasoae, Lesser Long-nosed Bat

A resident of desert-scrub country, the lesser long-nosed bat occurs in the southwestern U.S. to southern Mexico. It is colonial, occupying mines and caves at the base of mountains where the alluvial fan supports agaves, yuccas, saguaros, and organ pipe cacti. Like other leaf-nosed bats, it will take flight when disturbed. When launching, it gives several strong wing beats, bringing the body into a horizontal position before releasing its grip. It is an agile flier, and can fly nearly straight up while maintaining a horizontal body position. Flight is rapid and direct, showing none of the fluttering movements characteristic of most insectivorous bats. It emerges late in the evening, about one hour after sundown. The long tongue, covered with hair-like papillae toward the tip, is well adapted for feeding at flowers. These bats may land on the flowering stalk of agaves and insert their long snouts into each blossom. After feeding, the stomach is so distended that the bat appears to be in late pregnancy. When the stomach is filled, they retire to a night roost where they hang up and rest. Nectar, pollen, and insects are consumed, but fruits are eaten after the flowering season is past. One baby is born in late May or June. Maternity colonies may number into the thousands of individuals. This bat appears to be locally common in southeastern Arizona.

Leptonycteris nivalis, Greater Long-nosed Bat

This bat is found from the Big Bend region of Texas, southward across most of Mexico to central Guatemala. It is a colonial cave dweller that usually inhabits deep caverns, but also can be found in mines, culverts, hollow trees, and unoccupied buildings. It occupies a variety of habitats from high-elevation, pine-oak woodlands to sparsely vegetated deserts. The muzzle is greatly lengthened and this bat has a long protrusive tongue, which is attached to the posterior sternum. There are rows of hair-like projections that cover the area near the tip of the tongue, which aid in acquiring nectar. It emerges relatively late in the evening to feed. It is an agile flyer, capable of quick maneuvering and relatively high-speed flight. It makes swooshing sounds as it flies and can fly straight up while maintaining a horizontal body position. It feeds primarily on nectar, pollen, insects, and soft, succulent fruits of cactus during the non-flowering season. When foraging at agaves, it crawls down the stalk, thrusts its snout into the flowers, and licks nectar from them with its long tongue, which can be extended up to 7.5 centimeters (3 inches) and can reach nectar at the base of the corolla of the flowers. It emerges from the flowers covered with pollen and is an effective pollinator of many cacti, agaves, and other plants. It gives birth to one baby in April, May, or June. It is rare in the United States.

Myotis grisescens, Gray Bat

The gray bat occupies cave regions of Arkansas, Missouri, Kentucky, Tennessee, and Alabama, with occasional colonies found in adjacent states. Gray bats are cave residents year-round, but different caves usually are occupied in summer and winter. Few have been found roosting outside caves. They hibernate primarily in deep vertical caves with large rooms acting as cold air traps (5-11°C or 58-77°F). Summer roosts are often in caves with domed ceilings capable of trapping combined body heat from clustered individuals. Because of their specific habitat requirements, fewer than 5% of available caves are suitable for gray bats. Males and non-reproductive females form bachelor colonies in summer. Gray bats primarily forage over water of rivers and lakes. Moths, beetles, flies, mosquitoes, and mayflies are important in the diet, but gray bats also consume a variety of insects. Mating occurs in September and October, and females enter hibernation immediately after mating. Females store sperm through winter and become pregnant after emerging from hibernation. One baby is born in late May or early June, and begins to fly within 20-25 days of birth. The life span may exceed 14-15 years. About 90% of these bats hibernate in only nine caves making them extremely vulnerable to destruction.

Myotis sodalis, Indiana Bat

The Indiana bat occupies cave regions in the eastern United States. They usually hibernate in large dense clusters of up to several thousand individuals in sections of the hibernation cave where temperatures average 3-6°C (38-43°F) and with relative humidities of 55-95%. They hibernate from October to April, depending on climatic conditions. Females depart hibernation caves before males and arrive at summer maternity roosts in mid-May. The summer roost of adult males often is near maternity roosts, but where most spend the day is unknown. Others remain near the hibernaculum, and a few males are found in caves during summer. Between early August and mid-September, Indiana bats arrive near their hibernation caves and engage in swarming and mating activity. Swarming at cave entrances continues into mid- or late October. During this time, fat reserves are built up for hibernation. When pregnant, females eat soft-bodied insects; they eat moths when lactating, and moths, beetles, and hard-bodied insects after lactation. Males also eat a variety of insects. One baby is born in June, and is raised under loose tree bark, primarily in wooded-streamside habitat. Life spans of nearly 14 years have been documented. The present total known population is approximately 350,000, with more than 85% hibernating at only nine locations making them extremely vulnerable to destruction. Populations continue to decrease in spite of recovery efforts.

***Corynorhinus townsendii*, Townsend's big-eared bat**

This species occurs in western Canada, the western United States to southern Mexico, and as a few isolated populations in the eastern United States. They hibernate in caves or mines where the temperature is 12°C (54°F) or less, but usually above freezing. Hibernation sites in caves often are near entrances in well-ventilated areas. If temperatures near entrances become extreme, they move to more thermally stable parts of the cave. They hibernate in clusters of a few to more than 100 individuals. During hibernation, the long ears may be erect or coiled. Solitary bats sometimes hang by only one foot. Maternity colonies usually are located in relatively warm parts of caves. During the maternity period, males apparently are solitary. Where most males spend the summer is unknown. No long-distance migrations are known. Like many other bats, they return year after year to the same roost sites. It is believed that they feed entirely on moths. Mating begins in autumn and continues into winter, sperm are stored during winter, and fertilization occurs shortly after arousal from hibernation. One baby is born in June. Babies are large at birth, weighing nearly 25% as much as their mothers. They can fly in two and a half to three weeks and are weaned by six weeks. Life span may be 16 or more years. They are locally relatively common in the western United States, but eastern populations (the Virginia and Ozark big-eared bats) are endangered. It is believed that fewer than 12,000 individuals exist in the eastern United States.

SUMMARY

Bats comprise an extremely interesting and highly beneficial segment of our fauna. They should be understood and appreciated, not feared and persecuted. Like many wild animals, they sometimes pose public health problems or become nuisances by residing where they are not wanted. However, their benefit as the only major predator of night-flying insects greatly outweighs their negative aspects. Although only seven U.S. bat species or subspecies are listed as endangered, most species seem to be steadily declining in number, some at a rapid rate. Human disturbance to hibernating and maternity colonies and the all too prevalent attitude that "the only good bat is a dead bat," have been important factors in declining bat populations. Habitat destruction and the use of pesticides and other chemical toxicants have no doubt also taken a heavy toll, not only of bats, but of many other fascinating and beneficial species as well. The steady decline in bat numbers, as well as that of many other species, represents much more than just a decrease in a population of organisms. It reflects a steady decline in our overall quality of life as well.

Status of U.S. Bats

END = Endangered Species or Subspecies • SC = Of Special Concern

Mormoops megalophylla, Ghost-faced Bat	
Macrotus californicus, California Leaf-nosed Bat	SC
Choeronycteris mexicana, Mexican Long-tongued Bat	SC
Leptonycteris curasoae, Lesser Long-nosed Bat	
L. c. yerbabuenae, Lesser Long-nosed Bat	END
Leptonycteris nivalis, Greater Long-nosed Bat	END
Artibeus jamaicensis, Jamaican Fruit Bat	
Myotis auriculus, Southwestern Bat	
Myotis austroriparius, Southeastern Bat	SC
Myotis californicus, California Bat	
Myotis ciliolabrum, Western Small-footed Bat	SC
Myotis evotis, Western Long-eared Bat	SC
Myotis grisescens, Gray Bat	END
Myotis keenii, Keen's Bat	
Myotis leibii, Eastern Small-footed Bat	SC
Myotis lucifugus, Little Brown Bat	
M. l. occultus, Arizona Bat	SC
Myotis septentrionalis, Northern Long-eared Bat	
Myotis sodalis, Indiana Bat	END
Myotis thysanodes, Fringed Bat	SC
Myotis velifer, Cave Bat	SC
Myotis volans, Long-legged Bat	SC
Myotis yumanensis, Yuma Bat	SC
Lasionycteris noctivagans, Silver-haired Bat	
Parastrellus (=Pipistrellus) hesperus, Western Pipistrelle Bat	
Perimyotis (=Pipistrellus) subflavus, Eastern Pipistrelle Bat	
Eptesicus fuscus, Big Brown Bat	
Lasiurus blossevillii, Western Red Bat	
Lasiurus borealis, Eastern Red Bat	
Lasiurus cinereus, Hoary Bat	
L. c. semotus, Hawaiian Hoary Bat	END
Lasiurus ega, Southern Yellow Bat	
Lasiurus intermedius, Northern Yellow Bat	
Lasiurus seminolus, Seminole Bat	
Lasiurus xanthinus, Western Yellow Bat	
Nycticeius humeralis, Evening Bat	
Euderma maculatum, Spotted Bat	SC
Idionycteris phyllotis, Allen's Big-eared Bat	SC
Corynorhinus rafinesquii, Rafinesque's Big-cared Bat	SC
Corynorhinus townsendii, Townsend's Big-eared Bat	
C. t. virginianus, Virginia Big-cared Bat	END
C. t. ingens, Ozark Big-cared Bat	END
C. t. pallescens, Western Big-eared Bat	SC
C. t. townsendii, Townsend's Big-eared Bat	SC
Antrozous pallidus, Pallid Bat	
Molossus molossus, Pallas' Mastiff Bat	
Tadarida brasiliensis, Brazilian Free-tailed Bat	
Nyctinomops femorosaccus, Pocketed Free-tailed Bat	
Nyctinomops macrotis, Big Free-tailed Bat	SC
Eumops glaucinus, Wagner's Mastiff Bat	
E.g. floridanus, Florida Mastiff Bat	SC
Eumops perotis, Greater Mastiff Bat	
E.p. californicus, Western Mastiff Bat	SC
Eumops underwoodi, Underwood's Mastiff Ba	

Bats of the Eastern United States

(East of the Mississippi)

(20 species)

FAMILY PHYLOSTOMIDAE – NEW WORLD LEAF-NOSED BATS

Artibeus amaicensis	Jamaican fruit-eating bat (FL Keys only)

FAMILY MOLOSSIDAE – FREE-TAILED BATS

Eumops floridanus	Florida bonneted bat (southern FL only)
Molossus molossus	Pallas’ mastiff bat (FL Keys only)
Tadarida brasiliensis	Mexican free-tailed bat‡

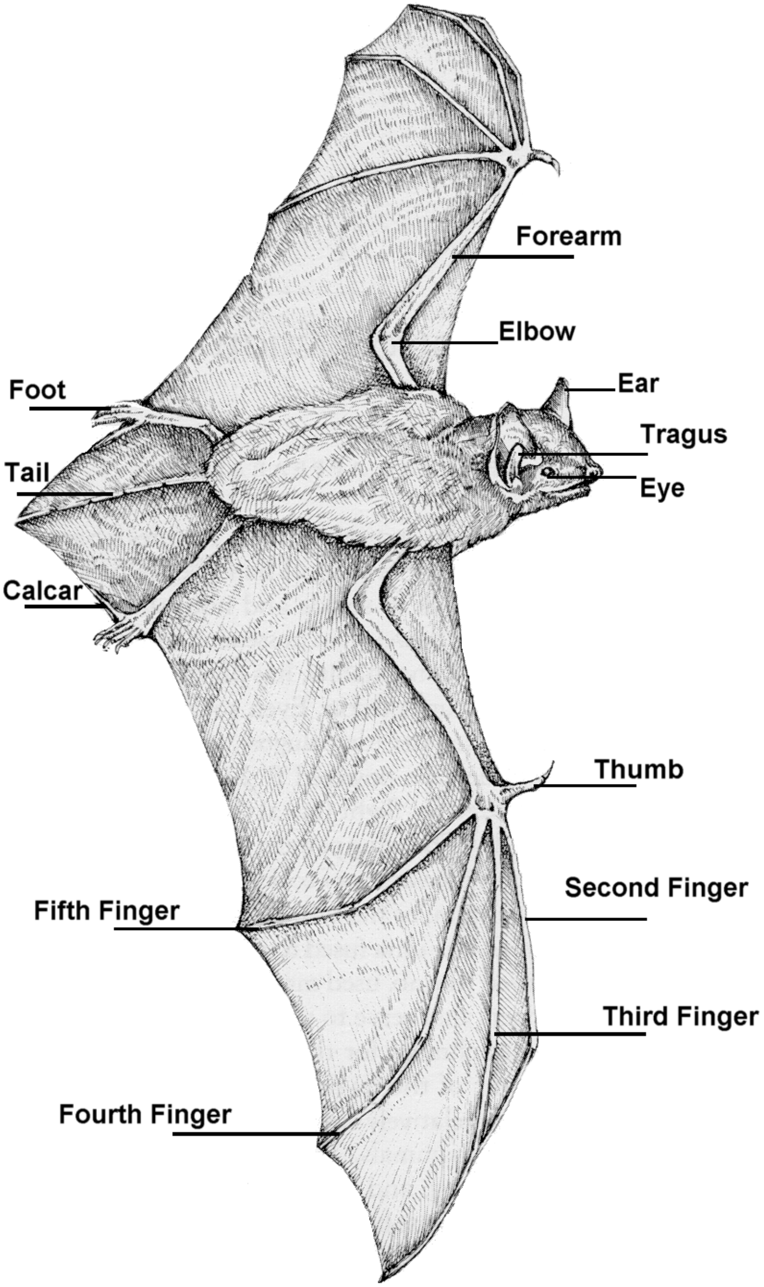
FAMILY VESPERTILIONIDAE – PLAIN-NOSED (VESPER) BATS

Corynorhinus (=Plecotus) rafinesquii	Rafinesque’s big-eared bat*
Corynorhinus townsendii ingens and *C.t. virginianus*	Ozark and Virginia big-eared bats*†
Eptesicus fuscus	big brown bat*
Lasionycteris noctivagans	silver-haired bat*
Lasiurus borealis	(eastern) red bat*
Lasiurus cinereus	hoary bat*
Lasiurus intermedius	northern yellow bat
Lasiurus seminolus	Seminole bat‡
Myotis austroriparius	southeastern myotis*
Myotis grisescens	gray myotis*†
Myotis leibii	small-footed myotis*
Myotis lucifugus	little brown myotis*
Myotis septentrionalis (formerly *M. keenii*)	eastern long-eared myotis*
Myotis sodalis	Indiana myotis*†
Nycticeius humeralis	evening bat*
Perimyotis (Pipistrellus) subflavus	*tri-colored bat (eastern pipistrelle)**

* range includes Kentucky
‡ vagrants can be found in Kentucky
†Federally Endangered Species and/or Sub-species

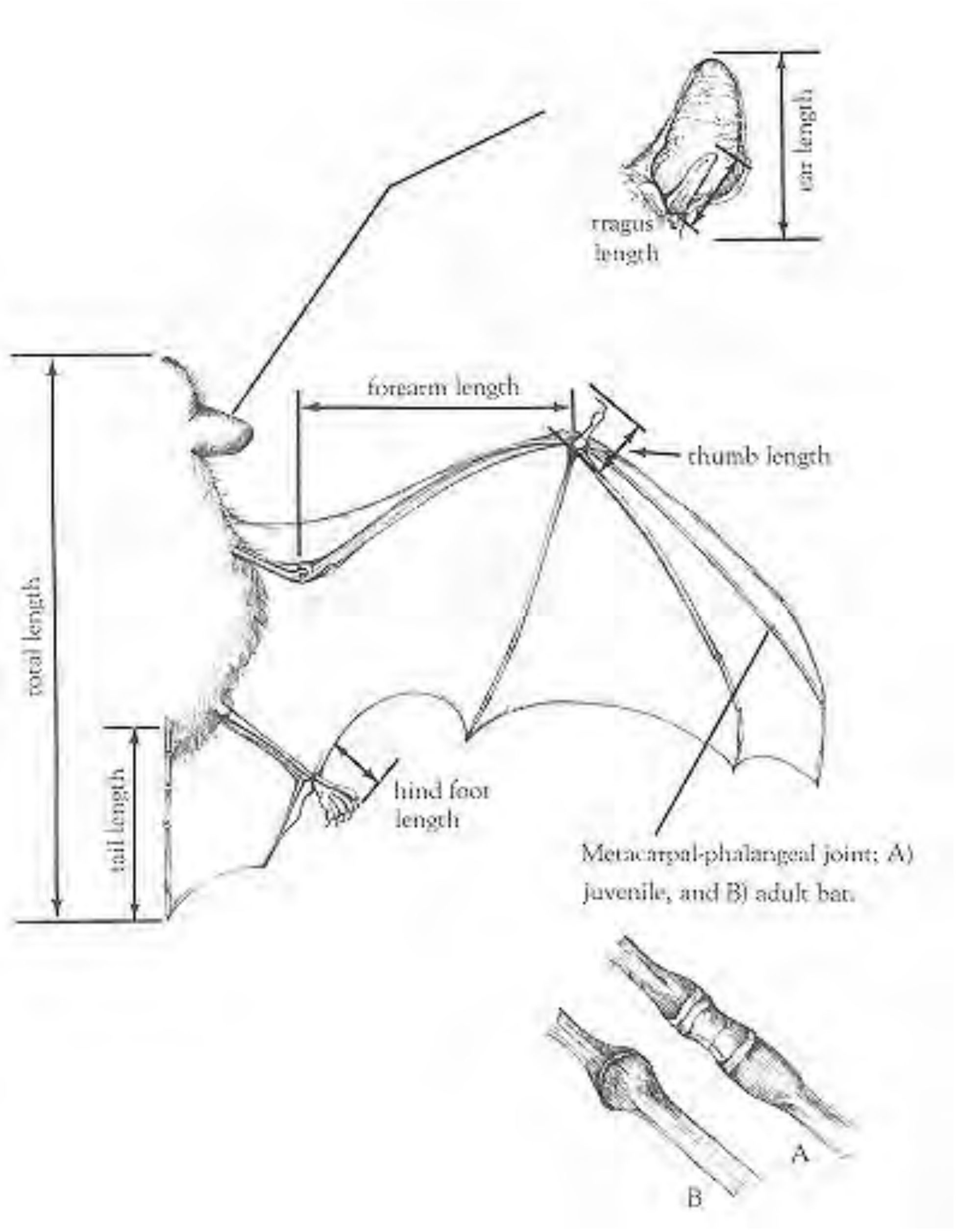
Source: Bat Conservation International. 2001. *Bats in Eastern Woodlands*, BCI, Austin TX, 301 pages. (electronic PDF copy available)

Bat Anatomy



After: Schmidly, David J. *The Bats of Texas*. Texas A&M University Press, College Station, 188 pages.
(Drawing by Christine Stetter)

Measurements Used in Species Identification Keys



Wing of a big brown bat (drawn semi-diagrammatically), labeled to show names of external parts and measurements used in key to Texas bats. The inset drawing is an enlargement of the metacarpal-phalangeal join in an adult (B.) and juvenile (A.) bat.

After: Schmidly, David J. *The Bats of Texas*. Texas A&M University Press, College Station, 188 pages.
(Drawing by Christine Stetter)

Common Measurements of U.S. and Canadian Bat Species

Adapted with permission from: Lollar, A. and B.A.S. French. 1998. *Captive Care and Medical Reference for the Rehabilitation of Insectivorous Bats*, 2002 (2nd Ed.). Bat World Publications, Mineral Wells, TX. 340 pages.

FAMILY MORMOOPIDAE

Species Name	Common Name	WT (g)	FA (mm)	WS (mm)	SOURCE
Mormoops megalophylla	Peters's ghost-faced bat	13-19	51-59	370	1

FAMILY PHYLLOSTOMIDAE

Species Name	Common Name	WT (g)	FA (mm)	WS (mm)	SOURCE
Artibeus jamaicensis	Jamaican fruit-eating bat	50-60	58-59*	‡	5,6
Choeronycteris mexicana	Mexican long-tongued bat	10-25	43-45	345	1
Leptonycteris curasoae	Lesser long-nosed bat	18-30	51-56	380	3,2,3
Leptonycteris nivalis	Mexican long-nosed bat	24	55-60	410	1
Macrotus californicus	California leaf-nosed bat	12-20	47-55	340	3,2,3

FAMILY VESPERTILIONIDAE

Species Name	Common Name	WT (g)	FA (mm)	WS (mm)	SOURCE
Antrozous pallidus	Pallid bat	12-17	48-60	353	1
Corynorhinus rafinesquii	Rafinesque's big-eared bat	7-13	40-46	270	1
Corynorhinus townsendii	Townsend's big-eared bat	7-12	39-48	293	1
Eptesicus fuscus	Big brown bat	13-20	42-51	325	1
Euderma maculatum	Spotted bat	16-20	48-51	365	1
Idionycteris phyllotis	Allen's big-eared bat	8-16	43-49	310-350	3,2,2
Lasionycteris noctivagans	Silver-haired bat	8-12	37-44	289	1
Lasiurus blossevillii	Western red bat	10-15	39-42	295	1
Lasiurus borealis	Eastern red bat	10-15	35-45	312	1
Lasiurus cinereus	Hoary bat	20-35	46-58	400	1
Lasiurus ega	Southern yellow bat	10-15	45-48	345	1
Lasiurus intermedius	Northern yellow bat	18-24	45-56	370	1
Lasiurus seminolus	Seminole bat	10-15	35-45	300	1
Lasiurus xanthinus	Western yellow bat	10-15	45-48	335-355	8,2,2
Myotis auriculus	Southwestern myotis	6-9	37-41	270	8,2,2
Myotis austroriparius	Southeastern myotis	5-7	36-41	254	1
Myotis californicus	Californian myotis	3-5	29-36	220	1
Myotis ciliolabrum	Western small-footed myotis	4-5	30-36	242	1
Myotis evotis	Long-eared myotis	4.2-8.6	36-41	275	4,2,2
Myotis grisescens	Gray myotis	7.9-13.5	40-46	275-300	7,2,2
Myotis keenii	Keen's myotis	4-5.9	32-39	228-258	4,2,2
Myotis leibii	Eastern small-footed myotis	4.1-5.5	30-36	212-248	7,2,2
Myotis lucifugus	Little brown myotis	7-9	34-41	239	1
Myotis occultus	Arizona myotis	7-9	34-41	239	1
Myotis septentrionalis	Northern myotis	5-9	32-39	241	1
Myotis sodalis	Indiana myotis	7-7.5**	35-41	240-267	7,2,2
Myotis thysanodes	Fringed myotis	6-11	39-46	285	1
Myotis velifer	Cave myotis	15	37-47	296	1
Myotis volans	Long-legged myotis	5-9	35-41	267	1
Myotis yumanensis	Yuma myotis	4-6	32-38	225	1
Nycticeius humeralis	Evening bat	5-7	33-39	263	1
Parastrellus hesperus	Western pipistrelle	3-6	27-33	190	1
Perimyotis subflavus	Eastern pipistrelle	4-6	31-35	237	1

FAMILY MOLOSSIDAE

Species Name	Common Name	WT (g)	FA (mm)	WS (mm)	SOURCE
Eumops glaucinus	Wagner's bonneted bat	30-47§	57-66	470	7,2,2
Eumops perotis	Greater bonneted bat	65	72-82	550	1
Eumops underwoodi	Underwood's bonneted bat	53-61	65-77	500-540	1
Molossus molossus	Pallas's mastiff bat	12-15	36-41	†	5,5
Nyctinomops femorosaccus	Pocketed free-tailed bat	10-14	44-50	345	1
Nyctinomops macrotis	Big free-tailed bat	24-30	58-64	426	1
Tadarida brasiliensis	Mexican free-tailed bat	11-14	36-46	301	1

This table is intended only as a very general guideline. The information was derived from a diversity of sources including some compiled from regional data only. For detailed information on these species, see Kunz (In press.) and Tuttle (In press.).
For bats found in the state of Texas, information was taken from (1) Schmidly, 1991.
For bats not found in the state of Texas, information was taken from: (2) Barbour and Davis, 1969, (3) Nowak, 1994, (4) Nagorsen and Brigham, 1993; (5) Emmons, 1990; (6) Eisenberg, 1989; (7) Mammalian Species Accounts; (8) Personal communications with researchers.

*58.18mm mean for males; 58.89mm mean for females.
**7.1g average winter weight for males; 7.4-7.5g average winter weight for females.
§ There is one record of 55.4g for a pregnant female of this species.
‡ Information not available from reference sources used.

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Nagorsen, D.W., and R.M. Brigham. 1993. *Bats of British Columbia*. Vancouver; Royal British Columbia Museum, University of British Columbia Press. 164 pages.
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Schmidly, D.J. 1991. *The Bats of Texas*. Texas A&M University Press, College Station, 188 pages.

Key to the Bats of the Eastern United States

(East of the Mississippi River)

A mm ruler is required to use this key. Select the appropriate alternative from each couplet (starting with 1a and 1b). Follow the number for the next pair of choices at the end of each statement, repeating the process until a name is reached instead of a number. Ear length is measured from the notch at the base of the ear to the ear tip. Forearm lengths (FA) are measured from wrist to elbow. (Information enclosed in parentheses is helpful but not essential.)

1a. Nose-leaf present (bat capture location is within flight range of Florida Keys)............... ***Artibeus jamaicensis***
1b. Nose-leaf absent.. **2**

2a. Tail extends at least 1/3rd its length past the terminal edge of tail membrane and appears thick and robust ... **18**
2b. Tail may extend past the terminal edge of tail membrane, but only slightly and is tiny **3**

3a. Ears 25mm or greater.. **4**
3b. Ears less than 25mm **5**

4a. Ear length 30-39mm, forearm 39-48mm, ventral fur tipped in tan, hair on toes short, does not extend past claws .... ***Corynorhinus townsendii***
4b. Ear length 28-38mm, forearm 39-48mm, ventral fur tipped in white, hair on toes long, extends well past claws .... ***Corynorhinus rafinesquii***

5a**.** Dorsal surface of tail membrane (TM) partially or entirely furred.. **6**
5b. Dorsal surface of tail membrane (TM) un-furred **10**

6a. Dorsal surface of TM furred on basal half; no white fur on wrists (FA 37-44mm) ..***Lasionycteris noctivagans***
6b. Dorsal surface of TM completely furred; white patches of fur on wrists present **7**

7a. FA > 45 mm (46-58mm); dorsal fur multi-colored yellowish and dark grayish, heavily tipped with white; fur around throat cream colored; ears light with contrasting black edges ....***Lasiurus cinereus***
7b. FA < 45 mm; short rounded ears without contrasting black edges.. **8**

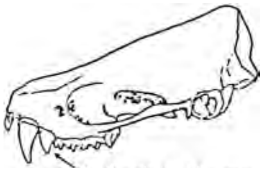
8a. Dorsal fur tipped in white, white patches at elbow, wrist, and thumb.. **9**
8b. Dorsal fur mono-chromatic, no white patches at elbow, wrist, or thumb......................... ***Lasiurus intermedius***

9a. Dorsal fur deep mahogany colored, tipped with white in females and first year males; muzzle and face dark brownish (FA=35-45mm).. ***Lasiurus seminolus***
9b. Dorsal fur reddish orange (males) or reddish to yellowish brown (females) w/whitish tips; muzzle and face light (same color as fur), FA = 36-43mm) .... ***Lasiurus borealis***

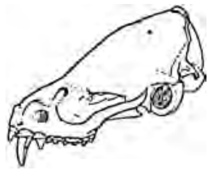
10a. Dorsal fur tri-colored when parted; dorsal surface of forearm reddish orange in sharp contrast to darker color of wing membrane; tragus bluntly shaped; FA 31-35 mm .... ***Pipistrellus (NDA Perimyotis) subflavus***
10b. Dorsal fur uni-colored or bi-colored, dorsal surface of forearm about same color as wing membranes.......... **11**

11a. Dorsal fur uni-colored, individual hairs on dorsal surface uniformly colored and grey from base to tips, forearm 41-46mm; ears grey and same color as fur, 13-16mm in length...............................***Myotis grisescens***
11b. Dorsal fur bi-colored.. **12**

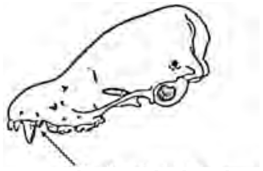
12a. Forearm 44 mm or larger (42-51mm), first upper pre-molar at least half as tall as canine ...... ***Eptesicus fuscus***
12b. Forearm 41 mm or smaller, first upper pre-molar less than half as tall as canine **13**



6a. Premolar ½ as tall as
canine, *Eptesicus fuscus*



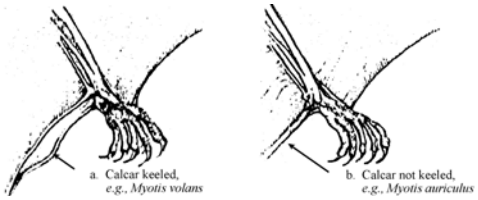
7a. Premolar less than ½
as tall as canine, *Nycticeius humeralis*



7b. Premolar less than ¼
as tall as canine, *Myotis sp.*

13a. Tragus wide and blunt; premolar one-fourth to one-third as tall as adjacent canine; FA 33-39 mm, body fur brown (calcar not keeled) .... ***Nycticeius humeralis***
13b. Tragus narrow and sharply pointed; premolar < one-fourth as tall as adjacent canine (sometimes too small to be easily seen), body fur brown or gray **14**

14a. Calcar keeled **15**
14b. Calcar un-keeled **16**



15a. Distinctive black face mask; body fur much lighter, typically light golden brown, sometimes medium brown; calcar keeled; foot about 8 mm long; FA 30-36 mm .... ***Myotis leibii***
15b. No distinctive black face mask (though facial fur may be slightly darker than body fur); calcar keeled body fur uniformly brown or gray, no or very short hairs on toes, forearm 35-41mm .... ***Myotis sodalis***

16a. Ears 14-19mm, extending approximately 4mm past nose when laid forward; forearm 32-39mm (no keel) .... ***Myotis septentrionalis***
16b. Ears 16 mm long or less, extending to tip of nose or barely beyond when laid forward **17**

17a. Fur wooly and highly variable in color, slate gray above, with white belly (in new molt) often fading to brownish gray or bright rusty red above and whitish tan below by mid-summer; individual body hairs are bi-colored especially on the dorsal surface with whitish tan tipped belly hairs with sharply contrasting black bases; FA 35-41 mm .... ***Myotis austroriparius***
17b. Fur smooth and glossy, brown above with tan belly; individual body hairs are bi-colored, even on ventral surface and darker at bases, but never black, but lighter at tips; FA 34-41 mm .... ***Myotis lucifugus***

18a. Deep vertical wrinkles on upper lips (FA36-46mm) .... ***Tadarida brasiliensis***
18b. No vertical wrinkles on upper lips **19**

19a. Forearm > 50mm (FA 57-66; bat capture location is near Florida Keys) .... ***Eumops floridanus***
19b. Forearm < 50mm (FA 36-41mm; bat capture location is in southern Florida) .... ***Molossus molossus***

Illustrations: *bat skulls – Hall, E.R., 1981.* The Mammals of North America, Volume 1, *John Wiley and Sons, New York, 600pp.*
bat calcars – Christine Setter in Schmidly, D.J., 1991. Bats of Texas, *Texas A&M University Press, 188pp.*

Annotated Key to the Hibernating Bats of the Northeast

(using non-handling methods of identification)

Finally, a bat key to the hibernating bats of Pennsylvania! This key is for cavers to use to try and familiarize themselves with the bats of PA and other Northeastern states. IT IS NOT SCIENTIFIC. It is a somewhat subjective way to identify bats, as most of the key characteristics require handling of the bat. Of course, looking closely at a bunch of bats will help anyone become more familiar with the subjective characteristics.

Characteristics which require the handling of bats are not included here, and is generally discouraged. Handling of bats should only be done by someone who has been vaccinated for the rabies virus and has a permit to handle live bats. Remember, it is against state law to handle hibernating bats in Pennsylvania (and in many other states)! On the other hand, it is beneficial for all cavers to know what species of bats are hibernating in the different caves. This key is designed to help cavers become familiar with the hibernating bats, and to identify them to species.

This key is designed to fit on the front and back of a single sheet of paper. It is recommended that the user copy this key double sided onto a single sheet, and laminate it against water damage. This way, a caver may take the key caving without destroying it.

Lastly, the key includes a bit of the ecology of each bat species. This is by no means an exhaustive account of the ecology of the species. It is merely to help sort out the bats based on their preference of temperature, desire to cluster, and typical in-cave habitat during the winter.

Anyone using this key can become reasonably proficient at identifying hibernating bats, but remember, there will always be a few individuals, which do not clearly fit the mold. Also, if you find you are caving amongst hundreds of bats, you should probably find out if the large hibernaculum is known to the bat researchers. There are only a dozen or so caves in PA known to have more than a hundred hibernating bats, but we are always looking for more.

Keith Christenson, Pennsylvania Game Commission 1997

1a. FA dark and uniform in color, possessing no more than a slightly orange streak along its length..................... **2**

1b. FA has distinctive orange stripe along its length, often visible from up to ten feet. .... ***Perimyotis subflavus***

DESCRIPTION The Eastern Pipistrelle (NDA “tri-colored bat”) is a small bat, with a forearm length averaging only 33 mm. They are usually a tawny brown color, but can range anywhere from blonde to brown to nearly auburn. They have a short, blunt tragus.

ECOLOGY *Found in many caves in the winter, the Eastern Pipistrelle prefers warmer areas in caves, and often is seen covered with condensation. They usually hibernate individually, rarely in clusters.*

2a. Tragus thin and somewhat pointed, FA < 39 mm. **3**

2b. Tragus broad and rounded, FA > 39 mm, fur chestnut brown and luxurious, muzzle broad ...... ***Eptesicus fuscus***

DESCRIPTION The Big Brown Bat is the largest hibernating bat in PA, and can often be identified solely by its size and long, luxurious brown fur. The broad muzzle and blunt tragus help distinguish it from all other PA cave bats. The ears are relatively short.

ECOLOGY *One of the hardiest bats known, the Big Brown Bat prefers to hibernate in only the coldest areas of caves, usually near the entrance or in a cold air trap. It will often wait until the first blizzard of the year before entering into hibernation, and has been shown to be able to survive sub-freezing temperatures for prolonged periods. They will occasionally hibernate in clusters, but are usually found in groups of three bats or less.*

3a. Bats hibernate individually or in clusters, but clusters are not intensely tight, most all clustered bats are visible, including head and part of the back fur. **4**

3b. Bats hibernate in extremely tight cluster, only noses, ears, and wrists visible. .... ***Myotis sodalis***

DESCRIPTION Only a very experienced person can distinguish an Indiana Myotis from a Little Brown Myotis without handling it. With careful observation it may be possible to notice the hairs on the feet, which do not extend beyond the toes of the Indiana Myotis. Some researchers also suggest that the lips of the Indiana Myotis are slightly more pinkish.

ECOLOGY *The Indiana Myotis is known to hibernate only in very cold areas, yet not near any entrances. There fore, they are found only in cold air sinks within the cave. They cluster so tightly that often only the individual bat’s noses are visible. Additionally, they are highly prone to disturbance, and the entire cluster can wake up with only a minor disturbance. Most reported sightings of Indiana Myotis turn out to be Little Brown Myotis.*

4a. Bat does not appear to be very small, and when looking directly into its face there is no obvious raccoon-like mask formed by ears and muzzle **5**

4b. Bat appears small with a raccoon-like mask extending from ear to ear. Ears are slightly large for such a small bat. Feet are small. .... ***Myotis leibii***

DESCRIPTION The Small-footed Myotis is PA's smallest bat. It is characterized by its size, as well as the black facial mask, and small feet. The dorsal fur tends to be a pale yellowish brown to golden brown. Belly hair is buff to whitish.

ECOLOGY *This bat hibernates in only in the coldest of cave areas, and often prefers very tight cracks. If the cave temperature is in the low to mid 40's, you may find this bat hibernating out in the open, but it usually can only be found very near cave entrances, often jammed into cracks only one quarter-inch wide. They will hibernate in clusters only if the thin cracks can accommodate several bats at once. In the open, they are usually alone.*

5a. Ears ~ 2 millimeters longer than most PA bats, and would extend beyond the nose if laid straight. Tragus long, pointed and dagger shaped; usually >1/2 length of the ear. .... ***Myotis septentrionalis***

DESCRIPTION The Northern Long-eared Myotis looks similar to the Little Brown Myotis and Indiana Myotis, but has a longer, more pointed tragus and longer ears. The ears will usually extend beyond the nose about 2 millimeters if laid flat. Also, the ears often look more 'mulish'.

ECOLOGY *This bat almost always hibernates individually, and often prefers the small recesses of caves. Seldom hibernating in tight cracks, this bat can usually be found in the folds of drapery formations, and sometimes out in the open. It seems to prefer colder areas more so than warmer ones.*

5b. Ears only to nostrils, if laid flat, well furred face, dark to buff brown in color with a rather pale underside, tragus is more blunt than pointed, and usually <1/2 length of ear. ....***Myotis lucifugus***

DESCRIPTION Often, the Little Brown Myotis is identified by process of elimination. It has a well-furred face, and is dark to buff brown in color. The underside is somewhat pale, usually grayish. The ears are relatively short and dark brown. The forearm is dark, but may have a slight reddish-pink tinge to it.

ECOLOGY *The Little Brown Myotis is the most common bat, which hibernates in Pennsylvania and throughout most of the northeast (prior to the spread of White-nosed syndrome (WNS) in bats. It will hibernate singly or in groups of up to several hundred, although not as tightly as the Indiana Myotis. It will use warmer roosts, but prefers cave temperatures to be in the 40's Fahrenheit. It can sometimes be observed soaking wet, which does not affect it while hibernating.*

Key to the Myotis of the Eastern U.S.

(presented in order of size; from largest to smallest)

SPECIES	FOREARM LENGTH	EAR SIZE (MM) AND COLOR	KEELED CALCAR?	FUR COLOR	ADDED CHARACTERISTICS
grisescens	40-46 mm	Short (9-15), dark, though often lighter at base near eye	no	gray, monochromatic *(unlike all other* Myotis*)*	The largest of the eastern *Myotis*. Wing-membrane attaches to the foot at the ankle instead of at base of toes as in all other *Myotis*.
austroriparius	36-41 mm	Short (11-15), pale (match body fur), has shortest, bluntest tragus of the Myotis	no	light gray to dark russet brown, often black at the base	Ventral fur is often much lighter tan with distinct whitish tips. Fur color is extremely variable, depending upon age and molt.
sodalis	35-41 mm	Short (9-14), rounded and dark (match body fur color)	yes *can be slight*	wooly brown	Fur is shorter and woollier than other *Myotis*. Muzzle and lips appear pinkish, especially when viewed head-on.
lucifugus	34-41 mm	Short (10-15), often darker than body fur color	no	glossy brown	Fur is longer and glossier. Tips appear reddish. Muzzle and ears darker than fur, but not black.
septentrionalis	32-39 mm	Long (14-19), with long, dagger-shaped tragus, pale, match fur color	no	light brown to pale gray-brown, lax	Long ears extend past the nose when laid forward. Distinct, well-organized horizontal striations on ventral surface of tail-membrane.
leibii	30-36 mm	Short (9-14mm), dark, nearly black, forming "mask" with dark muzzle	yes *prominent*	pale yellowish-brown to light golden brown	Face, ears, wings, and membranes are very dark brown to black, and when viewed straight on, mask is very distinct.
The small bats below are often confused with *Myotis* by novices. Their characters are listed here. Both have blunt tragi, distinct pre-molars, and are in different genera; thus, should never be confused with *Myotis*.					
Nycticeius humeralis	33-39 mm	Short (11-15), dark (darker than body fur color), rounded tragus	no	dull, medium brown to dark brown	Fur often appears shiny. In general, bat looks like a miniature big brown bat (without a keeled calcar).
Pipistrellus (Perimyotis) subflavus	31-35mm	Short (11-14.5), rounded, blunt tragus, match fur color	no exceeds tibia in length	pale yellow-orange to dark reddish brown	Fur is distinctly tri-colored with hairs dark at the base, light in the center, and darker at the tips. Forearms are pinkish in contrast to dark, nearly black wing membranes.

Sources: Barbour, R.W. and W.H. Davis. 1969. *Bats of America*. University Press of Kentucky, Lexington, 286 pages.
Nowak, R.M. 1994. *Walker's Bats of the World*. Johns Hopkins University Press, Baltimore, MD, 287 pages.
Schmidly, D.J. 1991. *The Bats of Texas*. Texas A&M University Press, College Station, 188 pages.

Roosting Patterns of U.S. and Canadian Bat Species

Adapted with permission from: Lollar, A. and B.A.S. French. 1998. Captive Care and Medical Reference for the Rehabilitation of Insectivorous Bats, 2002 (2nd Ed.). Bat World Publications, Mineral Wells, TX. 340 pages.

FAMILY MORMOOPIDAE

Species Name	Common Name	Hib?	Roosting Patterns
Mormoops megalophylla	Peters's ghost-faced bat	No	Do not cluster. Individuals roost about 6" apart in groups of up to hundreds of thousands; in caves, mines, and rarely buildings

FAMILY PHYLLOSTOMIDAE

Species Name	Common Name	Hib?	Roosting Patterns
Artibeus jamaicensis	Jamaican fruit-eating bat	No	Cluster in small bachelor groups or groups that include one male & several females. Several of these groups of males & their harems may roost in the same cave. Roost in tree hollows, foliage, & caves.
Choeronycteris mexicana	Mexican long-tongued bat	No	Do not cluster. Individuals roost about 1-2" apart. Roost in groups of up to several dozen in caves & mines & occasionally in other shelters such as buildings.
Leptonycteris curasoae	Lesser long-nosed bat	No	Cluster in groups of up to thousands. Generally found during the day in mines & caves, but may rest during the night in open buildings such as barns & carports.
Leptonycteris nivalis	Mexican long-nosed bat	No	Cluster in groups of up to thousands in mines & caves.
Macrotus californicus	California leaf-nosed bat	No	Do not cluster. Roost in groups of up to a hundred. Roost in abandoned mines and rock shelters during the day, but can also roost during the night in open buildings, bridges, mines.

FAMILY VESPERTILIONIDAE

Species Name	Common Name	Hib?	Roosting Patterns
Antrozous pallidus	Pallid bat	Yes	Cluster in groups of up to hundreds. During the day use rock crevices & buildings, but also sometimes in mines, caves, & hollow trees; night-roost in rock shelters, open buildings, bridges, & mines.
Corynorhinus rafinesquii	Rafinesque's big-eared bat	Yes	Cluster in groups of up to 100 in buildings, behind bark, & in hollow trees, caves, & mines.
Corynorhinus townsendii	Townsend's big-eared bat	Yes	Do not cluster. Roost in groups up to 1,000 although generally found in fewer numbers. Roost in caves & mines but are also found in buildings in the west where they night-roost in open buildings.
Eptesicus fuscus	Big brown bat	Yes	Cluster in groups of up to hundreds; in buildings, bridges, & behind shutters. Have been found roosting in rock crevices, swallow nests, hollow trees, & saguaros. In winter found roosting in caves, mines, quarries, & storm sewers.
Euderma maculatum	Spotted bat	Yes	Clustering information not available. Roost in cracks & crevices of high cliffs and canyons & possibly caves.
Idionycteris phyllotis	Allen's big-eared bat	§	Cluster in groups of up to 100 in caves, rock shelters, & mines.
Lasionycteris noctivagans	Silver-haired bat	Yes	Do not cluster. Solitary; roost behind loose bark, but have been found in buildings, mines, woodpecker holes, & bird nests. Found during migration in open buildings, lumber piles, & fence posts.
Lasiurus blossevillii	Western red bat	Yes	Do not cluster. Solitary; roost in tree foliage.
Lasiurus borealis	Eastern red bat	Yes	Do not cluster. Solitary; roost in tree foliage. Hibernate in leaf litter.
Lasiurus cinereus	Hoary bat	Yes	Do not cluster. Solitary; roost in tree foliage
Lasiurus ega	Southern yellow bat	§	Do not cluster. Solitary; roost in leafy vegetation.
Lasiurus intermedius	Northern yellow bat	§	Do not cluster although at least females appear to be colonial. Several may roost in same tree, Spanish moss, & palm leaves.
Lasiurus seminolus	Seminole bat	Yes	Do not cluster. Solitary; roost in Spanish moss.
Lasiurus xanthinus	Western yellow bat	Yes	Do not cluster. Solitary; roost in mostly dry leafy vegetation.
Myotis auriculus	Southwestern myotis	§	Do not cluster. Roost in buildings & caves but also will form colonies of up to 40 or more in tree hollows.
Myotis austroriparius	Southeastern myotis	Yes	Cluster in groups of up to thousands. Roost in caves, buildings, & hollow trees, although in winter they are also found in bridges, storm sewers, road culverts, & drain pipes

Species Name	Common Name	Hib?	Roosting Patterns
Myotis californicus	Californian myotis	Yes	Cluster in small groups in mines, caves, rock crevices, hollow trees, beneath loose bark, bridges & in open shelters such as garages, barns, houses, sheds, & porches.
Myotis ciliolabrum	Western small-footed myotis	Yes	Cluster in groups of up to 50 in mines, caves, buildings, & sometimes beneath loose bark.
Myotis evotis	Long-eared myotis	Yes	Do not cluster. Roost in groups of up to 30 in sheds, cabins, beneath bard, & in rock piles. Night-roost in caves.
Myotis grisescens	Gray myotis	Yes	Cluster in groups of up to thousands mainly in caves, although one maternity colony was found in a storm sewer.
Myotis keenii	Keen's myotis	Yes	Do not cluster. Solitary; roost in tree cavities, cliff crevices.
Myotis leibii	Eastern small-footed myotis	Yes	Cluster in groups of up to 50 in mines, caves & beneath rock slabs in quarries. Maternity colonies found in buildings.
Myotis lucifugus	Little brown myotis	Yes	Cluster in groups of up to thousands in mines & caves. In summer may also be found in buildings, bridges, & under bark.
Myotis occultus	Arizona myotis	Yes	Clustering is unknown. Maternity colonies found in buildings & a bridge. Scant hibernating records have all been in mines.
Myotis septentrionalis	Northern myotis	Yes	Small clusters of up to 30 have been found in maternity colonies; though generally roost singly in mines, caves, buildings, and beneath bark.
Myotis sodalis	Indiana myotis	Yes	Cluster in groups up to 100,000 in caves though maternity colonies use hollow trees. Also found in bridges & beneath loose bark.
Myotis thysanodes	Fringed myotis	Yes	Cluster in groups up to 300 in caves, mines, rock crevices, & buildings.
Myotis velifer	Cave myotis	Yes	Cluster in thousands in caves, mines, and sometimes buildings.
Myotis volans	Long-legged myotis	Yes	Cluster in groups of up to hundreds in buildings rock crevices and trees; night roost in mines and caves.
Myotis yumanensis	Yuma myotis	Yes	Cluster in groups of up to thousands in maternity colonies; adult males typically solitary; roost in buildings, under bridges, & in caves & mines.
Nycticeius humeralis	Evening bat	Yes	Cluster in groups of up to several hundred in buildings, tree cavities, & behind loose bark.
Parastrellus hesperus	Western pipistrelle	Yes	Do not cluster; relatively solitary, though maternity colonies of up to a dozen bats have been found in rock crevices and behind shutters. Roost in buildings, mines, and caves.
Perimyotis subflavus	Eastern pipistrelle	Yes	Do not cluster; relatively solitary, though small maternity colonies of up to 30 individuals have been found. Roost tin Spanish moss, caves, mines, rock crevices and buildings.

FAMILY MOLOSSIDAE

Species Name	Common Name	Hib?	Roosting Patterns
Eumops glaucinus	Wagner's bonneted bat	No	Clustering unknown. Found in groups of up to 8 individuals.
Eumops perotis	Greater bonneted bat	No	Cluster in groups of less than 100 in cliff crevices, rocky canyons, & sometimes buildings
Eumops underwoodi	Underwood's bonneted bat	No	Clustering information unknown. Have been found roosting in small groups in buildings & tile roofs.
Molossus molossus	Pallas's mastiff bat	No	Cluster in hundreds in tree hollows, rock piles & buildings.
Nyctinomops femorosaccus	Pocketed free-tailed bat	No	Cluster in groups of up to 100 in crevices of rocky out-crops & have also been found in tile roofs.
Nyctinomops macrotis	Big free-tailed bat	No	Clustering information unknown. Roost in rock crevices.
Tadarida brasiliensis	Mexican free-tailed bat	No	Cluster in groups of up to several million in caves, mines bridges, & buildings.

This table is intended only as a very general guideline. § Information not available from reference source used.

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Variation in the Cave Environment and its Biological Implications

by Merlin D. Tuttle and Diane E. Stevenson

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INTRODUCTION

Constancy of the cave environment has too often been assumed and emphasized. The most common generalization is that cave temperature varies only near entrances (the variable temperature zone) while that of a cave is constant (the constant temperature zone), with temperature closely approximating the local mean annual surface temperature. Humidity also is often considered to be near saturation and relatively invariant. These generalizations are true in some cases. Certainly, the cave environment is buffered in relation to the outside environment. Overall temporal and spatial variation of temperature and humidity among and within caves, however, is far greater than is generally suspected, and even a small amount of such variation can have great impact on cave faunas (Jegla and Poulson, 1969; Juberthie and Delay, 1973; Delay, 1974; Juberthie, 1975; Poulson, 1975; Tuttle, 1975, 1976; Wilson, 1975; Peck, 1976).

Although literature demonstrating considerable variation exists, it is scattered, often in foreign or little-known publications, and sometimes is authored by laymen who publish only once on the subject. Consequently, few individuals, even among biospeleologists, are adequately aware of much of the available literature and its biological implications. Another source of confusion has been the fact that many authors, while presenting a thorough discussion of one or more variation-producing factors, still have opened or concluded with general statements about the constancy of the cave environment.

Despite the confusion, in the existing literature a variety of factors-such as number, size, and position of entrances, passage size, contour and slope, overall cave volume, distance of greatest volume from entrances, amount and seasonal timing of entry of surface water, air flow, and the annual range of outside temperature-have been noted to strongly influence cave temperature and humidity (see Halliday, 1954; Moore and Nicholas, 1964; Plummer, 1964; Cropley, 1965; Geiger. 1965; Peters, 1965; Vandel, 1965; Conn, 1966; Barr, 1968; Daan and Wichers, 1968).

This paper integrates current knowledge of the cave environment with particular emphasis on air flow and temperature; it presents some of our data on the subject, and discusses the importance of such information to biological research and cave management. We believe that familiarity with factors influencing cave environments can be highly useful in biospeleology and cave management, both for the generation of hypotheses and predictions in ecological and distributional studies and for predicting the biological uniqueness and potential of any given cave under investigation.

METHODS

From 1960 to 1975 the senior author visited several hundred caves, primarily in Alabama, Florida, Tennessee, and Virginia, and recorded temperatures at hundreds of winter and summer roosts of the gray bat (*Myotis grisescens).* Temperature and humidity readings were recorded using a Bendix Psychron motor-driven psychrometer. Since gray bats prefer caves that provide the greatest possible deviations from mean annual surface temperatures, the caves visited during these bat studies provided examples of strikingly different structures and temperature regimes. Many other caves, not used by gray bats, provided additional comparisons.

From the winter of 1975-76 through the winter of 1976-77 a more detailed study of cave temperature was conducted. Thousands of temperature measurements were made in 25 caves and mines from Wisconsin to Florida, in an effort to test the predictions generated incidental to the previous bat studies. A quick, accurate temperature measuring device was essential, and a Bailey Thermalert, Model TH-2 digital readout thermometer with a 1-mm diameter thermister probe was used initially. Testing in controlled water baths at temperatures of 0-30°C demonstrated precision of +/-0.1°C. However, accuracy under field conditions varied with the temperature of the instrument itself, forcing one to carry it beneath one's coveralls and to repeatedly recalibrate against a laboratory-tested Wesco mercury thermometer. Though readings could be made in only a few seconds, accuracy with the Thermalert in the field was only +/-0.3°C.

Accuracy was greatly improved with the purchase of an IMC Digital Thermometer, Model 2100 (produced by

IMC Instruments, Inc., Glendale, Wis.), with a range of -40° to +250°F. This thermometer proved far more suitable for use in caves. It weighed only about 500g, (including batteries), was extremely sturdy, provided accuracy and precision of +/-0.1°F, and continued such reliability over an instrument temperature range of 0 to 110°F. Using a sensor probe 2.2 mm in diameter, this instrument had a response time of 3 seconds in liquids, 30 seconds or less in air, and from 45 seconds to several minutes (depending on density of solid) for surfaces. Most air and wall temperatures reported in this paper were taken with this instrument.

Although the data are not presented here, gross daily and seasonal temperature variation was recorded in five cases using Weksler maximum/minimum thermometers, and 24-hour comparisons between inside and outside temperatures were made using Bacharach Tempscribe recording thermometers, in order to verify our findings. Mean annual surface temperatures (MAST) were obtained from U.S. Department of Commerce (1975a-c) publications. A steel tape or, for the longest distances, a Model 100 Optical Tapemeasure (produced by Ranging Inc., Rochester, N.Y.) were used for cave measurements.

Data from only a few representative caves in the study could be included here, but the omitted observations agree well with those selected for discussion.

FACTORS THAT INFLUENCE CAVE TEMPERATURE

Conduction from Cave Walls

If one surface of a very large limestone block were exposed to a seasonal cycle of temperature, “it may be predicted that its interior temperature would remain very close to (mean annual surface temperature (MAST)] within a very few feet of its surface.” A time lag in temperature adjustment of approximately 7 days for every foot of depth produces this constancy (Cropley 1965). Cropley described as Zone III an area of a cave where isolation from outside conditions is such that “no temperature variations occur except those that are initiated by the conduction of heat from the surface through the cave roof.” Although this is the characteristic of the constant temperature cave of popular legend, he found no instance of a “true Zone III location,” but concluded that relatively isolated rooms “are sufficiently common that the legend is perpetuated.” The main effect of cave wall conduction will be seen to be the tendency to gradually return differing air or water temperatures to mean annual surface temperature--the more isolated from outside influences an area is (whether by distance or physical barriers) the more nearly its temperature will approximate MAST.

Geographic Location

Vandel (1965) listed geographical location and altitude as important factors affecting cave temperature; their major influence is on the range and mean of the annual surface temperature and on standard barometric pressure. Since the amount of variation from mean annual surface temperature that can be achieved in any given cave is directly proportional to the annual range of surface temperature (see discussion below), caves in tropical regions would be expected to exhibit only the slightest deviations from MAST. To a lesser extent, fluctuations also should be reduced in caves on islands, peninsulas, or even in coastal areas. Within a given area, cave entrances on north versus south slopes, those at different elevations, and those on exposed surfaces versus in deep, protected valleys or sinks will face different means and ranges of surface temperature, which often result in detectable differences in internal temperatures.

Another geographic factor is the nature of the geological structure present; caves of certain configurations may exist primarily in certain areas. Barr (1961:13) documented the existence of strong geographic tendencies in the distribution of caves of “essentially horizontal” versus “steeply or moderately inclined beds.” Such structural tendencies would be expected to be reflected in geographic trends in cave temperature and humidity. This in turn may have important zoogeographic implications.

Water Circulation

In order for internal temperatures to vary above or below mean annual surface temperature, a cave must have a route of communication with the temperature fluctuations of the outside atmosphere. With cave wall conduction exerting only infinitesimal effect extremely short distances from the surface, the two main routes of communication are circulation of air and water. Water is most likely to cause deviations from mean annual surface temperatures when it enters directly from the surface in seasons when surface temperatures deviate farthest from the mean annual temperature (Cropley, 1965) or, in rare instances, when it enters from thermal springs (Geiger, 1965). Flooding, as noted by Barr (1968), can produce sudden and pronounced temperature changes and can play a vital role in triggering reproduction of aquatic troglobites (Poulson and Smith, 1969; Jegla and Poulson, 1970). The “disrupting” influence of outside water will, of course, last only until it has flowed a distance sufficient to allow it to reach thermal equilibrium with the cave walls.

Air Circulation

Although exceptions do occur, the impact of air circulation in caves is generally far greater than that of water, if for no other reason than the fact that whereas most known caves have some air circulation (those isolated by water sumps being an exception), a much smaller proportion have major water circulation. The four main causes of air circulation affecting cave temperature (see Plummer, 1964) will be discussed. It will be seen that the magnitude and type of impact of all air flow types is overwhelmingly determined by the structure (passage configuration) of the cave itself.

Barometric pressure -- Atmospheric (or barometric) pressure frequently has been cited as a primary factor influencing within-cave air movement and temperature fluctuation. Although other factors such as solar-induced atmospheric tides can produce slight pressure changes (Encyclopedia Britannica, 1975), the relatively greatest fluctuations in barometric pressure at any given altitude are directly the result of temperature changes (Moore and Nicholas, 1964).

At one location pressure changes can, of course, occur that are due to temperature changes (and the resulting winds) at another distant location, as in the case of changes preceding storm fronts. It is only these non-temperature associated pressure changes that can be discussed meaningfully as barometric pressure influences on cave climate. Changes in the outside air temperature obviously will be accompanied by changes in barometric pressure, since the latter is determined by the weight of air (colder = heavier). In this paper, however, references to barometric pressure effects will refer only to the non-temperature-associated changes; temperature-associated pressure changes will be considered synonymous with temperature fluctuation.

At certain times, as noted by Porter (1974), “All caves should exhibit an airflow into the entrance when the outside atmospheric pressure rises, and should emit air when the pressure falls.” Nevertheless, the overall impact of this circulation appears to be relatively minor (Moore and Nicholas, 1964; Plummer, 1964), especially when compared to that of thermal convection. Its effect certainly is more gradual, transitory, and of less magnitude. Apparently rare cases exist where caves, such as Wind and Jewel Caves in South Dakota, have extremely large volumes and generate significant winds through barometric pressure interactions alone (Conn, 1966). Even in these caves, however, internal temperatures probably are affected little, compared to the amount that would occur if thermal convection were directly involved.

Surface wind. -- Surface winds carried into or through caves by their own force may be of some importance in certain instances (Plummer, 1964; Geiger, 1965), but most examples are limited to a cave with a short simple tunnel between its two or more entrances, or to a relatively shallow cave with a large entrance. Plummer (1964) discussed the flow of surface winds through caves with entrances a large distance apart, but points out that in such cases the “motion is not properly ‘caused’ by the surface winds.” He contends that “both the cave and surface winds result from the same difference in barometric pressure between the locations of the entrances.” This effect would be most likely to occur in a cave shaped like a nearly level tunnel.

Resonance. -- Schmidt (1959), Eckler (1965), Peters (1965), Moore and Nicholas (1964), Plummer (1964), Porter (1974), Russell (1974) and others have discussed this potential cause of cave "breathing" through a single entrance. The oscillation of air has been attributed to movement of outside air across the entrance, creating resonance similar to that which “produces a sound when a person blows across the mouth of a coke bottle.” (Cave 3 of Fig. 1 is of the “jug” shape postulated as suitable for resonance.) Schmidt (see Barr, 1968) also suspected that such resonator effects could explain air flow oscillations in passages at the bottom of large “elevator shaft” types of passages; he hypothesized that “vertical air column of considerable height” in the tall passages could produce effects similar to surface winds.

Although we have not attempted to investigate this phenomenon in any detail, we doubt that the above explanations are of more than rare importance. We have observed both regular and irregular breathing cycles in caves of a variety of structures, and note that oscillations are most likely to occur when outside temperature is fluctuating around or is close to inside temperature. Furthermore, such oscillations often persist in the absence of outside wind. When marked outside temperature changes are occurring, as during a storm (for an example, see Eckler, 1965), breathing easily can be explained by thermal convection; Peters (1965) has discussed differing cave structures and how they might cause patterns of breathing.

Moore and Nicholas (1964) have pointed out that the now famous Breathing Cave in Virginia is itself probably a multiple-entrance cave dominated by air currents caused by thermal convection. They point to internal complexity of structure as the probable source of breathing and discount the idea that the air flow oscillations are caused by outside wind blowing past its entrance. An alternative explanation (using thermal convection as opposed to resonance) will be proposed to explain air flow oscillations in caves of Type 3 (Figure 1) in the section, "Cave Structure and Volume."

Thermal convection. -- The impact of thermal convection on air movement in and out of caves (and therefore on cave temperatures) is well known; thermal convection is generally believed to be the most important factor in determining the direction and amount of air exchange with the surface (Halliday, 1954; Plummer, 1964; Geiger, 1965; Peters, 1965; Daan and Wichers, 1968; Porter, 1974; Russell, 1974). The principle of thermal convection in caves is that air escapes (rises) through an upper entrance (or through the top of a single entrance) when it is warmer than the outside air. Conversely, air will escape through a lower entrance (or through the bottom of a single entrance) when it is cooler than the outside air. The greater the inside-to-outside temperature gradient, the faster the rate of air movement; flow ceases when the temperatures are the same. (This equilibrium condition theoretically should be reached when the outside temperature equals mean annual surface temperature for the area. Different cave types may deviate so markedly from MAST, however, that this equilibrium point may be

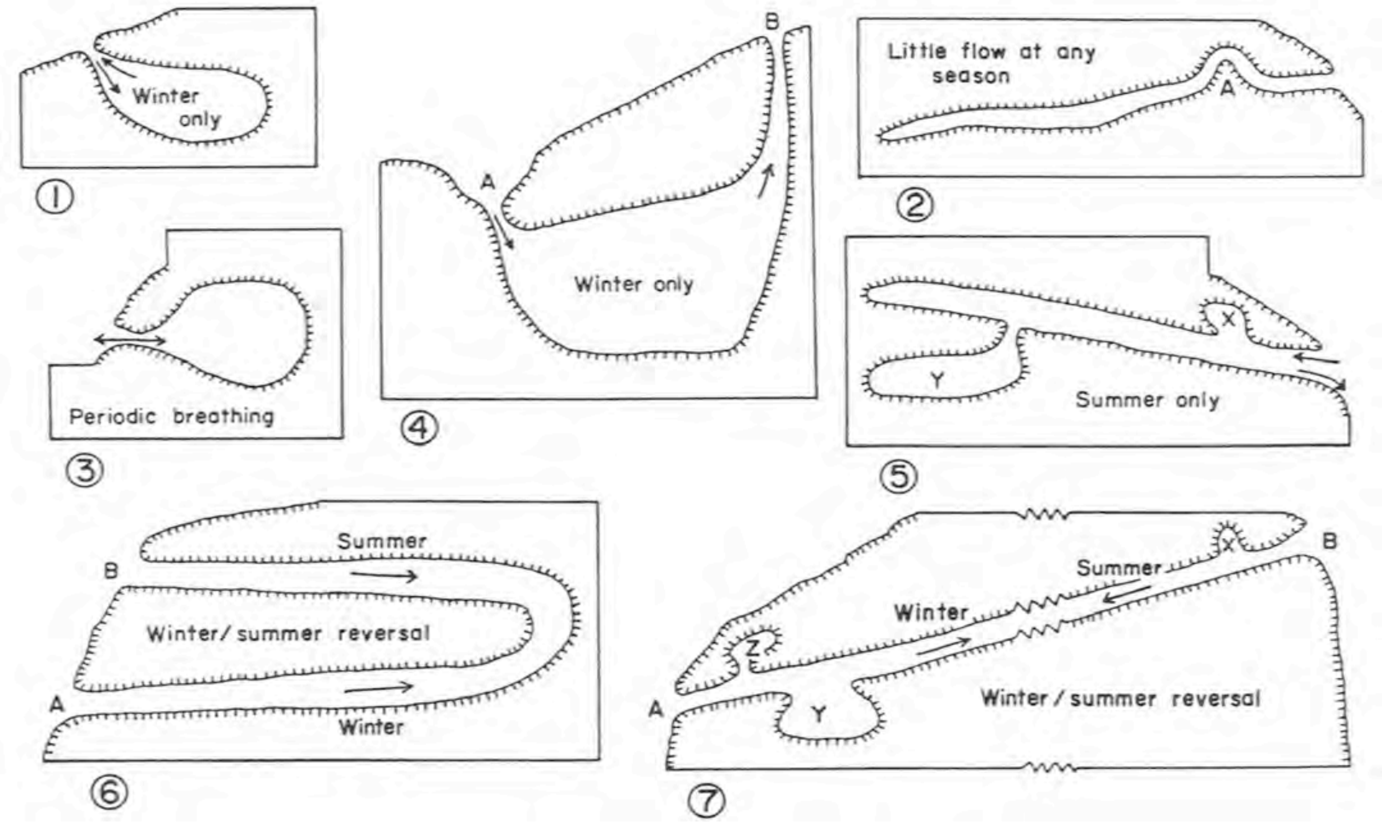

Figure 1. Simplified cave structures. Air flow indicated as occurring in "winter" wil generally occur when outside temperature is below mean annual surface temperature (MAST); flow marked "summer" will occur when outside temperature is above MAST. *Type 1*: Breathes (as indicated by arrows) in winter; stores cold air in summer. *Type 2*: Undulation at A acts as dam inhibiting air flow; temperature relatively constant beyond dam. *Type 3*: "Jug" shape often postulated to exhibit resonance; may have pulsing in and out air movement, especially when outside air deviates from MAST. See text for alternate explanation for the oscillation of air. *Type 4*: Strong air circulation from A to B in winter; stores cold air in summer. *Type 5*: The reverse of Type 1; warm air enters along ceiling in summer wile air cooled by cave walls flows out along floor. No flow in winter. X is a warm air trap, Y stays a relatively constant temperature. *Type 6*: Strong air flow from A to B in winter; equally strong air flow in opposite direction in summer. *Type 7*: Same as Type 6, with a warm air trap (X) cold air trap (Y), and an area of relatively constant temperature (Z). Distance between and elevational displacement of the entrances are critical factors in the air flow direction in these two cave types; the flow of air (cooled relative to outside temperatures by the cave walls) down in summer must be strong in order to overcome the tendency for warm outside air to rise into A. Similarly, in winter the "negative pressure" created by air (now warmer than the outside air due to the MAST effect of the cave walls) rising out of B must be strong enough to pull cold air up into A.

shifted at times.) Caves can exhibit such air flow seasonally, on a daily cycle, or in response to passage of weather fronts. Direction and timing (and to a certain extent, rate) of flow will be determined by the structure of the particular cave.

Cave Structure and Volume

Figure 1 presents several simplified examples of how air circulation works in caves of different structure. Although the number of entrances (including cracks too small for human passage) is an important variable of air circulation, the elevational difference between multiple entrances is of primary importance for thermal convection-induced temperature variation, as noted by Halliday (1954), Plummer (1964), Geiger (1965), Porter (1974) and others. Negative pressure (as described by Peters, 1965, and Daan and Wichers, 1968) can create powerful chimney effects in caves with entrances at different elevations (Figure 1, Types 4, 6 and 7). Halliday also pointed out that other factors, such as irregular, tortuous passages or narrow entrances, "will act as baffles to air currents." We have noted that vertical undulations are especially effective natural dams against the free flow of convection currents (see Figure 1, Type 2).

The location of a cave's greatest volume relative to its entrance(s) is also of great importance. Distance of a cave's greatest volume from the entrance(s) has been shown to be of importance in determining depth and pattern of air movement in and out of caves where movement is the result of changes in barometric pressure (Conn, 1966). Elevational displacement of cave volume from an entrance(s), however, is perhaps the most important single factor affecting cave temperature (see Figure 1, Types 1, 4, 5, 6 and 7). As noted by Geiger (1965), "if a cave slopes downward from the entrance, cold air flows downward inside it and is no longer affected by warmer and lighter air. Caves of this type are called sack caves and act as cold reservoirs . . . The opposite thermal effect is obtained when a cave slopes upward from its single entrance." Caves with their greatest volume above the entrance can act as warm air traps; cooled air sinks out as warm air rises in. These considerations also apply to cave chambers or passages that extend above or below passages with air flow, as illustrated in Figure 1, Types 5 and 7.

Small passages, in addition to acting as baffles, also dampen temperature fluctuations through their increased cave wall-surface-to-volume ratio -- the tendency of the walls to return air to mean annual surface temperature will have maximum effect. Halliday's (1954) study of ice caves demonstrated not only the importance of having the volume below the lowest entrance but also the necessity of large volume for cold air storage. Halliday, in discussing classical examples of limestone ice caves, repeatedly noted the presence of very large volume. He mentioned room sizes of 100 feet by 30 feet, 200 feet by 50 feet, and 300 feet by 50 feet, and described another as "one immense room of ballroom proportions."

Thermal convection and the distribution of a cave's volume in relation to its entrance also could provide an alternate explanation of breathing (air flow oscillations) in caves of Type 3, Figure 1. With its volume approximately equally distributed above and below the entrance, such a cave could be expected to have warm summer air entering along the entrance ceiling, with cooled air spilling out along the bottom of the entrance. The reverse flow pattern would occur in winter. If the entrance were sufficiently constricted, however, breathing could be predicted to occur. There no longer would be room for air to move simultaneously in opposite directions; density differentials should lead to a pulsing action. At some point, further increases in entrance passage length and constriction should almost completely inhibit exchange of inside and outside air in caves of this type.

INTERACTION OF CAVE STRUCTURE AND AIR FLOW

The following examples of specific caves (see Figures 2 and 3) were taken from our studies in the southeastern United States and will illustrate the extent and nature of cave structure/air flow interactions. Cave names and locations are withheld because most of the caves discussed contain populations of endangered bats or other cavernicolous faunas. This information will be provided, on request, to those documenting *bona fide* need.

Seasonally Reversing Air Flow

Cave number 1 of Figure 2 is an excellent example of Type 6/7, Figure 1. Due to its relatively simple shape, large passage diameter, and 43-meter elevational difference between entrances, air flow is direct and rapid. We have observed a strong (unmeasured, although probably sometimes exceeding 15 KPH) flow of air exiting the lower entrance and entering the upper on hot summer days, with the reverse being true on cold days in winter. Temperatures at the entrances in February (Figure 2) show the effect of the cold air entering the low entrance, and warmed air exiting the upper one. Local residents and the cave's former owner report complete or nearly complete cessation of air flow, either in or out of either entrance, when the surface temperature is approximately 60°F (15.6°C). Air flow cessation would be expected in this general temperature range due to its proximity to mean annual surface temperature (15.7°C)

As a consequence of its strong, seasonally reversing air flow, this cave shows the greatest annual range of temperature of any of the hundreds of caves observed in this study. Note the extremes of deviation from MAST at locations H and D in July and February (outside temperatures approximately 34°C and -30°C respectively). Certainly a temperature of 0.6°C 350 m inside an Alabama cave requires exceptionally strong circulation of outside air. This reading, and the high summer temperature at H, are all the more surprising since the cave passages slope in the “wrong” way: down from K between J and I and up from A to D. Both readings are attributable to the dramatic impact of the negative pressure created by air exiting such a large cave--in summer cool air pours out of the bottom entrance in such a quantity that warm air is "sucked" in the upper entrance and down the slope. In winter the reverse occurs, when warm (relative to outside) air escaping through the upper entrance creates a partial vacuum which "sucks" cold air into the lower entrance and deep into the cave. Lower outside temperatures in January undoubtedly produced below-freezing temperatures as far in as site D.

Cave number 2 of Figure 2 is a nearly horizontal, two-level tube which, according to Barr (1961), ends at point F. Mean annual surface temperature is probably 12°C or slightly below; temperature recording stations within 70 km on opposite sides from the cave have MASTs of 12.4° and 13.4°C, but the cave is at a higher elevation than either station. This cave is a good example of how knowledge of cave temperature variation can lead to prediction of undiscovered sections. Our observations of a seasonally reversing air flow (into the known entrance in winter and out of it in summer) strongly point toward the existence of a second, previously unsuspected entrance.

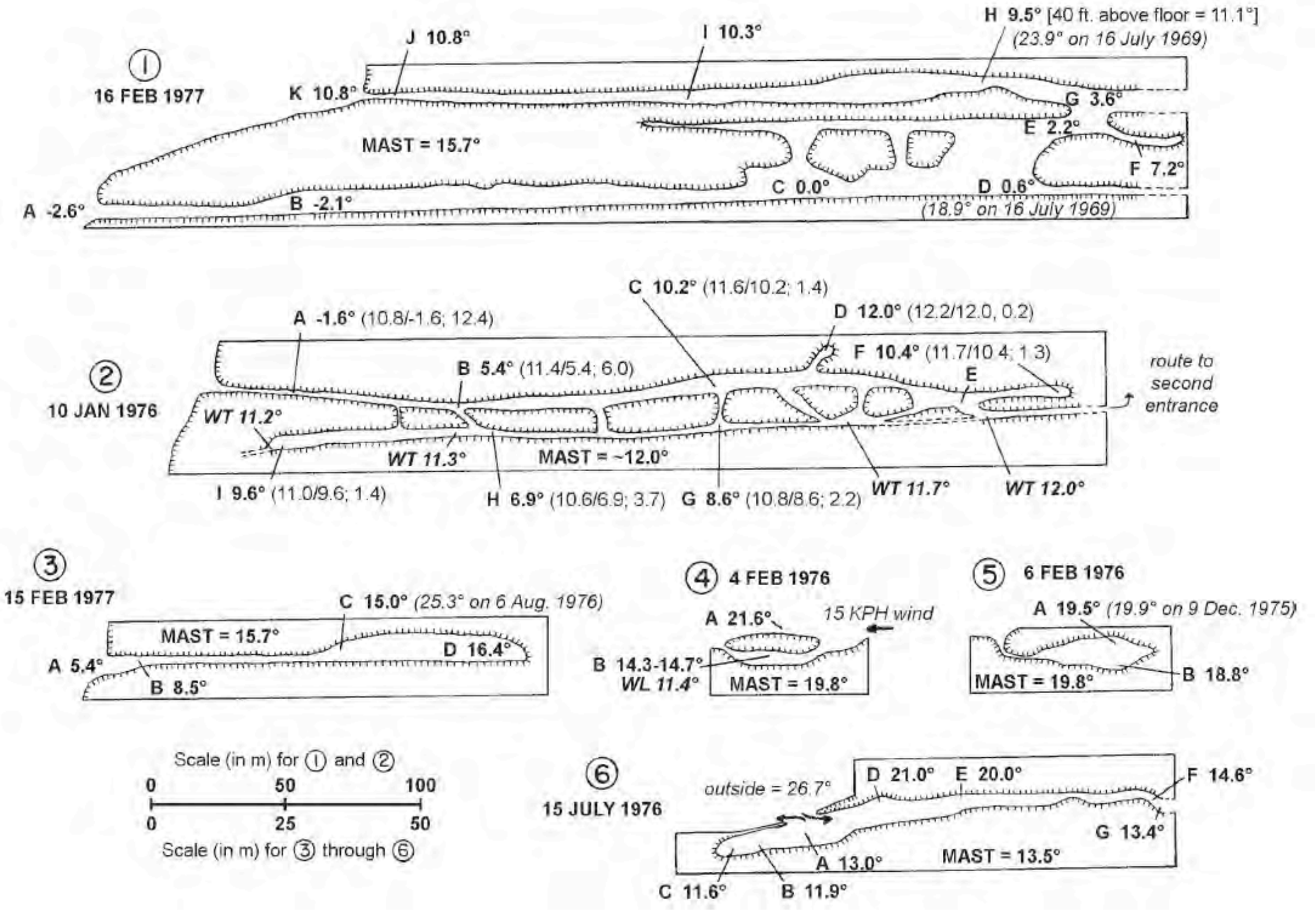

Figure 2. Six southeastern eaves and temperatures (in °C) at some sites for the date indicated near the cave number. Temperatures on additional dates may be given in parentheses. MAST = mean annual surface temperature, WL = wall temperature, WT = water temperature. For cave 2 the range of temperatures from January through August is given in parentheses (maximum/minimum; number of degrees in the range). Streams flow from right to left through the lower levels of caves 1 and 2.

Furthermore, the direction of flow requires that the second entrance be higher in elevation than the one known, making this cave an example of Type 7, Figure 1. The tell-tale air flow is quite strong in the stream passage beyond point E, indicating that this passage leads toward the undiscovered entrance. Further evidence of a second entrance can be seen in the relative fluctuations of air and wall temperature in the cave, to be discussed later.

Given postulation of this second entrance, the pattern of temperatures observed within the cave are what would be expected. Location A shows the lowest January reading and the greatest January to August fluctuation, with B, H, and G following, in decreasing order. This follows the flow pattern of cool dense air from the entrance, and the entire lower cave level is a cold air trap. It is not as cold as might be expected; cold air settles into this low area, but it is warmed by the stream which pools there before disappearing in a sump. Note the cooling effect of the lower cave on the stream, which enters the known cave (near E) at 12.0°C and progressively cools to 11.2°C at I. C is little affected by air from either entrance; it is too high relative to the known entrance to be cooled in winter, and too distant from the other to be greatly warmed in summer. Warm summer air being drawn into the upper entrance evidently has been cooled approximately to MAST by the time it reaches the known cave. D is an example of a relatively constant-temperature room such as Z, cave type 7, Figure 1. Distance from the warm air (upper) entrance, plus small volume, prevent it from being a warm air trap. Temperatures at F are slightly lower than the presumed MAST, indicating that it is probably nearer to the known cooling entrance than to the undiscovered upper one; its overall temperature stability, however, is indicative of its isolation from both entrances.

The above two caves illustrate the impact of seasonally reversing air flow in multi-entrance, multilevel caves. Cave number 6 of Figure 2 illustrates a more subtle example of seasonally reversing air flow. Its moderately large, sloping entrance, simple structure, and the distribution of volume both above and below entrance level allow year-round air flow through the single entrance. When outside temperature rises above internal cave temperature, cool air spills out the bottom of the entrance. The "negative pressure" so created enhances movement of warm air through the upper part of the entrance into the upper sections of the cave. The size of the entrance is sufficient to allow the two opposing streams of air to pass simultaneously, and they are easily detected by an observer. In winter the relatively warmer cave air will rise through the entrance, being replaced by denser, colder air from outside (air flow arrows would reverse directions). In this type of cave, relative velocities of flow, summer versus winter, depend on the amount of volume above versus below the entrance.

It is important to note that the two ends of the cave will have their major circulation at different times. The lower end will have greatest air flow in winter, and be a cold air trap in summer; the upper end will have greatest air flow in summer and act as a warm air trap in winter. Periods of temperature stability (deviating from MAST in opposite directions within the same cave) will be much longer and more predictable in this cave than in caves 1 or 2 of Figure 2. The range of temperatures between points C (below MAST) and D (well above MAST), and their relationship to MAST and the outside temperature illustrate the difference between the two “trap” areas. The narrow, undulating passage creates a relatively stable MAST regime beyond F. On the day of observation there was no detectable air flow at B and C despite the rapid movement of air above. The outward moving flow of air along the ground outside (1.5 m below the point registering 26.7°) was 18.4°C.

Non-reversing Air Flow

Cave number 3 of Figure 2 illustrates the impact of having all of the cave volume above entrance level. Its air flow pattern is like that of Type 5, Figure 1, although its elevational rise is only slight. The room containing C and D is a warm air trap, as demonstrated by an August temperature considerably in excess of MAST. Despite strong winds which buffet the entrance from across a large reservoir, the large entrance size (2 m high by 11 m wide), the cave length of only 76 m, a direct, relatively unobstructed path from the entrance to the innermost volume, and its relatively small total volume, this cave does not become cold in winter; the warm air is trapped and very little flow occurs. Even at the end of a record cold winter in 1977, location D remained slightly above the local MAST. If there were a strong upward slope between points B and D and/or if the volume from C to D were greater in an upward direction, this cave's winter temperature would be even higher. Nevertheless, its annual average is well above that expected based on MAST.

Some of the most remarkable thermal gradients known to occur in caves are found in those which have “sack” structures similar to that illustrated in type 4 (Figure 1). A cave located in eastern Tennessee (see Figure 3), where the MAST is approximately 14°C illustrates this. Entrance A, just above the rim of a large sinkhole, slopes upward into the main chamber; entrance C, located 11 m below the rim in the bottom of the same sink, slopes down into the cave. Entrance B, slightly below C, opens directly into the main chamber. In summer, cooled air from the upper portion of the chamber spills out into the sink, which acts as a large dam. Consequently, on 18 July 1976, when the outside temperature at the rim of the sink (site 1) was 23.6°C, the temperature near the bottom of the sink (site 2), outside entrance C, was 14.0°C (approximately MAST). A thermal range of 6.7 (site 3) to 23.5°C (site 4) existed in the main chamber (35 m tall, 54 m long and 12 to 20 m wide). A mild negative pressure created by the escape of cold air probably aids in drawing warm summer air in through A and B; the temperature at the very top of the room may have been even warmer than that recorded at site 4. Though slight air flow is possible in summer, the cave's only strong air flow is limited to periods of cold winter weather. Multiple entrances and its greater overall volume above the highest entrance and below the lowest one, allows this cave to function as a more efficient cold and warm air trap than cave 6, Figure 2.

Data from a second cave of very similar structure illustrate an annual temperature cycle in such a cave (Figure 4). Again, there is an elevational increase (roughly 35 m) from the bottom of the cave's main, large room to the cave's upper entrance. In this cave the main entrance room is 46 m long, 18 m wide and 15 m high, with several major passages extending out to the sides and downward. A single large canyon passage approximately 25 m tall and 1.5-2 m wide connects the lower cave to an upper room that is approximately 27 m long, 18 m wide and 4 m high. The upper room exits to the surface at a level about 1 m below its upper end through an entrance less than 1 m in diameter. The larger lower room is entered through either of two entrances near the upper end of its ceiling, both of which average about 1 m wide by 2 in. high. Though this cave is more complex than the last, it serves as another good example of the fourth type shown in Figure 1.

The record of air temperature from location A (Figure 4) in this cave is from a deep, inner room, protected from air flow by a very narrow irregular passage and several vertical turns that act as ideal dams (as in Figure 1, example 2) against flow of either warm or cool air. As expected, air temperature there closely approximates MAST and shows an annual fluctuation of only 1.1°C. Even this small fluctuation is thought to have been caused by the occasional use of the room as a roosting place for several thousand bats. Location B was in a major side passage roughly half way between upper and lower levels of the cave. Here air temperature varied by only 0.6°C, despite relatively free circulation of air, but constantly was below MAST. Site C was located in the uppermost room 18 m from the upper entrance. At this location small amounts of cold air "leaked' in, lowering temperatures in winter, while slight summer loss of cool air from the lower entrances created sufficient negative pressure to draw warm outside air down into the room, resulting in a nearly 12°C annual fluctuation. The temperature record for site D, located near the bottom of the main, lower room, 40 m from the lower entrances, shows an annual fluctuation of 5°C with the annual high temperature still 7.3°C below that expected based on MAST. Its large volume below the lowest entrance makes this main room an exceptionally efficient cold trap. As in the previous example, the lower entrances were surrounded by a deep sinkhole which reduced loss of cold air. Summer air movement was slow enough that it was detected only at the small upper entrance. During cold winter weather a strong flow of cold air enters the lower entrances, while relatively warm air exits through the single upper entrance.

Air Flow Prevention

As previously discussed, lack of elevational differences between multiple entrances, small entrance size (particularly in single-entrance caves), and natural dams can reduce or nearly eliminate air circulation. When these characteristics are present, singly or in combination, the result generally will be caves or sections of caves with the relatively constant temperatures of popular legend.

Cave 5 (Figure 2) provides a very simple example of the impact of a small entrance. The entrance passage into this cave includes a 5 meter-long horizontal section that is only 1/4 m in height and 1.5 m wide. With an enlarged entrance, this cave would be of type 1 (Figure 1) and would fall well below MAST in winter, yet due to its restrictive entrance size and shape, its average air temperature on 6 February 1976 was less than a degree below MAST. The 18.8°C temperature near the lowest point in the cave may have reflected the impact of cold surface water flowing into the sinkhole entrance during winter rains. A prominent factor in reducing air exchange with the outside in this cave is the cross-sectional shape of the entry passage. If the passage were simply turned 90°, placing its greatest width in a vertical plane, this cave's annual temperature fluctuation likely would increase considerably. Warm and cool air could then exit and enter simultaneously.

Surface Wind

Cave 4 (Figure 2) of this study illustrates the relative ineffectiveness of surface wind, even on a tunnel-like cave only 17 m long with two entrances (4.9 m wide by 1.4 m high and 3.5 m wide by 0.8 m high). Although a 15 KPH surface wind was blowing in the same direction as the cave passage, the air temperature in this cave at 1700 on 6 February 1976 was more than 7° below the outside temperature and approximately 5°C below MAST. Despite this cave's small size, simple shape, relatively large entrances, and its directional orientation, the surface wind had only moderate impact; slight directional air flow along the cave ceiling in the expected direction was noted, and the 3° difference between air and wall temperature demonstrated that a relatively rapid rise in air temperature had occurred during the day. This cave and cave 3 (Figure 2) demonstrate that surface winds probably have little effect on any but the smallest and simplest caves.

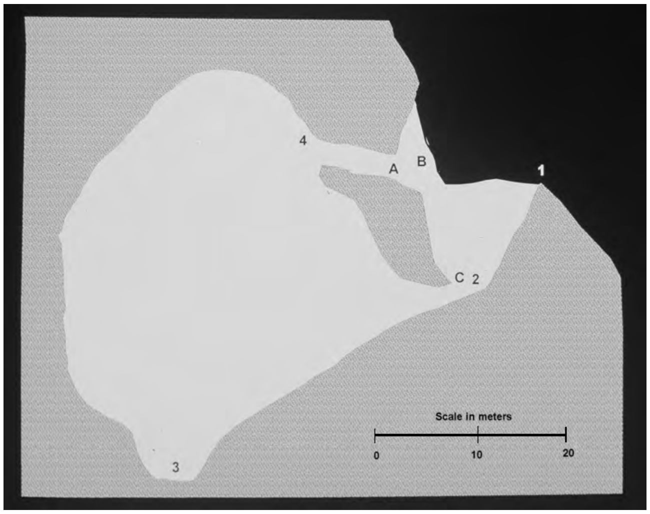

Figure 3. Cross section of an eastern Tennessee cave which acts as both a cold and warm air trap. Air circulation is greatest in winter.

EFFECT OF WATER ON CAVE TEMPERATURE

A central Tennessee cave with a single vertical entrance (6 m deep and 4 m in diameter; located in the bottom of a shaded, 8-m-deep sinkhole) provides an excellent example of the potential impact of surface water on cave temperature. A 100-m section of passage below the entrance averages 11 m wide and 3 m tall and would be expected to have an average air temperature below the mean annual surface temperature of 14°C. Even if air circulation were poor, a cave below such a single sinkhole entrance should not exceed MAST. However, on 30 July 1976 we found that the air temperature 90 m inside the described large passage was 21.1°C, some 7°C above MAST. This could be accounted for only by the presence of a large stream flowing through the main passage below the cave entrance. Though the stream clearly fluctuates in size, at the time of our visit it averaged 7 m wide, 0.25 m deep, and was flowing rapidly.

At its point of entry, the water temperature was 21.3°C (0.2°C warmer than the air 2 m above), but 90 m downstream it already had lost 0.1°C to the surrounding cave. Cave air at that point (nearly directly below the entrance) was 20.3°C. Approximately 100 m farther downstream the air temperature was 19.4°C. At this point an upper level passage, averaging about 2 m in diameter slopes very slightly upward and continues for at least 100 m, and probably much farther. Air temperatures near the ceiling 25 and 75 m into this side passage were 17.2° and 15.3°C, respectively. At 95 m, just past the first downward dip in the passage, the air temperature near the floor was 14.3°C, approximating the expected temperature based on MAST. Clearly, the high temperature of this cave's stream had measurable impact on the cave's air temperature, even at a considerable distance beyond the main stream passage. Due to the structure of the cave's single entrance, it is very unlikely that warm air entered from outside.

While working in caves of northwest Florida in winter, we repeatedly observed not only the impact of cold surface water, but also that of deep pools of subterranean water. Two caves less than 5 km apart illustrate these temperature differences. On 3 February 1976 the first cave was approximately half-full of surface water from winter rains, and the water temperature was 11.4°C. Air temperature 1.5 m above the water ranged from 11.3° to 12.4°C. The second cave, visited 5 February 1976, sloped sharply downward from its 2-m entrance and had an easily detected flow of cold air along its floor, with warm air exiting along the ceiling. Despite these characteristics (which favored entrapment and storage of cold air) its air temperature 28 m inside and 1.5 m above a pool of water roughly 30 m long, 12 m wide and more than 12 m deep ranged from 16.6° to 17.8°C. The water was of subterranean origin, and its temperature was 19.9°C, only 0.1°C above the MAST reported by a nearby weather station.

RELATIONSHIP BETWEEN AIR AND WALL TEMPERATURE

Wherever air in a cave is isolated from the external atmosphere it should come into thermal equilibrium with surrounding cave walls. As already noted, the locations of such protected places are highly predictable, as are the locations of probable large differentials between air and wall temperatures. The magnitude of difference in air and wall temperature provides a test of one's assumptions regarding constancy of temperature for any given location: areas of assumed constant temperature should show consistent equilibrium of air and wall temperatures. (It should be remembered, however, that even areas of great fluctuation may frequently exhibit air/wall temperature equilibrium, for example, during sustained periods of minimal air flow.) Air/wall temperature differences should be greatest near cave entrances where air enters. Near such "sucking" entrances, air temperature should average above wall temperature in summer, while it should average below wall temperature in winter. However, these expected differences will decrease with distance of air flow through a cave, so that even rapidly moving air exiting through distant entrances may have reached equilibrium with surrounding walls.

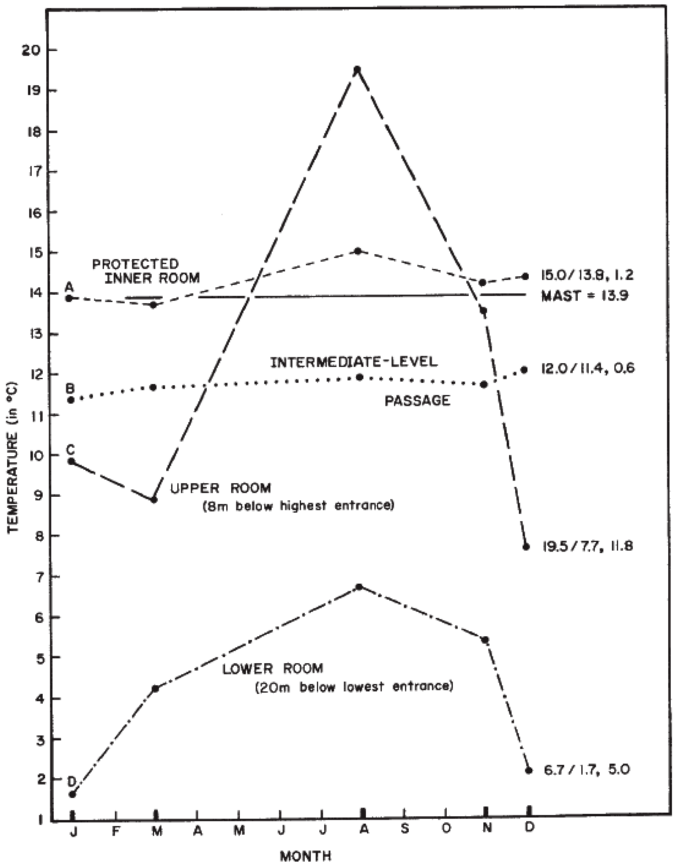

Figure 4. Air temperatures (maxiumum/minimum, number of degrees in the range) at four sites in a northeastern Tennessee cave on 18 November 1975, and 13 January, 9 March, 1 August and 20 December 1976. The cave is similar to Type 4, Fig. 1, with the addition of a warm air trap near entrance B. MAST = mean annual surface temperature.

Accordingly, analysis of air/wall temperature differences (Figure 5) in cave 2 of Figure 2 provided additional evidence in favor of the existence of a second, unknown entrance, as noted previously. Near the known entrance (site A), which "sucked" air in winter, the greatest differences between air and wall temperatures occurred in November and January (air temperature below wall temperature). Differences were very small in March, May, and August (with air slightly higher than wall in temperature, and both still below MAST), when the entrance was "blowing." The reverse was true at site F near the end of the known cave, on the way to the undiscovered entrance; the greatest difference occurred in May (air higher than wall temperature), and the least in January. Clearly, "warm" air was passing this location during the spring on its way from the undiscovered to the known entrance. The relative slowness of wall temperature response to air temperature fluctuations is pointed out by the August-November and January-March readings at sites A and F where air temperature drops below wall temperature with the beginning of cold weather, and rises above wall temperature in spring. Finally, site C, which is relatively isolated from either entrance and from air flow (as noted previously), exhibits the expected minimal air/wan temperature difference.

When comparing differences in air and wall temperatures it is important to remember that, regardless of season, both the amount and direction of air flow will be determined by the amount and direction of differences between inside and outside temperature. These differences may fluctuate widely, not only as a result of the passage of storm fronts, but also on a daily basis, due to night-day changes. Although we visited the respective locations of temperature measurement in cave 2 at approximately the same time of day each visit (to maximize comparability of readings among visits), we recorded several day-to-day and within-day fluctuations between air and wall temperatures at location A in order to illustrate the potential extent of such fluctuations.

On 28 December 1976 the air temperature in front of the known entrance was +8.6°C at 1145 hr and -2.8°C at

2250. At 1200 the air temperature at location A was fluctuating from 5.8 to 6.1°C, and the wall temperature was 3.9°C. (Unfortunately no temperatures were recorded at location A at 2250.) Clearly, outside temperatures during the previous night had fallen well below freezing, and the cave walls, cooled by that incoming night air, were now being warmed but were still cooling incoming air to below the higher daytime temperature.

The reverse situation is well illustrated by data from the following exceptionally cold day. At 1250 on 29 December 1976 the outside temperature was -6.1°C, and at 1935 the temperature had fallen to -8.2°C. Inside the cave at 1300 the air temperature at location A was fluctuating from -3.3 to -2.9°C, and the wall temperature was 0.8°C. At 1925 the air temperature at this site had continued to fall, varying from -4.7 to -4.5°C, and the wall temperature was -1.4°C. On this day continually falling outside temperature prevented the situation recorded on the previous day when inflowing air was warming the cave walls. On the second day incoming air ranged 2.1 to 3.3°C lower than wall temperature, as opposed to 1.9 to 2.2°C above wall temperature on the previous day. The first day's data are undoubtedly more representative of average daily cycles.

These data probably can explain the contradiction between our findings and those of several previous authors who claimed that wall temperatures in caves are normally about 1☜C lower than that of adjacent air masses (Twente, 1955; Nieuwenhoven, 1956, Hall, 1962; McNab, 1974). These researchers limited their investigations to winter studies of hibernating bats. Bats normally hibernate in caves whose structures act as cold air traps, and such caves tend to take in more and colder outside air at night than during the warmer days. By mid- or late morning, when researchers generally arrive at their caves, air flow often has slowed considerably and may have stopped altogether. Nevertheless, the last air drawn in was probably considerably warmer than the coldest night air, leading to the observation that air temperatures are generally higher than those of adjacent walls.

RELATIONSHIP BETWEEN AIR MOVEMENT, TEMPERATURE, AND HUMIDITY

A thorough study of cave humidity and the subtle interrelationships between humidity and the many factors that may bear upon it is far beyond the scope of our research. We did, however, make sporadic comparisons among humidity, temperature, and air movement in 10 of the caves investigated. Substrate type, ground moisture, and the presence of streams or standing water all contribute to basic cave humidity levels. Superimposed upon these basic factors, rates of air flow, nearness to a "sucking" entrance and the humidity and temperature of air entering from outside compared to existing cave conditions were found to be of importance in determining daily and seasonal patterns of humidity.

Regardless of season or temperature of the inflowing air, relative humidity was lowest near the entrance where outside air entered. A gradient of increasing relative humidity existed between the places of entry and exit of the flow. Further, in caves with seasonally reversing air flow, passages that have low relative humidity at one season may have high relative humidity at another. These patterns are illustrated by our recordings from cave 2 (Figure 2). On 10 January 1976 when air movement was past locations A, B, H, G, and E, in that order, sample relative humidities were as follows: B -- 49 percent; halfway between H and G -- 82 percent; halfway between

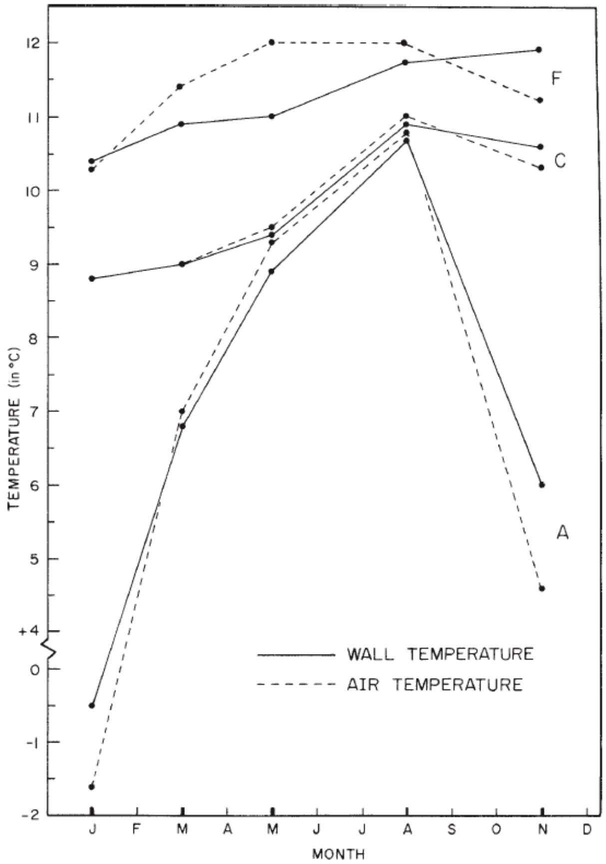

Figure 5. Air and wall temperatures through a seasonal cycle at 3 sites in cave number 2, Fig. 2. Dates of the measurements are 15 November 1975, and 10 January, 6 March, 16 May and 18 August 1976.

G and E -- 86 percent; halfway between E and D (upper cave: air flow nearly nonexistent) 98 percent. The movement of outside air through the cave clearly affected relative humidity levels along its route. On 16 May, when the direction of air flow had reversed (passing from E to D, C, B, and A), the relative humidity halfway between E and D had dropped as expected (to 88 percent). No other measurements were taken on that visit.

Strong air flow has been considered by some to be closely associated with low humidity throughout a cave (Vandel, 1965; Barr, 1968). Although it is true that air flow often can be a desiccating influence, particularly near "sucking" entrances in winter, ground moisture or areas of water can increase relative humidity of even strongly flowing air to near saturation as it passes through the cave. For example, despite the fact that troglobitic trechine beetles are limited to areas where the relative humidity is 98 percent or above (Barr, 1959), a number of individuals of three species have been observed feeding in a "wind tunnel" in a Kentucky cave where the air flow exceeded 40 m per minute (Barr, 1968). Barr seemed puzzled by this apparent contradiction, but we suspect that the contradiction was only apparent --as we have pointed out, rapidly moving air in caves is not necessarily dry. One of us (Tuttle) once made a similar observation of trechine beetles in a "wind tunnel" in a Kentucky cave; the relative humidity was 98 percent, despite the strong air flow.

In reference to the relationship between the total volume of air flow through a cave system and the cave's humidity, it also is important to note that air flow rates will vary greatly in different sections of the cave even along the main route of flow. For example, in a single passage, diameter and shape may vary dramatically, so that a given volume of air flow through the area would be rapid and potentially very influential on humidity in a narrow section while remaining virtually undetectable in a very large area. Within the parameters discussed in this section, however, our limited data indicate that overall patterns and timing of relative humidity changes are largely correlated with, and dependent upon, predictable daily and seasonal patterns of air flow.

Finally, although it is usually relative humidity which is reported in the literature, it is important for cave biologists to keep in mind the distinction between this measurement and absolute humidity (mass of water vapor present in a unit volume of atmosphere). In some instances the two measurements follow the same relationship from site to site. This is the case for the cave 2 example above--absolute humidities (in the same site order, in g/m^3) on 10 January were 2.6, 7.5, 8.0 and 9.9. The 16 May absolute humidity had dropped to 8.8. In other cases, high relative humidities at low temperatures actually may be more potentially dessicating than lower relative humidities at higher temperatures, due to the lesser amount of water vapor present in the air in the former case. For example, in the cave discussed in Figure 4 the relative humidity at location C on 10 January 1976 was 99 percent. On 1 August 1976 it was only 92 percent. Although the August relative humidity was lower, absolute humidity was nearly two times higher--15.5 g/m^3 in August versus 8.4 g/m^3 in January. In a similar cave (Figure 3) the relative humidity on 18 July 1976 was only 70 percent in the path of incoming air (site 4), while it was 100 percent at the floor of the same room (site 3) and 99 percent just inside entrance C (where air exited very slowly). These relative humidities follow the pattern discussed in the paragraph above but, due to the great temperature gradient in the room, absolute humidities (14.1, 7.6 and 8.8 g/m^3 respectively) are totally reversed in relationship among sites. Temperature of the air, due to its effect on absolute humidity, must be included in the list of factors considered in evaluating the impact of a cave's humidity regime on its faunas.

BIOLOGICAL IMPLICATIONS

Humidity is a very important environmental parameter for many terrestrial cavernicolous animals (Barr, 1959, 1961, 1967; Vandel, 1965). Cold dry air entering a cave in winter, as it warms inside, certainly can be a dessicating influence to organisms in that area. In particular, respiratory water loss for an animal with a body temperature warmer than the air will be more severe the greater the temperature difference. It is important to note, however, that besides the large-scale factors influencing humidity (discussed in the previous section), a number of other considerations influence the effect of given levels of air flow and humidity on organisms. The size of the boundary layer associated with a particular organism's coupling with its environment is proportional to the size of the organism and the roughness of the substrate on which the animal rests, as well as to the wind speed (see Juberthie, 1969, for a cave study of microclimate). Substrate moisture in many situations, then, may be of more importance to small arthropods than air moisture. In other words, in addition to the fact that flowing air in a cave is not always dry, different organisms in a particular area of cave in fact may be exposed to very different environments--low air humidity (relative or absolute) may have little effect on a small terrestrial arthropod on a rough, moist floor compared with its effect on a bat.

Air flow, despite its potential for lowering humidity, should not be assumed to be entirely bad for most or even any cave organisms. It may be of considerable importance as a directional cue for some cave animals. Trechine beetles are reported to be highly sensitive to air flow (see Barr, 1968), and two species of cave crickets *(Ceuthophilus conicaudus* and *Hadenoecus subterraneus)* are believed to use air currents in their orientation to and from cave entrances (Reichle *et al.*, 1965; Campbell. 1976; Levy, 1976). Additionally, air flow and associated patterns of temperature and humidity are as predictable in many caves as are many other cues that are used by surface animals. Many cavernicolous animals are thought to be extremely sensitive to even slight changes in air flow, temperature, and humidity (Barr, 1959, 1961, 1964, 1967; Vandel, 1965), and the role of air flow as a seasonal or daily cue may be of major importance in some caves.

Beyond the cue effects of air movement and temperature, temperature directly affects a variety of trogloxenes (animals that live in caves but cannot complete their life cycles without leaving caves). Bats will be discussed in detail later. Our casual observations indicate that cold caves which harbor hibernating bats often additionally serve as hibernating sites for a variety of otherwise surface arthropods (e.g. culicine mosquitoes and the noctuid moth *Scoliopteryx libatrix)* that were not often found in warmer caves. On the other hand, these same cold caves rarely contained amphibians, such as *Eurycea lucifuga* and *Plethodon glutinosus* (even when relative humidity remained high), which often were abundant in other caves nearby. Even if the major effects of air movement and temperature were limited to determining the within and among cave distributions of such trogloxenes as bats and cave crickets, they ultimately could exert strong indirect effects on troglobitic (animals that are so highly specialized that they cannot live outside of caves) and troglophilic (animal that often live their entire lives underground but also can live in moist places under rocks or logs on the surface) cave animals that depend on these animals as primary sources of energy.

Dependable food sources in a cave environment are of vital consequence to its fauna; whether they be guano from bats and crickets, entrance litter, or detritus from floods, supplies vary seasonally (Barr, 1967). Strong selective pressure must exist for the development of responses to such available cues as changes in water temperature, pH and oxygenation (for aquatic animals), air flow, temperature and humidity (for terrestrial animals), and flooding. In fact, initial studies indicate that many troglobites, both terrestrial and aquatic, use seasonal flooding to time peaks of reproduction (see Barr, 1968; Poulson and Smith, 1969; Juberthie, 1975, among others).

Clearly, the potential impact of the above environmental factors in determining species survival and distribution is great and the problems complex. We make no pretense of understanding more than the potential importance of these variables. It is important, however, to note the extent to which the environment of the cave depends on its exchange of air and water with the outside. Hopefully, our discussion of cave structure and the causes and predictability of daily and seasonal patterns of air flow, temperature, and humidity will act as a stimulus for much further investigation of these potentially important environmental parameters.

Temperature Constraints on Cave Bats

For most bats, and especially for cave dwelling species, the selection of appropriate roosting temperatures is of critical importance (Harmata, 1973). Twente (1955) noted that it was vital for bats to choose roosts with temperatures appropriate to the desired metabolic processes: warm for digestion and growth in the summer, and cool for torpor in the fall and winter, with the exact optimum temperatures varying somewhat among species. McManus (1974) found that hibernating *Myotis lucifugus* in a New Jersey mine "demonstrated a clear preference for temperatures near 2EC the temperature at which Hock (1951) found the species' oxygen consumption to be lowest. Harmata (1969) demonstrated that *Rhinolophus hipposideros* could select "the proper temperature of hibernation" with accuracy as near as 0.8°C.

Whatever the mechanism of selection, microspatial distribution preferences and movements along temperature gradients also have been demonstrated in summer roosts of many species, with clustering playing a role in behavioral temperature regulation then as well as in winter (Licht and Leitner, 1967; Harmata, 1969, 1973; Tuttle, 1975; Trune and Slobodchikoff, 1976, among others). A number of authors have noted the high metabolic cost of the wrong ambient temperature for bats (Hock, 1951; Herreid, 1963; Stones, 1965; Davis, 1970; McManus, 1974).

For cave dwelling species, caves with roosts of appropriate temperatures are limited in number. At extremely high latitudes caves may be too cold for use at any time. At somewhat lower latitudes, where MAST ranges 2 to 12°C, caves often provide appropriate hibernating quarters but are normally too cold to permit summer use. In areas of intermediate latitudes (MAST 12 to 20°C most caves are too warm in winter and too cold in summer, and few are used by bats in any season. At lower latitudes nearer the equator, increasingly warm caves are ideal for maternity use but unsuitable for hibernation (Dwyer, 1971).

Throughout most of the cavernous areas of the United States, caves are of the intermediate type with regard to temperature. Consequently, although bats may be able to utilize them in spring or fall when their temperatures may be acceptable (Harmata, 1973), most U.S. caves are unsuitable for bat use for summer nurseries or winter hibernacula. Thus, those species that use caves are often severely roost limited. (The problem is compounded for species which use caves in summer, since the cave must have not only appropriate temperatures available but also must be close enough to proper feeding habitat.) Distribution of caves of appropriate temperature, then, likely plays an important role in the determination of many distributional boundaries (McNab, 1974; Humphrey, 1975).

For example, although numerous caves and mines exist in Utah, Twente (1960) concluded that virtually all were of inappropriate structure to provide temperature ranges essential to bat hibernation. He did not find a single suitable cave or mine among more than 500 examined. Additionally, the endangered gray bat (*Myotis grisescens)*, a species which uses caves year-round, appears to be limited in its north-south distribution primarily by the absence of warm caves for rearing young in the north and by a lack of cold hibernating sites in southern caves (Tuttle, 1975, 1976). Few caves anywhere within its range provide roosts of appropriate temperature, and even in Alabama, where gray bats probably were once most abundant, this species is not known to have ever occupied more than 2.4 percent of the area's 1635 known caves in summer or 0.1 percent in winter (Tuttle, in press). This is despite the fact that this species is behaviorally able to reduce thermoregulatory costs during summer by clustering together in large numbers in ceiling domes or in restricted passages where heat can be trapped (Tuttle, 1975), thereby utilizing otherwise marginal caves.

Since most U.S. caves are in the intermediate, unusable range of temperature, cave bats generally are forced to select the very few caves that have structures permitting them to deviate well above MAST (for summer use) or below (for winter use). Structures of caves chosen for winter hibernation are easily predictable. Except at high latitudes or elevations, they almost invariably fall into categories 1, 4, 6 or 7 (Figure 1). Of these, Type 4 is by far the best. Without a cold air trap, Type 6 does not provide adequate stability. A midwinter period of outside warmth could prove highly detrimental to bats (many of which cannot go out to feed) hibernating in a simple cave of this type. A small, simple cave of Type 1 could prove equally unsatisfactory in an unusually cold winter. Accordingly, among the eight largest bat hibernating caves known in the Southeast, five are of Type 4 and three are Type 7. All of these occupied caves are large and have structural complexity adequate to provide temperatures ranging from near freezing to 12 to 15°C.

Summer maternity roosts usually are restricted to heat traps, especially in caves of Type 6 (if a trap exists) and 5 and 7 (where the rooms marked “X” probably would be best). *Myotis grisescens*, despite its ability to heat summer roosts by aggregating in large colonies, still prefers caves of these types; one of the largest maternity colonies ever known existed in Cave 3 (Figure 2), a Type 5 cave. Although few observations of summer cave colonies of *Plecotus rafinesquii* have been made, the several maternity colonies observed by us in southeastern caves each numbered fewer than 200 individuals. Such small colonies lack the ability to heat roosts of marginally low temperature, and as might have been expected, each was located in a heat trap of the kind illustrated by Xs in Types 5 and 7 (Figure 1). Temperatures in these roosts were all between 21° and 25°C, although MAST ranged only 14° to 16°C. Other examples could be presented, but it is sufficient to point out that bats must either abandon caves during the maternity period, seek exceptionally efficient heat traps near cave entrances, or heat their cave roosts by clustering together in very large numbers on domed ceilings (a strategy for which any benefit must be balanced against the cost of increased intraspecific competition for food). Successful growth and survival of young gray bats depend on the success of one of the last two strategies (Tuttle, 1975).

Finally, the ideal bat cave is generally one which offers a large thermal range. Ability to move among temperature zones within a cave can allow bats to control embryonic development (thereby synchronizing parturition time--Racey, 1969; Dwyer and Harris, 1972), to achieve deeper torpor when stressed by inclement weather during summer or when fat acquisition becomes important in late summer, or to adjust to temperature fluctuations throughout a season or between years. Obviously, structural and elevational complexity and increased cave size generally will contribute to this desired thermal range. Tall canyon passages often provide especially suitable temperature gradients for winter hibernation.

It is rare for any one cave to provide sufficient thermal complexity for year-round occupation; seasonal migration between caves is usually necessary for bats which use caves year-round (see Tuttle, 1976). Two caves discussed in this paper, however, are important to bats both in winter and summer. The cave (discussed in the section on Nonreversing Air Flow) from which the readings in Figure 4 were taken houses one of the largest winter populations of *Myotis grisescens* known, as well as a sizeable summer bachelor colony of the species. The hibernation roosts are in areas of the cave which are protected from freezing but are well ventilated by cool winter air; the summer roosts are in warm areas much higher in the cave.

The second such cave, Cave 1 of Figure 2, contains the largest summer colony of *Myotis grisescens* known. The main roost, located in the dome-like area around H, is warmed by the summer air sucked in from entrance K by the strong air circulation discussed previously, and by the body heat of the colony of 128,000 bats (formerly more than 250,000). In winter, the appendix-like area (F), due to its configuration and location, traps and stores air of low temperature, providing a hibernation roost of relatively constant temperature for a number of bat species, including *M. grisescens* and *M. sodalis*.

MANAGEMENT IMPLICATIONS

Choosing Caves for Protection

Clearly, knowledge of cave structure and its relation to temperature and humidity is of potentially great importance in predicting species distributions within and among caves, and in determining the relative merits of any given cave for protection. Data on such factors as number, size, shape and location of entrances, internal passage size, contour and slope, distribution and amount of volume relative to cave entrances, and source and amount of water flow (if any), can be used to predict and/or verify the probable seasonal temperature and humidity regime of a cave.

Given the limitations of resources, time and manpower, it often is important to establish criteria for recognition of caves of special or unique merit. Obviously no single structural type can be singled out for exclusive protection, since each cave type presents a potentially different setting for the evolution of different faunas and survival strategies. In fact, a wide variety of cave types should be protected. For example, caves that are good for bat hibernation may not be good for some terrestrial cavernicoles, and vice versa. Frequently the object of cave protection is centered around one or two endangered species. In such situations it is vital to ascertain not only the species' temperature, humidity, and other microhabitat requirements, but also its food requirements and sources when relevant, in order to guarantee that all important parameters are adequate.

For bats, when food supply availability and other external variables are equal, caves of greatest structural and therefore thermal complexity generally are best. Nevertheless, in the case of maternity colonies, where warmth is of primary concern, even simple caves (for example cave 3, Figure 2) may be of great importance. Also, in the case of endangered bats, their present usage of a cave often is not a reliable indicator of its suitability for use. The best caves often have been heavily disturbed and now contain very few bats. On the other hand, other nearby caves, of very marginally suitable temperature but less disturbed, may contain more bats. In many cases the most important cave, in terms of the species' longterm survival, is the one that presently has few bats.

A good example is illustrated in Figure 3. As a result of this cave's popularity with local cavers, it has not housed major bat populations for perhaps as long as 50 or more years. Although no bats were present at the time of our visit, scattered recent droppings indicated that some bats continue to visit the cold area at night in the summer and probably in the fall. If the cave were protected, it could potentially become an important bat hibernating site, as it undoubtedly once was prior to disturbance. In addition to its cold trap characteristics, which make it suitable for hibernation, there is evidence (in the form of feces) in the warmest area, which indicates that some bats continue to attempt to use the area as a summer roost. Similarities with known roosts suggest that the species involved may be *Plecotus rafinesquii*. In this case as in many others, then, the cave's structure and resulting environment can tell more about its importance to bat populations than does its present degree of usage. This is almost certain to be true for caves valuable to other animals as well.

Means of Protecting Caves

Knowledge of factors affecting cave environments also is of great importance in determining the proper means of cave protection. In a number of instances, improper gating of caves has reduced or destroyed the bat populations intended for protection, either through reducing free access by the bats or reducing the air flow necessary for maintenance of appropriate temperature and humidity (Mohr, 1972; Tuttle, 1977). Creation of additional entrances also can have disastrous results. Specific recommendations for cave protection through gating or fencing are provided by Tuttle (1977). In brief, structures which in any way alter air flow should be avoided. Any structure which blocks an entrance can affect not only air flow, but also the supply of food (in the form of entrance debris) for those cavernicoles requiring within-cave sources. In general, it is sound policy to simply avoid tampering directly with an entrance unless absolutely necessary.

It is of interest to note that alterations in temperature and humidity can have negative effects not only on cave life, but also on cave formations by altering development. Furthermore, protection or destruction of one species may influence the survival of a whole group of other species; for example, protection of a summer bat colony protects the whole guano ecosystem which may be present. Another vital factor for the public and individuals responsible for caves to be aware of is that even actions outside of caves can have great impact inside; in particular, smoke from fires built in or near an entrance can be drawn into a cave, as McCavit (1975) noted. At the very least, unnecessary disturbance is the result; at the worst, whole populations of bats and perhaps other animals may be killed.

Hopefully, this discussion of the factors influencing cave environments and our examples will prove useful to those who deal with caves in a scientific, managerial, or recreational capacity. It is apparent that, at times, lack of understanding of the many complexities involved has impeded the progress of both research and protection of faunas. Improved understanding of these factors, combined with increased knowledge of cavernicolous species habitat requirements, should provide guidelines for utilization and/or protection of valuable cave resources.

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Guidelines for the Protection of Bat Roosts

J. Mamm., 73(3):707-710, 1992.

The American Society of Mammalogists recognizes the need for guidelines to regulate activities in and around bat roosts. In developing these guidelines, the Conservation of Land Mammals Committee has weighed the need for protection from disturbance against the needs for legitimate scientific inquiry and or monitoring declining bat populations. These guidelines are intended to assist field biologists and state and federal agencies charged with the granting of permits. They also reaffirm the Society's commitment toward high professional standards and its opposition to activities that could endanger bat colonies.

The preservation and conservation of bat roosts, especially caves, is probably the most important issue in bat conservation, particularly since many roosts are traditional and used by successive generations of bats over many years (Hill and Smith, 1984). One of the most important factors in the decline of bat populations in the United States and around the world is the destruction of roost sites. Roost sites (caves) are a limited resource that seasonally contain a high proportion of many species. Bats, particularly when concentrated in caves or other structures, are extremely vulnerable. Despite their generally small size, bats have low reproductive rates and long generation times and cannot sustain elevated rates of mortality or depressed levels of recruitment (Hill and Smith, 1984; McCracken, 1989). Of the 39 species of bats in North America north of Mexico, at least 18 species rely substantially on caves as roosting sites, and many of the remaining 21 species rely on caves during some time of the year (Barbour and Davis, 1969; McCracken, 1989). The fact that large numbers of individuals often are concentrated into only a few specific roost sites results in high potential for disturbance. Cave-dwelling bats are especially sensitive to both direct disturbances, such as human entry, and indirect disturbances to the roost and surrounding habitat. Persons entering maternity colonies can cause bats to abandon young or drop them to the floor from where they are usually not retrieved and subsequently die (Gillette and Kimbrough, 1970; McCracken, 1989). In addition, the handling of pregnant females has been known to cause abortion (Gunier, 1971).

Disturbance during hibernation may cause bats to arouse prematurely, elevating their body temperatures and utilizing stored energy reserves, which usually cannot be spared. Bat specialists have estimated that each arousal of hibernating bats can rob them of 10 to 30 days of stored fat reserves (Thomas et al., 1990; Tuttle, 1991). Bats may return to a state of torpor after disturbance, but then may not have sufficient energy to survive the rest of the winter. In addition, bat caves are vulnerable to habitat alteration and degradation. Changes in cave microclimate (e.g., humidity, temperature and air flow) are imposed through modification of cave entrances. Clearing trees from around cave entrances may result in an overall increase in summer temperatures or a decrease in winter temperatures, both of which may render a cave uninhabitable. The natural air flow in and out of a cave or its humidity may be altered to such an extent that the habitable portions are reduced or eliminated (Hill and Smith, 1984). Disturbance and destruction of roosts, especially caves, have contributed to the listing of many species and subspecies of bats on the U.S. Fish and Wildlife Service's list of endangered and threatened species (McCracken, 1989; Mohr, 1972). Such designations and the subsequent recovery efforts require bat specialists and wildlife managers to monitor remaining populations. Guidelines presented herein should be considered as minimum precautions when dealing with roosts containing endangered or threatened taxa. These guidelines should also be considered when working with other bat roosts as well, because severe reduction or elimination of populations through careless entry may eventually lead to additional species and subspecies being threatened. In addition, we know very little regarding the actual status of some populations of most bat species, and many species that are not listed as threatened may warrant listing and need the protection that goes along with it (McCracken, 1989; Stebbings, 1980). Moreover, several species of bats often use the same roost; thus, a roost containing mostly non-endangered species may also harbor endangered ones (Hill and Smith, 1984; McCracken, 1989). This lack of knowledge regarding the status of bat populations emphasizes the real need for precautions around roosts of all bats (Stebbings, 1980). As an additional precaution, we recommend that any species of cave-dwelling bat be treated as though their populations are in decline; exceptions should be limited only to those cases for which substantial evidence exists to the contrary.

Recommended Guidelines

1. Avoid revealing exact locations of bat roosts. Many bat specialists have already adopted this practice, often after declines in populations, damage to roosts, or both, have taken place soon after a publication revealed the roost location.

2. Caves or other structures designated as critical habitat for endangered or threatened species should not be entered except by federal or state management biologists or researchers with valid permits when bats are present.

3. Caves protected by fences or gates should not be entered except by special permit holders, regardless of species of bat present.

4. Caves protected by warning signs about bat nurseries or hibernating bats should not be entered during the times of year specified on the sign. Entry can be permitted at those times of year when bats are not present, so long as the cave is left unaltered and unpolluted.

5. Although species' tolerances differ, maternity colonies of endangered or threatened bats should not be visited, unless there is a special need and a federal permit has been obtained. Maternity colonies of non-endangered or non-threatened bats generally should not be disturbed. It is highly recommended that if maternity colonies must be visited that it be done at night while the adults are away from the roost.

6. For bats whose populations are either known or suspected of being in decline, most field research, including banding, should be discontinued while the bats are hibernating. Even for monitoring purposes, disturbances should be as brief as possible and should occur no more than once per winter, preferably in alternate years. In general, winter banding efforts for any bat population should be minimal and clearly warranted because arousing bats to band them can cause excessive mortality.

7. Persons entering bat roosts should reduce their impact by minimizing noise and the number of participants. Lights should be limited to those powered by batteries or cold chemicals such as cyalume. Persons should avoid passing too closely to roosting bats, and should leave no refuse or other signs that they were there.

8. Research on federally listed bats should be carried out through stringent adherence to the terms of federal and, when applicable, state permits.

9. Persons collecting bats need to be aware of federal and state laws governing the collection and transportation of bats, and must be in possession of the appropriate scientific collecting permits before the study is undertaken. When bats are collected for laboratory research, proper handling and transportation of captured animals should be practiced to minimize injuries and/or deaths, and therefore the actual numbers taken from a roost.

10. In nearly all cases, collecting should be done at, near or outside roost entrance rather than inside the roosts. Collecting is usually done with harp nets placed at or near roost entrances or with mist nets placed outside roost entrances. A limited amount of collecting can be safely done inside large cavern systems or in some man-made structures. Collectors should avoid captures in excess of numbers needed by estimating the size of colonies before setting up nets.

11. Collections should be minimal, including only a small fraction of the population of any given colony, should not be redundant with existing collections, and should be sufficiently infrequent to ensure that healthy colonies are sustained. Collecting should only be done as a means of furthering our knowledge and understanding of bats and not just because the bats are there.

12. Collecting should be done so as to avoid any damage to the cave or other roost structure.

13. Firearms, open-flame torches, smoke or toxicants (including pesticides) should never be used inside bat roosts.

14. Despite their genetic, ecological and economic importance, bats have an image problem and are not popular with most of the public. Current public attitudes towards bats threaten their survival, especially since the first reaction of most people to their presence in houses or buildings is to eliminate or remove them as quickly as possible (Hill and Smith, 1984). Because popularity is a major stimulus for conservation, we recommend that wildlife agencies, spelunking societies, colleges and universities, and nature centers, in conjunction with bat specialists if possible, increase their efforts to educate the public about bats. These efforts could include newspaper and magazine articles and talks directed at school

children, conservation groups, spelunking clubs and land owner groups. In addition, we recommend continuing education programs dealing with bats be directed at wildlife managers, conservation officers, wildlife commissioners, animal damage control agents and veterinarians. Adequate protection for bats may be next to impossible without an educated public (Tuttle, 1979). Through such education efforts, the public can be made more receptive to restrictions on human activities in or near bat roosts.

15. Although many of the guidelines proposed herein call for various permits for research, we do not imply that merely holding permits will ensure against detrimental effects of study. The American Society of Mammalogists expects that scientists will maintain high professional standards when conducting research in and around bat roosts.

16. We recognize that special circumstances may require these or any other guidelines to be violated for the welfare of an endangered or threatened species. Decisions on such matters will have to be made on an ad hoc basis by bat specialists and recovery team members in conjunction with the appropriate wildlife agencies. We intend these guidelines as general guidelines only, subject to modification under extenuating circumstances or as new information becomes available.

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On Cave Gates

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National Speleological Society, Huntsville, Alabama. 615 pp.

Editors' Note*: In this chapter, dimensions for materials deviate from the standard metric/English format used elsewhere in this volume because construction materials are usually sold in English units in the United States.*

Cave gates. There are hardly two words that polarize cavers as much as these. Even the most vocal anti-gate cavers admit that gates serve an important function in protecting irreplaceable cave assets, and in reducing the liability of cave owners. Yet all too often land managers turn to gates as quick and easy solutions to complex cave management problems.

Cave gates can be an important part of a comprehensive cave management plan, but there is much more to gating a cave that just welding steel. This chapter will not tell you everything you need to know about gates and gating, but it will give you an overview of the planning, design, building, and monitoring process and will direct you to additional expert resources.

Is a Gate Needed?

First, determine if a gate is truly necessary. Since a gate is a somewhat permanent structure that requires great expenditures of resources and may negatively impact the cave environment, it should be installed only after careful planning and design. Other protective methods may be more efficient or effective and should be explored first.

Other protective measures for cave habitats include but are not limited to the items in the following list.

- Administrative closures
- Signage
- Fencing
- Redirecting trails
- Public education
- Protective stewardship
- Electronic surveillance

While carefully designed and constructed gates have minimum effect on the cave environment, poorly placed gates can be very detrimental to the cave and its resources. If a gate is needed, it should have minimum impact on the cave.

Editor's Note*: If a cave gate will change air currents that originally flowed through breakdown or small openings, then measure the natural airflow before the gate installation begins. Design and construct the gate to mimic the original airflow. (See virgin digs, page X265.)*

Types of Protective Closures

Next decide on an appropriate gate design. In this section, the term cave gate is used for any type of lockable barricade that prevents human access to the cave, including fences, doors, and bars. Some types of closures, such as a simple chain across a passage restriction, are less secure than others.

The majority of this chapter focuses on various types of bat-friendly horizontal bar gates, which are suitable for most situations and are very secure. In rare instances that require an environmental seal, such as a newly opened cave or section of cave with no natural entrance, bat-friendly gates would be inappropriate. In those cases, air lock gates may be necessary to prevent drying air currents and contamination by outside organisms or materials such as mud.

Bat Friendly Gates

Most cave gating scenarios call for a bat-friendly gate. Fortunately, there are many types of gates that incorporate bat-friendly features. Standard bat-friendly gates are designed with widely spaced uprights and 5-3/4inch (146-millimeter) spacing between horizontal bars. The actual design depends on the amount of human vandalism pressure, the bat species present, and the way the bats use the cave. For instance, we must be aware that some species of bats do not tolerate cave gates at all, and others only at certain times in their life-cycle. The size and angle of the cave entrance may also dictate innovative adaptations of the standard bat gate designs. (See drawings for the horizontal bar gate, figure 3.)

After carefully choosing a location and initiating the actual construction, observe the effectiveness and impact of the gate over time. If the gate is creating negative impacts, quickly modify or remove it. Routine maintenance tasks should be planned before commencing the actual construction. Maintenance schedules may be required to repaint the gate if necessary, remove sticks and leaves or flood debris, change locks before they stop working, and remove rocky debris that accumulates around the gate. Signs, fences, and gates are also susceptible to vandalism, and repairs or replacement may be necessary.

Cave	Significance	Threats
1	paleontology, recreation, pristine	few due to difficult access
2	possible bats in winter, recreation	highly visible, liability (pit)
3	bats in winter	small, hard to find, rarely visited
4	recreation, speleothems, possible invertebrates	heavy traffic, increasing damage
5	Invertebrates	unintentional traffic from Cave 4

Table 1. Set Up a Table to Prioritize Actions

Selection of Protection Method

Before installing a gate at a cave entrance, many factors must be considered.

Issues to examine can be divided into two broad categories.

- Evaluate the cave resources themselves.
- Assess the level of threat to the cave resources.

Obviously, an easily accessible cave is more in need of protection than a rarely visited cave in a remote wilderness area. Likewise, a cave with a wealth of speleothems, important biota, or archeological and paleontological remains, is more in need of protection than a small, featureless, relatively sterile cave. We believe that all caves have value. But how do we determine what is significant and threatened?

Ideally, a complete resource inventory is done for the cave in question, with periodic monitoring up to the time of the actual gating. In reality, this rarely happens. Even caves that have been known and visited for decades hardly ever have simple baseline data, like temperature and invertebrate studies.

Often a gate is planned because the cave owner or manager is reacting to a crisis—the discovery of a rare and threatened resource, advanced loss of cave resources, sharply increased visitation, or liability concerns. No matter what the impetus for protection, we should consider all users and resources when designing a gate or other type of protective closure.

Five Possible Scenarios

This process can be illustrated by a hypothetical example. Assume that we have five caves on a 1,000-acre (405-hectare) parcel of land.

Cave 1. This cave is located on a remote back corner of the property, accessible only by fording a shallow river. It is backed by several hundred contiguous acres of forest under other ownership. It has a few thousand feet of passage, some fun climbs, and ancient bear den sites.

Cave 2. This is a shallow, 25-foot (8-meter) pit leading to 300 feet (90 meters) of easy canyon and crawlway. This cave is very near a road, and an obvious trail leads to its entrance. No bats or other obvious wildlife have been noted, but the temperatures are very cold, even in the summer.

Cave 3. This cave is on a distant hillside and has a small obscure opening that leads through breakdown and crawls to a fairly large room. Endangered bats hibernate in this cave during the winter.

Cave 4. This is a large, well-known system with several horizontal entrances. Several entrances have obvious trails leading to them, and one entryway is small, torturous, and rarely used. There are many delicate and unusual speleothems in this cave, and damage has been steadily increasing for many years.

Cave 5. This is a small crawl cave with records of endangered invertebrates. Because it is near the fourth cave, it is often mistaken as an entrance to Cave 4 and receives unnecessary traffic.

What to do with these? Gating all the entrances would be time-consuming and expensive, would likely aggravate those people currently visiting them, and might cause overflow problems in neighboring caves. We already have some resource information on the five caves, so we can prioritize their significance. We also have information on the level of disturbance and threats to these caves, so we can determine the level of urgency for protecting each one. Now we have to determine exactly how we will protect each cave.

Cave 5. This cave appears to have an urgent need for protection because of its endangered fauna and the unintentional traffic. This reality would need to be weighed against the population size of the invertebrates, and the numbers of those species in other caves. Since this is a relatively small cave with a well-known entrance and no bats, a gate could be appropriate.

Cave 4. This cave needs a more thorough resource inventory. Its proximity to Cave 5 indicates a likely connection. Although it is viewed primarily as a recreational cave, the possibility of finding endangered invertebrates there is high. There are too many unknowns at this time to make a good decision. Perhaps the entrances can be gated. A small internal gate might allow access to only part of the cave. Signs and a permit system might reduce the number of visitors to a sustainable level. We need to know more.

Cave 3. This cave might be categorized toward the opposite end of the spectrum. Rarely visited and obscure, it faces no immediate threats. The only critical time of year is winter when the bats are hibernating. Winter visits could be curtailed simply by doing public education through the local grottos. Because the entrance is obscure, a gate or signs might draw unnecessary, detrimental attention to the cave.

Cave 2. This cave presents a different challenge. It is easily accessible and well known, so rerouting the trail would make little difference. A combination of educational signage and a bat-friendly fence could prove beneficial, and would not detract from the aesthetics of the pit. If the fence is repeatedly damaged, and if the cave is suitable for bats, a cupola-style bat gate could be installed over the entrance (Figure 4). Since temperatures are suitable for hibernating bats, we might conclude that bats are no longer in that cave due to disturbance, so fencing or gating should allow for their eventual re-colonization. A thorough in-cave survey for old guano or roost stains would help with this decision (Figure 1). As with any site where there is a strong history of visitation, the reputation for open access must be broken, even if it means patrolling the site and arresting violators.

Cave 1. This is a relatively pristine wild cave. However, traffic may increase if other nearby caves are gated. The paleontological resources are very vulnerable. A permit system, combined with increased caver education, might work here if the location is protected by the terrain and the remoteness of the site. If natural site protection is not adequate, the cave might need a gate. Since the threats are not immediate, protective efforts for this cave are not as urgent.

Figure 1. Bat roost stains on cave walls provide evidence of bat population even when bats are not present. In the image, a 3-inch (80-millimeter) HOBO® Pro data logger is used for scale. (See page 5 of color section.) © Merlin D. Tuttle, BCI

Summary of Assessment

Careful assessment of a cave's resources and threats is necessary before installing any protective device on a cave—particularly more permanent structures like gates. Public input from concerned user groups should be solicited, especially if those groups oppose closure and may damage or destroy protection efforts.

It is essential that gates and other protective structures be continually monitored, not only for structural damage, but also for their impact on the cave ecosystem. Gates, culverts, or fences that cause a negative effect should be modified or removed. Cave gating is not a quick Band-Aid approach to cave management. Gating is merely one tool a cave manager can use. Maintenance schedules should be established because gates need attention and review after installation.

Certain types of protective efforts may have an opposite effect than that intended. For instance, several species of North American cave-dwelling bats do not tolerate any type of gate at all. Some species only tolerate gates during one part of their life cycle and not at other times of the year.

Always consult experts early in the planning stages of any gating project and be sure to get the most current gate design recommendations through Bat Conservation International, the National Speleological Society, and the American Cave Conservation Association.

Location and Design

Placement of a fence or gate is as critical as the actual design of the structure. Poorly located gates may increase flood damage to the cave, accumulate debris and restrict airflow, and restrict movement of bats or other wildlife. Poorly placed gates may also be more susceptible to natural damage or vandalism, and may increase predation at the cave. Much depends on the size, shape, and orientation of the opening, but in general, bat gates should not be situated in natural passage constrictions, and fences should not interfere with the flight path at the entrance.

It must be stressed that cave gating is not a cookie-cutter management technique. Simply because a cave has bats does not mean that one can dust off a gate design and build it in the cave mouth. But even if a cave does not have bats, the cave may need a bat-friendly gate. The approach to protecting each cave should be based on the configuration of the cave itself, the species using it, the season bats occupy it, the proximity to civilization, and so on.

There is not a one-size-fits-all solution to cave protection. Poor gate design or placement can render the cave unsuitable for bats. Consult the experts listed in the resources section at the end of this chapter.

Gate Location

As mentioned above, cave gates should not interfere with the natural flow of air, water, nutrients, or wildlife to and from the cave. Gates should never be in a constricted part of the passage. The bottom of an entrance slope should also be avoided since it will catch debris that will pile up against the gate. In cave entrances that have inflowing streams this can be a very serious problem. The gate on the North Entrance of Bat Cave (Carter County, Kentucky) failed in the spring of 1996 as flood debris lodged against the gate, backing up water until the increased pressure finally collapsed the gate. The resultant flood pulse destroyed many low-roosting Indiana bats, a federally listed endangered species. (See Indiana bats, page X57.)

Predation Dangers

Predation can also increase dramatically because of badly located gates. Most bat predators rely on vision when hunting, so gates in the daylight or twilight zone may enhance the predators' foraging success. When bats slow down to negotiate the gate bars, or back up behind the gate waiting their turn to pass through, they are easily captured by enterprising raccoons, ringtails, and feral cats.

Gates installed beyond the twilight zone eliminate the predators' advantage. The old gate to the lower entrance of Sinnett–Thorn Mountain Cave (Pendleton County, West Virginia) had piles of Virginia big-eared bat wings around it from the nightly predations of local house cats. The gate was removed in October 1998 and a new gate was built in a tall area approximately 75 feet (23 meters) further in, despite having to maneuver the steel and equipment through a crawlway. The new gate, in the dark zone, has eliminated the predator problems.

Figure 2. This is a poorly designed gate, constructed of 1-inch (25-millimeter) round bars. It is not very secure—the bars maybe easily bent and the welds are small. The small rectangular openings in the narrow vertical entrance make the gate difficult for bats to fly through. On this type of platform gate constructed in a vertical entrance, branches and leaves can collect to restrict airflow and light. © 1989 Jim Kennedy, BCI

Cupola or Cage Gates for Vertical Entrances

Vertical or near-vertical entrances pose their own set of problems. A horizontal gate at such an entrance accumulates debris, makes a perfect feeding platform for predators, and is very difficult for most bats to negotiate.

To solve these problems, a raised gate called a cupola gate or cage gate can be used. Generally, the longer and narrower the opening, the larger and taller the cupola gate should be in order to give the bats adequate space to gain altitude and avoid predators. Cupola gates are not practical for very large openings, and fencing may be the only option. For vertical entrances with very short drops, a standard gate may be installed deeper within the cave where the passage begins to be more horizontal (when the vertical entrance itself is not a liability concern).

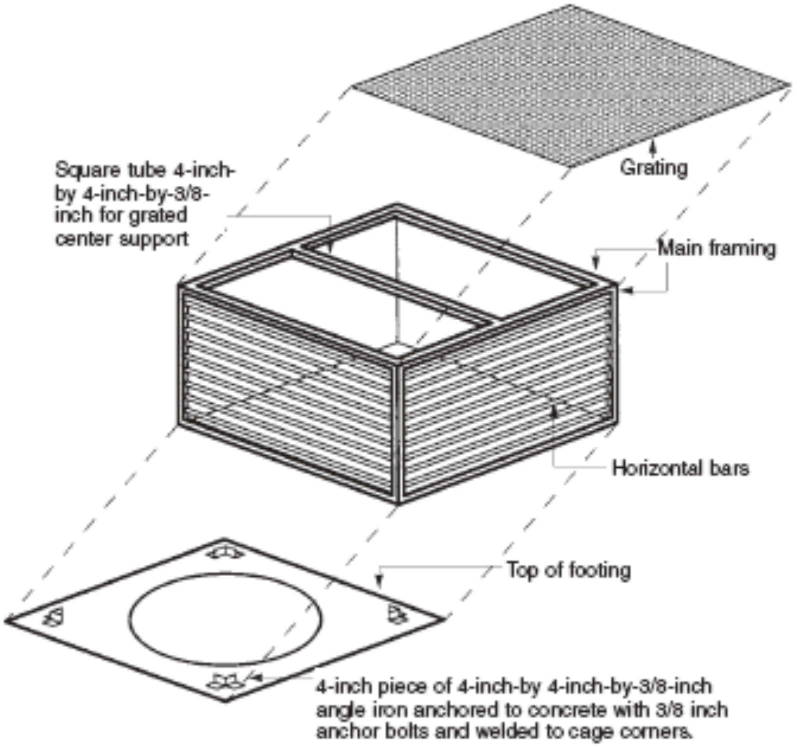
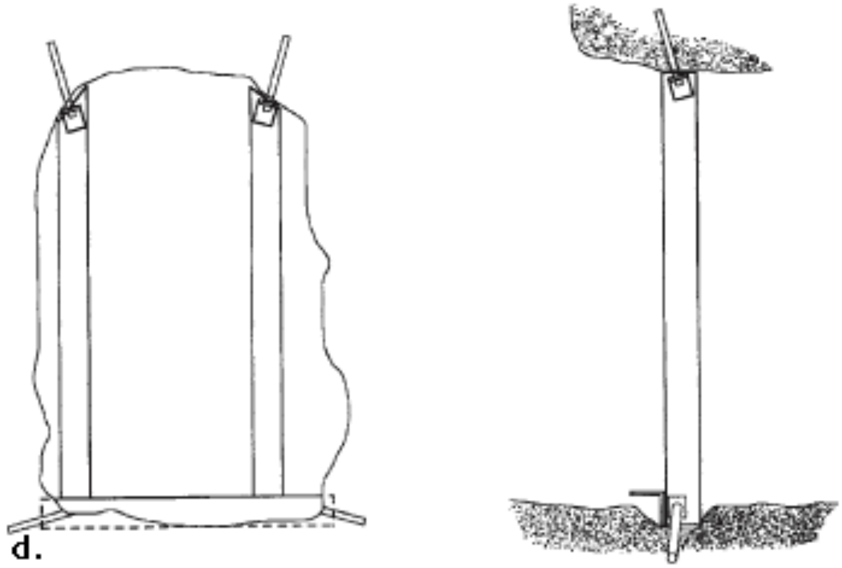


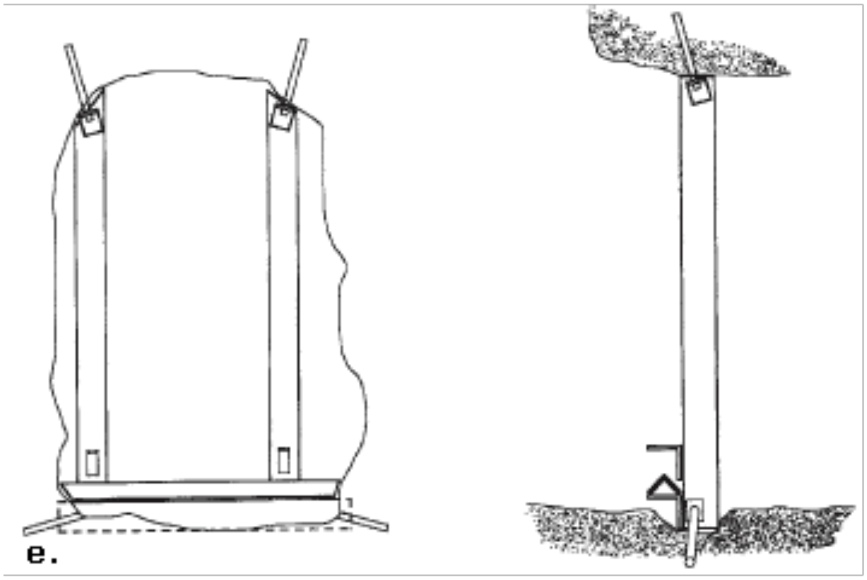
Figure 4. A cupola or cage gate is often used in vertical or near-vertical entrances.

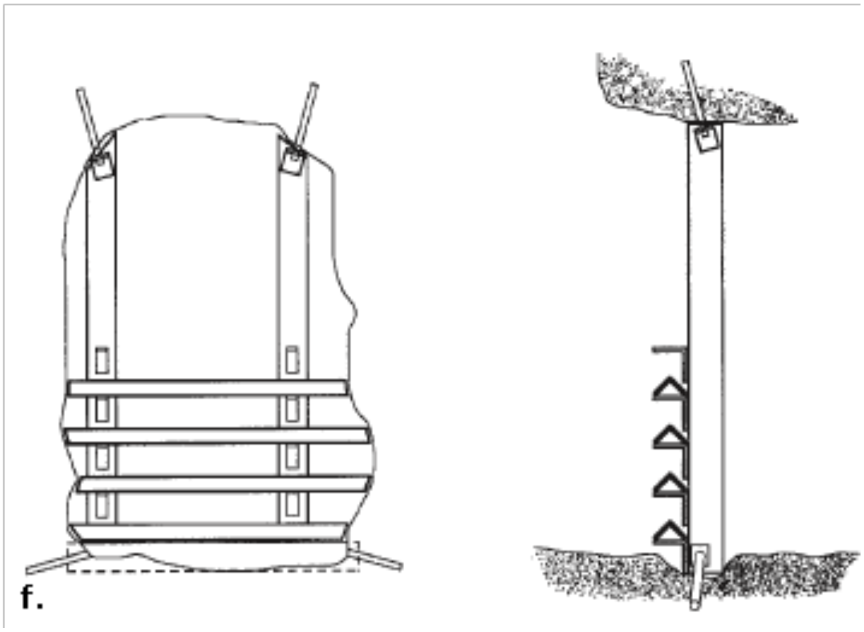
Chute or "Window" Gates

A recent innovation, since the late 1990s, is the chute gate, sometimes called a window gate. An otherwise standard horizontal gate is modified with a rectangular opening boxed in with additional angle iron and expanded metal mesh. This design allows sufficient opening for emerging bats and makes it very difficult for trespassers to breach the opening. The chute is usually angled to make it more difficult for humans to enter. This particular gate design is especially useful in caves with large bat populations, such as gray bat maternity colonies, which have entrances that are too small for traditional half gates or flyover gates. Because of the weight extending out from the main (standard) part of the gate and the resulting mechanical stresses, extra attention is needed in the design and construction to prevent future cracked welds and gate failure. Chute gates have been used successfully on numerous Alabama, Kentucky, Missouri, and Tennessee caves, and are well accepted by bats.

Figure 5. Chute gate at McDowell Cave, Missouri © 2001 Sheryl Ducummon







3d. Installation and securing of uprights.

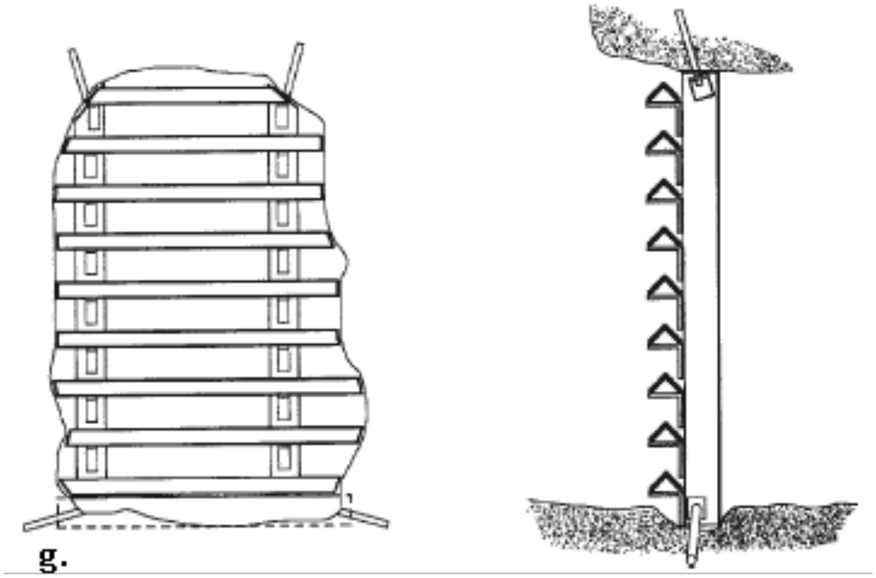
3e. Installation of bottom bar and hangers for second bar.

3f. Continuation of hangers and horizontal bats (for clarity, removable bar is not shown).

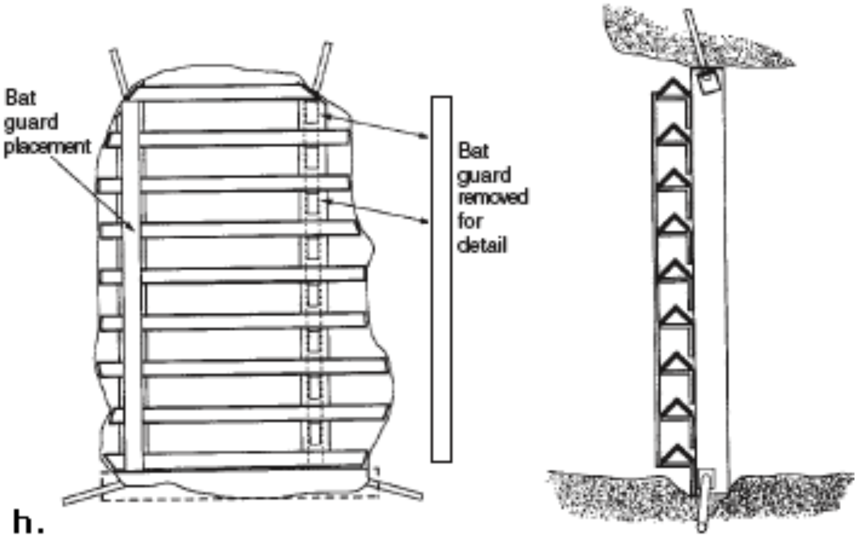
3g. Completion of horizontals.

3h. Placement of bat guards.

3i. Completed gate



g.



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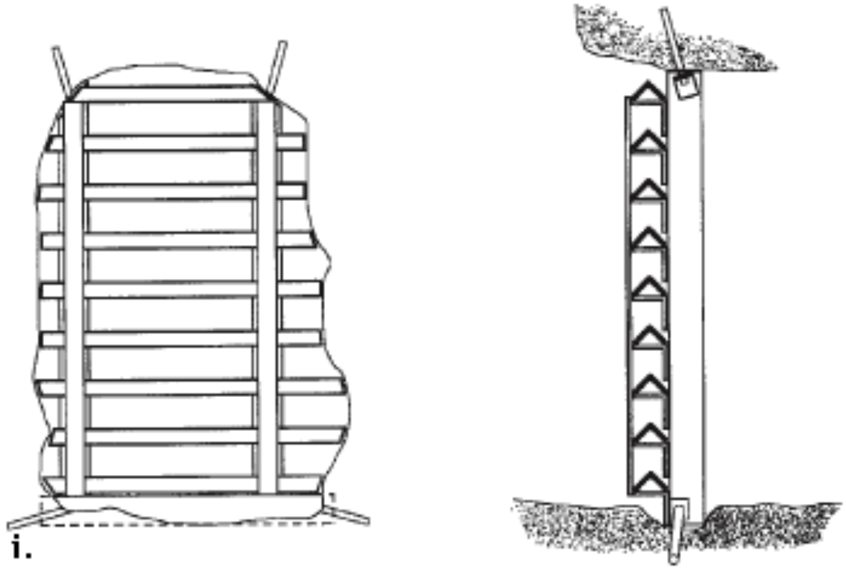


i.

Nonstandard Gates

Caves that are entirely unsuitable for bats (as opposed to sites where bats are not currently found) may be candidates for gates that are not bat-friendly. However, the bat-friendly design is the preferred solution for most caves, except those that have no natural entrance and require some sort of environmental seal. Sometimes the availability of materials and volunteer labor, or the lack of adequate funds will dictate construction of a nonstandard (not bat-friendly) gate. Nonstandard gates are almost always poor substitutions.

Educational Signage

All finished gates require signs stating the purpose of the gate and contact numbers for more information. The penalty for entering the cave or vandalizing the gate can be written in small print, but this should not be the focus of the sign because it is often taken as a dare by would-be vandals. Educational material is less antagonistic.

Signs themselves sometimes become collectors' items, or are needlessly damaged by thwarted cave visitors. Permanent signs mounted inside the gate where they can be read, but are out of harms way, will last longer. Paper and wooden signs are highly susceptible to weather, decomposition, and the gnawing teeth of rodents. Metal or plastic signs are preferred. (See protective signs in caves, page X187.)

Construction Logistics

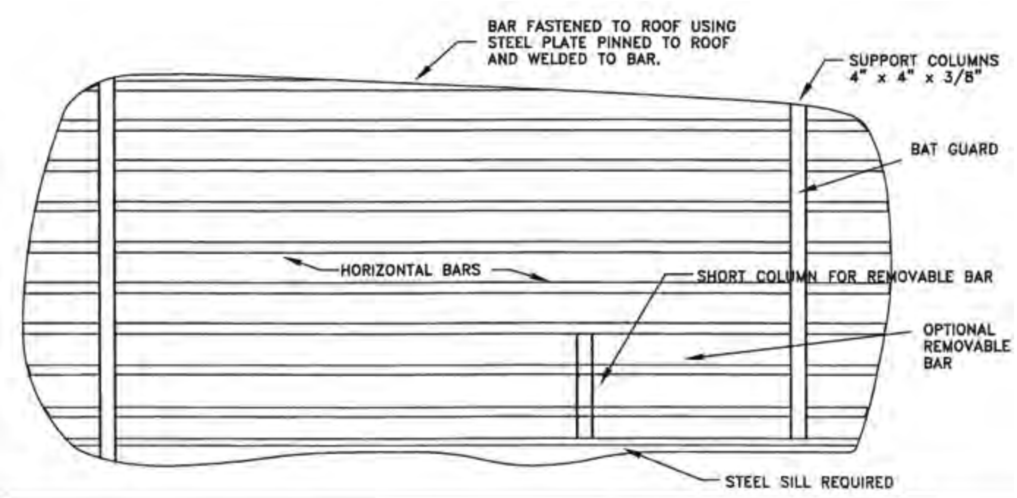
This cave-gating chapter is no substitute for a more complete cave gating manual or training workshop. While it covers the rudiments of cave gating to assist resource managers in making better-informed decisions, it is too brief to help with actual design and installation. Nevertheless, here we provide information for better planning of gating projects. Further assistance is readily available on request. (See cave gating resources, page X168.)

Timing

Construction should take place during seasons when human activity is least disturbing to the cave resources. For bat caves, this means the work must be done when the bats are absent. Some caves may be used as both summer and winter roosts, which leaves only short periods

Figure 9. Half or "flyover" gate. Note the removable bar at bottom right. Expanded metal mesh covers the overhanging top portion, making it extremely difficult to climb over. Coating the overhang with grease also helps repel trespassers. © 1997 Keith Christenson, BCI

Figure 6 (top). Typical bat gate (not to scale).



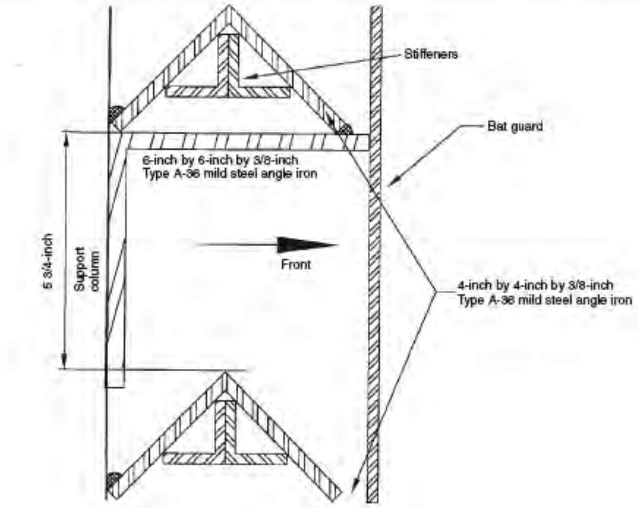
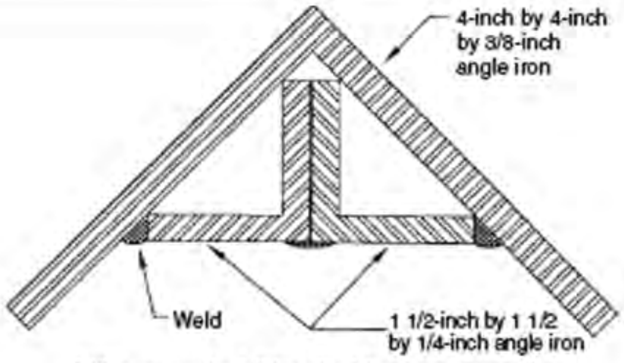


Figure 7. (middle) Horizontal bar spacing, typical detail (not to scale).



Stiffeners run the full length of the the horizontal bar, except for being 2-inch shorter on each end

Figure 8. (bottom) Stiffener detail horizontal bars (not to scale).

in the spring and fall for construction. Seasonal temperature variations may also cause reversals in the cave's airflow. If the cave is drawing in air, it may be necessary to install temporary plastic curtains inside the construction site to keep smoke and noxious welding fumes out of the cave. (See toxic fumes, page X49.)

Materials

Ordering adequate materials depends on accurate estimates of the area to be covered. Gate construction projects require accurate measurements and scale drawings of the finished gate. Materials should be ordered well in advance of the actual gating and may need to be stored off-site in a secured area before being transported to the cave. Always order a little extra for emergencies.

Supplies

To help ensure completion of the project, carefully calculate welding gases, welding rods, grinding wheels, and other expendables. It is much easier to return unused supplies, or save them for the next project, than to run out before the new gate is finished.

Tools

The remoteness of the site will dictate the type of tools needed, but almost every gating project requires an electric generator or two to run the welders, grinders, and lights. Most projects need the following equipment.

- Electric generator(s)
- Extension cords
- Oxy-acetylene torches (with spare tips and regulators)
- Chipping hammers and wire brushes
- Tape measures, levels, and squares
- Ladders (for tall gates)
- C-clamps
- Portable work lights
- Hammer drills and hand-held grinders
- Digging and rock breaking tools to prepare the site

Also, provide the following safety equipment at cave gating sites.

- Rakes and water for fire control
- Buckets
- Welding vest, hood, and gloves
- Cutting goggles, and so on

Always plan for things to break, so have backups on site or readily available. Other equipment such as come-alongs, pulleys, chainsaws, all terrain vehicles, or in extreme cases, a helicopter may be needed to move materials to the site.

Short, 8-foot (2.5-meter) lengths of 1-inch (25-millimeter) tubular nylon webbing tied in loops make excellent carry handles for moving lengths of steel. Tools should be color-coded or labeled so they get back to their proper owners. Be careful to keep track of tools and equipment. Tools are especially easy to lose in or around the cave area.

Transportation of Materials

Many ingenious methods have been developed for moving materials to cave sites. Rarely can the delivery truck drive to the cave mouth. For long hauls, caver power may suffice, given a large enough workforce. Animal power (horses, mules, and burros) is sometimes used. All-terrain vehicles are sometimes used in non-wilderness areas with adequate trails. Boats or rafts may be necessary along rivers or lakes.

Materials may even need to be airlifted in extremely rugged terrain. Airlifts are sometimes accomplished with the cooperation of a local military reserve unit (the project may be used as a training mission). But during the course of most projects, all materials must be carried by hand. Keep in mind that a 20-foot (6-meter) length of 4-inch (10-centimeter) angle iron, 3/8-inch (9.5-millimeter) thick, weighs about 196 pounds (89 kilograms). Avoid pinched fingers and crushed toes by keeping safety in mind.

Personnel

The gate designer should oversee construction—this person is most important in any gating project. Currently, there are very few people in North America with the experience needed for all but the simplest jobs. (See contact list, page X170.)

Next comes the welder, who may be an agency employee, a volunteer, or a person hired specifically for the project. Depending on the size of the gate and the amount of work necessary, it is usually good to have several welders (people and machines) available to make the work go faster and to offer rest breaks.

Gating projects also need one or more welding assistants, anticipating the next piece to be cut, handing tools, taking measurements, and generally facilitating the workflow so that no one is standing around idle.

Finally, a project needs sufficient labor to prepare the site, carry items from the cutting area to the gate location, carry the steel from the drop point to the work area, and clean up afterwards. These workers can be hired with the welder, be provided by the responsible agency or organization, or be volunteers such as local cavers.

In several gating projects, prison labor was arranged for much of the heavy work. Using volunteers is beneficial because it involves the cave's user groups, educates them about purposes for the gate, and lessens potential for opposition and future vandalism to the gate.

Don't forget to take care of the safety and wellbeing of your workers. Provide plenty of food and drinks, and give adequate recognition after the project is finished.

Safety

Every cave gating work plan needs to address the protection of the cave and surrounding site as well as the safety of the workers involved. Prevent ground fires from starting at the work site. It may be necessary to temporarily remove dead leaves or grasses in the areas where cutting, welding, and grinding occur. As a precaution, have plenty of water and fire fighting tools (rakes and shovels) on hand. An Indian Pump or chemical fire extinguisher is also handy.

All workers should wear leather work boots, preferably steel-toed, as well as leather gloves, hardhats (caving helmets are fine), long pants, long-sleeved shirts or coveralls, protective eyewear, as well as hearing protection, especially when working around the welders, torches, and grinders. Caution all workers not to look directly at the torch flame or welding arc. Brief the crew on hot metal, heavy objects, potential dangers from the tanks of welding gases, and any other hazards specific to the site (loose rock, steep slopes, poison ivy, and the like). Keep a well-stocked first-aid kit on site. Also, be aware of the dangers of exhaustion, dehydration, hypothermia, and heat-related illnesses. Be sure the team takes breaks, eats during the day, and keeps hydrated.

Site Restoration

It may be difficult, but try to minimize disturbance of rocks, vegetation, and ground cover during steel hauling and other work. Natural contours should be restored after the gating is completed, unless the work on the cave entrance includes retuning it to a former historic configuration in an attempt to restore internal conditions. Sites may need re-vegetation, and trails may need to be blocked to divert casual hikers from the cave. All trash should be picked up and removed, including all scrap metal and as much welding waste as possible, including welding rod stubs. Cave gates, after painting (if necessary), should blend in rather than attract attention.

If an entrance was previously modified or enlarged, gating processes may provide a perfect time to restore the entrance to a former ecological state. Keep in mind that, relatively speaking, caves are short-lived geologic features that constantly change.

Entrances open and close naturally during the life of some caves, sometimes repeatedly. Choosing the historic baseline configuration is sometimes a judgment call based on the special resources for which the site is actively managed. For declining populations of endangered Indiana bats, for instance, we would aim for restoration to a time frame of pre-European settlement, but post-Pleistocene.

Locks and Removable Locking Bars

Since the main purpose of a cave gate is to secure the site from intrusion, the choice of locking mechanism is critical. Many modern gates now dispense with hinged doors entirely and use removable locking bars. The removable bars can be secured with standard padlocks or with specially keyed bolts, similar to automotive locking lug nuts. Removable bars have several advantages.

- Removable bars are easy to construct.
- They disguise the obvious entry point.
- They eliminate the use of moving parts.
- They reduce maintenance tasks.

All padlock mechanisms must be designed to protect the lock from damage. Locks should be inspected regularly and replaced at the first sign of trouble or failure. No gate is completely vandal proof, but the idea of building a strong gate secured by a weak lock is ridiculous. If the cave is worth gating, make it as secure as possible.

Monitoring and Maintenance

So, you have finished building the gate and restored the entrance zone to a natural appearance. Job well done, right? More like job half done. There are no guarantees that the gate will accomplish your objectives despite your most careful planning.

Instead of helping maintain or restore the cave's ecosystem, a gate may cause further problems. Only long-term monitoring and assessment will tell. For bat caves this entails nightly and seasonal observations to monitor and ensure the bats' behavior is unchanged and uninterrupted. For other critters, monitoring might involve population estimates via specific sampling techniques. Monitoring requirements also point out the need to establish good baseline data before gate installation so comparisons can be made with post-gating data. At the minimum, temperature and airflow should be recorded, but observations of moisture and humidity, animal distribution, and nutrient flow are also useful.

If the gate is not doing its job, then it should be modified or removed. Many bat caves gated in the 1970s and early 1980s were thought to be protected and were largely ignored thereafter. Continuing bat population declines puzzled researchers, who believed the caves were protected and looked for other reasons to explain decreases.

Recent advances in gating knowledge show that the gates themselves were causing negative impacts on the caves because they were poorly designed or placed, or because the entrance was modified during the gating process. In an extreme case, the temperature of the cave was raised by as much as 5°F (2.8°C). Temperatures were restored and the population began to increase when the original gate was replaced with a better-positioned and better-designed closure. Monitoring programs are now initiated early in gating projects to identify and correct bad situations before human modification results in tragedy.

Gates must also be monitored for the inevitable breaching attempts. Certain segments of our society delight in trying to break into places where access is denied. Proper signage will go a long way toward educating most of the public about the reasons the cave was gated. Signs should point visitors to more information and contacts for access. Gaining the trust and cooperation of user groups and local cavers during the planning and construction processes will also alleviate potential animosity and break-in attempts.

Repairing Damage

Any damage to the gate should be repaired immediately—otherwise, you will be repairing more damage and dealing with illegal entries. When design flaws and weaknesses are discovered, you have the obvious opportunity to modify the gate and make it stronger. As noted gate expert Roy Powers says, "We have to keep one step ahead of the vandals." Be careful not to negatively impact the cave environment with security modifications. Recurring vandalism may require increased security measures, such as surveillance. Sometimes trustworthy local cavers can be named as volunteer cave stewards who can provide much-needed manpower for patrolling the site. A well-publicized arrest of trespassers vandalizing a posted cave gate makes a wonderful deterrent to other would-be lawbreakers. Many other clever techniques have been utilized to deter vandalism, including fake monitors and signs announcing (usually nonexistent) alarm systems. Real alarms can also be used, triggering a dispatch to the agency office or local law-enforcement authorities.

Cave Gating Resources

If, after reading this, you feel overwhelmed and want to stay as far away from cave gating issues as possible, RELAX! There are several sources of excellent assistance available to help you. Modern, bat-friendly cave gates (also called zero-airflow-reduction bat gates) are the result of many years of experimentation and development, supplemented by field observation, strength testing, and wind tunnel testing.

The design presented in this chapter is the standard accepted by most federal and state agencies that manage caves, and by organizations such as The Nature Conservancy and Bat Conservation International. The leading force behind bat-friendly gate development has been the American Cave Conservation Association, particularly Roy Powers. Detailed drawings may be requested from them. Across the country, there are examples of many adaptations showing varying degrees of success. Successful gate designs provide entrance security and avoid the blockage of airflow, water, nutrients, and animals.

Current Books on Cave Gate Design

Bat-friendly gate designs are also widely used for closing abandoned mines. Mines and caves are similar, but not equivalent management concerns. Mines usually lack the complex ecosystems and recreational values that caves offer, and mines often pose bigger liability problems. Mines are extremely short-lived in comparison to caves. Stabilizing or closing mine entrances to achieve desired conditions does not have the ramifications that such actions cause in undisturbed caves. Bat Conservation International (BCI) has produced a free booklet, Bats and Mines, that discusses in detail the suitability of mines as habitat, addresses the dangers associated with them, and includes full plans for both standard and cupola gates. The booklet also offers excellent template forms for conducting external and internal summer and winter bat site assessments. (In the additional reading list for this chapter, see Tuttle and Taylor 1998.)

The authors and editors know of no modern, comprehensive, published gate plans for caves that have no bats or other vertebrates. Trap door gates and air lock gates are common in several parts of the United States but are usually built by local experts.

A detailed book on cave gating has been developed by the US Fish and Wildlife Service, the USDOI Office of Surface Mining, Bat Conservation International, the American Cave Conservation Association, the National Speleological Society, and numerous other sponsors. It includes the entire proceedings from the groundbreaking conference on cave and mine protection options held in Austin, Texas, in March 2002. It is available through the National Speleological Society and covers the entire gating process in detail. (In the additional reading list for this chapter, see Vories and others 2004.)

Cave Gating Seminars

To get hands-on training, participate in one of the Cave Gating Seminars cosponsored by the American Cave Conservation Association, Bat Conservation International, the US Fish and Wildlife Service, and the USDA Forest Service. These workshops combine evening slide lectures and discussions with hands-on gate building experience. The small group residential setting teaches design and placement philosophy, covers design options and case studies, and offers an opportunity to interact with some of the most knowledgeable cave gaters in the country. Contact the American Cave Conservation Association or Bat Conservation International for dates and locations of upcoming workshops.

Cave Gate Contractors

There are also several private individuals and firms that will contract gate-building projects. The best of these have many years experience or are graduates of the Cave Gating Seminar. Names of those known to be knowledgeable and reliable can also be obtained from Bat Conservation International or the American Cave Conservation Association. (See the contact list at the end of this chapter, page 170.)

Summary

Cave gating is only one form of cave protection. It should not be undertaken without sufficient study and planning. There are many types of gates and the manager should choose the type that best protects the resources within the cave and best fits the cave configuration.

Planning, construction, and follow-up activities are time and resource intensive. Gating projects may require a lot of manpower and other resources, including volunteers as well as specialized equipment. There are several sources of expertise and possible funding assistance for gating projects. Gating experts should always be contacted before any work begins.

Additional Reading

Anon. 1985. Volunteers protect Tennessee bats. American Caves 1(2):8-9.

Anon. 1993. James Cave receives new gates for bats. Bats 11(3):4.

Anon. 1993. BCI helps protect Pennsylvania mine for bats. Bats 11(4):16-17.

Anon. 1995. New ACCA gates protect Kentucky and Tennessee caves.

American Caves 8(1):10-11.

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Does Competition for Roosts Influence Bat Distribution in a Managed Forest?

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ABSTRACT

Previous studies disagree regarding the mechanism that determines distributions of neartic bat species. Many papers suggest that competition for foraging areas is important and is dictated by morphological characters or roost diversity. Here, I present evidence that suggests that local bat distribution, diversity, and population size in managed forests are related to interspecific competition for limited roost sites, and to intraspecific division by sex that depends on local population numbers.

INTRODUCTION

Findley (1993) summarized relationships between bat morphology, diet, and ecological niches to define a bat community in attribute space. Using work of Findley and Wilson (1982), Findley and Black (1983), and Aldridge and Rautenbach (1987), Findley states ‘‘ . . . it is possible to have a reasonable amount of confidence in the ability of morphology to provide an insight into the feeding and foraging of insectivorous bats. Bat reproduction, occurrence, and abundance are related to food abundance, and in that sense food is clearly limiting to animals.’’ Humphrey (1975), however, found a strong correlation between the diversity of physical structure and the diversity and richness of colonial bats. Perkins (1993) reported that the distribution of bat species in a neartic managed forest is not random, and speculated that forest bat distribution is a result of roost availability, insect concentrations, or competition between species resulting in displacement. Perkins and Peterson (1995) concluded that the distribution of reproductive female bats in a managed forest was affected by availability of roosts. In areas where harvest of large, older trees was highest, statistical analysis indicated a significant over-representation of the largest bat species. In areas where timber harvest was non-existent or minimal, the only competition exhibited at foraging sites was between the three species that forage exclusively or primarily on moths (*Corynorhinus townsendii*, *Myotis thysanodes*, *Myotis volans*). In contrast, Bell (1980) reported no foraging competition between paired bat species at concentrated insect patches in similar forested and Great Basin habitat.

Here, I examine data regarding male and female distribution, prey, and roost selection in a managed forest. I hypothesized that (1) the males forage separately from females of the same species; and (2) the determinant of the presence of any paired species at foraging sites is not solely foraging competition, but also involves roost availability.

STUDY SITE

My study area is in northeastern Oregon on the Wallowa-Whitman National Forest (44° 44’ to 46° 00’N, 116° 30’ to 117° 45’W; Figure 1). I sampled 140 sites distributed arbitrarily throughout four ranger districts: Hells Canyon National Recreation Area, Wallowa Valley Ranger District, Eagle Cap Ranger District, and Pine Creek Ranger District. Over 486,000 ha (1.2 million acres) of public and private forest and canyons comprise the study area. Ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), Douglas-fir (*Pseudotsuga menziesii*), and white fir (*Abies grandis*) are the dominant tree species. I divided the study area into three habitat blocks, based on vegetation and management practices: Forest, Forest/Canyon Edge, and Canyon. Roost habitat surrounding Forest sample sites is limited to trees, snags, stumps, and a few buildings. This habitat comprises the largest area, had the most sample sites, and has had the greatest timber harvest in past decades. Roost habitat in the Forest/Canyon area included trees, snags, stumps, cliffs, talus, mines, and buildings. This was the second-largest sample area, had fewer sample sites, and the least impact in terms of timber harvest. Canyon habitat is not considered in this analysis. I have recorded by capture or audible call signatures 13 species from the study area. Four of these species were not considered due to their low capture rates (*Lasiurus cinereus*, *Euderma maculatum*, *Corynorhinus townsendii*, and *Myotis yumanensis*).

MATERIALS AND METHODS

I sampled Forest and Forest/Canyon sites by setting mist nets over open water. Mist netting occurred from 1 June to 1 September 1984–1994. Netting periods lasted at least two hours after sunset. Bats were identified to species, sexed, aged, weighed, and morphological measurements were taken.

To test for division of foraging sites by sex, I used the chi-square test (Williams 1993). *Lasionycteris noctivagans* data are from Perkins and Cross (1992). To test for independence of distribution at foraging sites I paired each possible group of species and applied Fisher's exact test. Netability varies among species. To minimize this bias, I assigned a value for each species at each site as either present (1) or absent (0).

RESULTS

Chi-square analysis of exclusivity in male and reproductive female foraging patterns resulted in statistically significant separation between the sexes for all eight species for both portions of the study area, regardless of timber impacts (Table 1). However, Fisher's exact test indicates that when reproductive status is not considered, paired *M. californicus, M. ciliolabrum*, and *M. thysanodes* in both habitats had no foraging separation between the sexes. *M. californicus, M. ciliolabrum*, and *M. thysanodes* were the species that I captured the least of the eight considered. In the Forest/ Canyon habitat, *M. evotis* and *M. lucifugus* also had no significant segregation by sex.

If we divide the bats into morphological sizes based on forearm length, skull size, and mass, we get a large bat group (*E. fuscus, L. noctivagans*), a middle-sized group (*M. evotis, M. volans, M. thysanodes*), and a small group (*M. lucifugus, M. ciliolabrum*, and *M. californicus*). The occurrence of large and small species together at sites was less than expected by chance in 67% (32 of 48) of the cases. Middle-sized bats and small bats were less frequently associated than expected in 73% (35 of 48) of cases.

In terms of foraging ''style,'' gleaners (*M. evotis, M. thysanodes*) show competitive exclusion for both sexes. Forest and clearing aerial-insectivores (*E. fuscus, L. noctivagans, M. californicus, M. ciliolabrum*, and *M. volans*) produced mixed results indicating lower competition. In pairs of these species, 58% of cases indicated significant avoidance (29 of 50). *M. lucifugus* is the only water-surface forager, but significantly avoided other species in 68% of cases (19 of 28). There was a slight difference in frequency of significant avoidance between the two habitats (when I excluded same species/different sex pairs). In the Forest habitat, competition was indicated in 70% of cases (74 of 105), while in the Forest/Canyon habitat competition occurred in 60% of cases (63 of 105).

DISCUSSION

My results indicate that the long-held assumption that sexes forage in separate areas is valid, particularly for the larger species, and those which form larger colonies outside of human structures. The lack of foraging habitat segregation by sex in the small and less numerous bat species (*M. californicus, M. ciliolabrum, M. lucifugus*, and *M. thysanodes*) suggests that prey biomass is not a critical factor in determining distribution or foraging sites when numbers of resident individuals are low. Analysis of species pairs by sex seems to validate the concept of competition for foraging areas as a factor influencing distribution (Findley 1993). If one takes into account prey species and foraging techniques, it is difficult to imagine how *L. noctivagans* or *E. fuscus*, who forage at tree-top level at dusk, compete with *M. lucifugus, M. californicus*, or *M. ciliolabrum*, who forage low over meadows, water, in clearings, or under canopies in riparian zones.

Whitaker et al. (1977) demonstrated that diets of *M. californicus* and *M. lucifugus* only overlap with the middle-sized and large bat species in consumption of Diptera and Lepidoptera. *M. lucifugus* and *M. californicus* consume (by volume) mostly Diptera, while for large and middle-sized bats, Diptera make up less than 10% of consumed volume. Lepidoptera seem to be the prey common to all bat species represented on the study area. Prey analysis indicates that the small bat species eat less Lepidoptera by volume by at least a factor of two when compared with the larger bat species. Dietary competition is most likely to occur in consumption of lepidopterans: *L. noctivagans* (32% of prey volume), *E. fuscus* (21% of prey volume), *M. evotis* (46% of prey volume), *M. thysanodes* (46% of prey volume), and *M. volans* (78% of prey volume) (Whitaker et al. 1977; Whitaker et al. 1981). However, if prey competition is important, why is there inconsistent evidence of foraging competition between *E. fuscus* and *M. volans*, and between *L. noctivagans* and *M. volans*?

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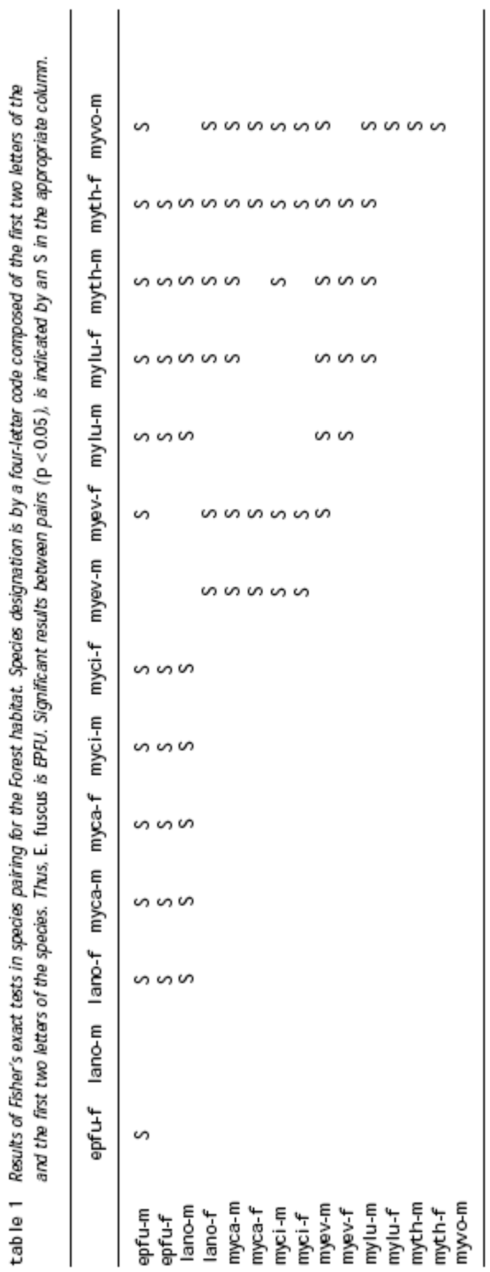

table 1 *Results of Fisher's exact tests in species pairing for the Forest habitat. Species designation is by a four-letter code composed of the first two letters of the and the first two letters of the species. Thus,* E. fuscus *is EPFU. Significant results between pairs* (p < 0.05)*, is indicated by an* S *in the appropriate column.*

	epfu-f	lano-m	lano-f	myca-m	myca-f	myci-m	myci-f	myev-m	myev-f	mylu-m	mylu-f	myth-m	myth-f	myvo-m
epfu-m	S		S	S	S	S	S		S	S	S	S	S	S
epfu-f			S	S	S	S	S			S	S	S	S	
lano-m			S	S	S	S	S			S	S	S	S	
lano-f								S	S		S	S	S	S
myca-m								S	S		S	S	S	S
myca-f								S	S				S	S
myci-m								S	S			S	S	S
myci-f								S	S				S	S
myev-m									S	S	S	S	S	S
myev-f										S	S	S	S	
mylu-m											S	S	S	S
mylu-f														S
myth-m														S
myth-f														S
myvo-m														

close inspection of roosting behaviour provides the most likely answer. *E. fuscus*, *L. noctivagans*, and *M. volans* females all prefer abandoned woodpecker holes as maternity roosts, while males of these three species generally use crevices (Barclay 1985; Vonhof 1994; Kalcounis 1994; P. Ormsbee, pers. comm.). If roost availability is the determining factor in the significant differences in paired bat distributions, then female *L. noctivagans*, *E. fuscus*, and *M. volans* should rarely occur together. Indeed, my data suggest that this is the case. Other bat species of both sexes seem to rely mostly on crevices in cliffs and trees, or exfoliating bark, in the absence of human structures (Perkins 1993; Kalcounis 1994; P. Ormsbee, pers. comm.). If we assume that roosts adequate for *M. californicus* are also adequate for other crevice-roosting bats, I would expect that ‘‘might makes right,’’ and the larger and more aggressive bat species out-compete the smaller and the less aggressive species.

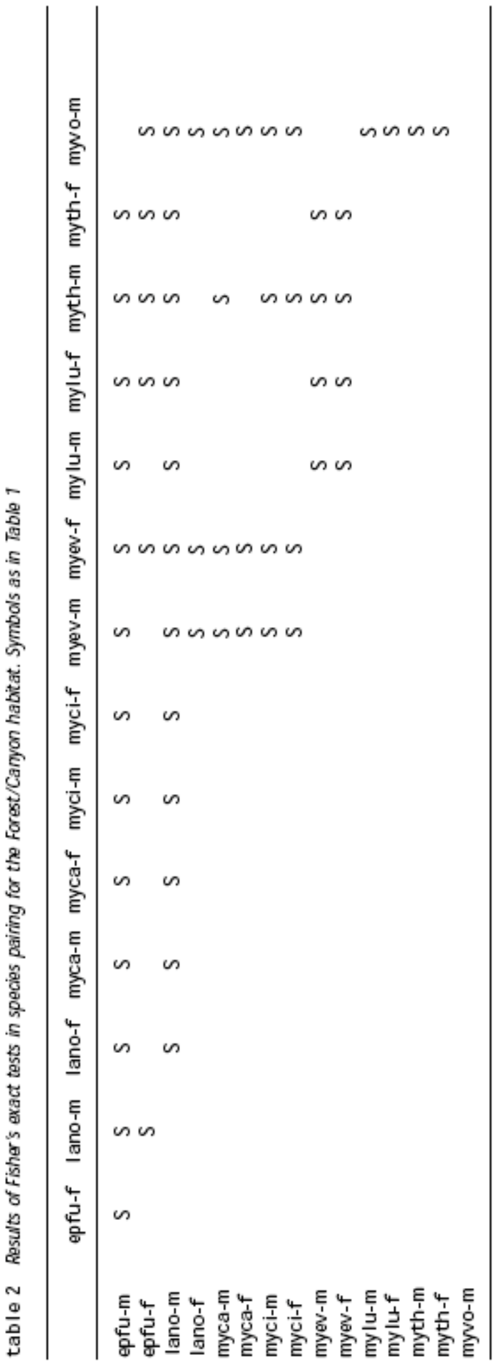

table 2 *Results of Fisher's exact tests in species pairing for the Forest/Canyon habitat. Symbols as in Table 1*

	epfu-f	lano-m	lano-f	myca-m	myca-f	myci-m	myci-f	myev-m	myev-f	mylu-m	mylu-f	myth-m	myth-f	myvo-m
epfu-m	S	S	S	S	S	S	S	S	S	S	S	S	S	
epfu-f		S							S		S	S	S	S
lano-m			S	S	S	S	S	S	S	S	S	S	S	S
lano-f								S	S					S
myca-m								S	S			S		S
myca-f								S	S					S
myci-m								S	S			S		S
myci-f								S	S			S		S
myev-m										S	S	S	S	
myev-f										S	S	S	S	
mylu-m														S
mylu-f														S
myth-m														S
myth-f														S
myvo-m														

Differences in the distribution of bats between the two habitats in the study area can be attributed to the greater harvest of trees in the Forest habitat. As well, in the Forest/Canyon habitat, alternate roost sites such as cliffs, caves, and human structures are more abundant than in the Forest habitat, thereby lessening competition. Perkins and Peterson (1995) noted potential foraging competition only among reproductive females of three bat species that are moth strategists (*M. thysanodes*, *M. volans*, and *C. townsendii*), and only in the Forest/Canyon habitat. Other significant differences noted in Tables 1 and 2 could be attributed to foraging interactions, but results here, and those of Perkins (1993), Perkins and Peterson (1995), Humphrey (1975), and Bell (1980) all agree that bat distribution is more likely dependent upon roost availability and interspecific competition for roosts rather than dietary competition. Sexual segregation in foraging areas occurs in most species, and may be correlated with local population densities of a given species

IMPLICATIONS

If competition for roosts and roost availability is important in determining the distribution and success of bat species in neartic forests, several questions arise:

1. Are present harvest practices especially harmful to smaller and less aggressive bat species?
2. Will future harvest practices result in lower population densities?
3. If competition for roosts is reducing populations of small and less aggressive species in the summer, what are the effects for species that depend on forest tree-roosts for hibernation?

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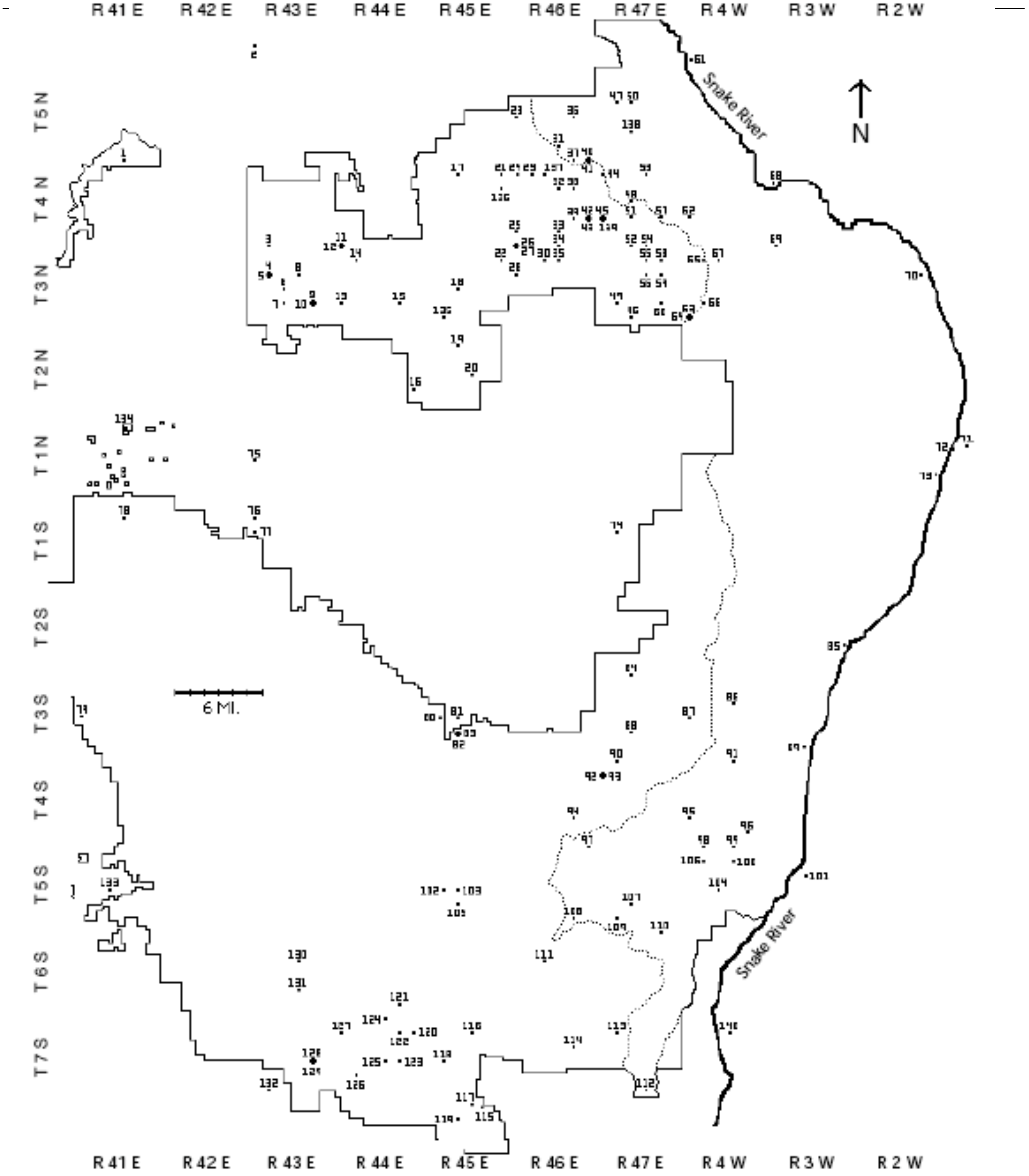

FIGURE 1. Study area, WWNF, Oregon, U.S.A. Thin line indicates forest boundary. East of the broken line is the HCNRA. Small dots represent single sample sites to nearest section. Large dots show two sites within section.

Response of Northern Bats (*M. septentrionalis*) to Prescribed Fires in Eastern KY Forests

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Prescribed fire is becoming a common management tool for restoring forests of North America; however, effects of prescribed fire on forest-dwelling bats remain unclear. During 2006 and 2007, we monitored prey availability, diet, foraging behavior, and roost selection of adult female northern bats (Myotis septentrionalis) before and after 2 prescribed fires in dissected terrain of the Red River Gorge on the Daniel Boone National Forest in eastern Kentucky. Size of home ranges and core areas did not vary between bats radio-tracked before and after fires. Bats foraged more often in the vicinity of pine stands than hardwood or mixed stands, and along ridges and mid-slopes than lower slopes, regardless of burn condition. Home ranges were closer to burned habitats following fires than to unburned habitats. Abundance of coleopterans, dipterans, and all insects combined captured in black-light traps increased following prescribed fires. Fecal samples of bats demonstrated lepidopterans, coleopterans, and dipterans to be the 3 most important groups of insect prey, with consumption of dipterans increasing after burning. Bats chose roosts that were taller in height and in earlier stages of decay than random snags, and after prescribed fires chose roosts in trees with a greater number of cavities and a higher percentage of bark coverage. More roosts were observed in burned habitats (74.3%; n 5 26) after fires than in unburned habitats (25.7%; n 5 9). The results of this work suggest that northern bats are tolerant to prescribed fire on the landscape pattern and scale observed in this study. Northern bats responded to habitat alterations resulting from prescribed fires through shifts in the location of foraging areas as bats tracked changes in insect availability, and through shifts in the selection of roost trees by occupying trees and snags possessing more potential roosting microsites.

Key words: diet, fire ecology, foraging habitat, habitat selection, home range, insect communities, *Myotis septentrionalis*, northern bats, prescribed fire, roost selection

Fire alters composition, structure, and functioning of forests (Fulé et al. 1997; Moritz 1997; Mushinsky and Gibson 1991). Fire is known to modify habitat conditions for birds (Finch et al. 1997) and mammals (Keyser and Ford 2006); however, data on the effects of fire on habitats of forest-dwelling bats and on the behavioral responses of bats to fire remain limited (Carter et al. 2002). Fire in winter is known to disturb red bats (*Lasiurus borealis*) roosting in litter on the forest floor (Moorman et al. 1999; Saugey et al. 1989), and growing- season fires likely disrupt red bats presumably due to effects of smoke and heat reaching where these bats roost (Rodrigue et al. 2001). Fire can produce but also destroy standing snags that are suitable for bark- and cavity-roosting bats (Carter et al. 2002). A study of snag production and loss associated with prescribed fires in western North American forests demonstrated losses of up to 20% of the standing snags, whereas few new snags were created (Randall-Parker and Miller 2002). Nevertheless, examination of data on roosting behavior of evening bats (*Nycticeius humeralis*) in deciduous forests in Missouri suggests extensive use of snags in stands treated with prescribed fires (Boyles and Aubrey 2006). Vulnerability of bark- and cavity-roosting bats to heat and smoke during fires is unknown, although a simulation study using models of roosting structures demonstrated smoke concentrations inside roosts to be comparable to that of ambient levels (Guelta and Balbach 2005). Activity by bats in response to prescribed fires in pine (*Pinus*) forests in South Carolina did not differ across 2 growing seasons among stands treated with prescribed burns, stands thinned and burned, and control stands (Loeb and Waldrop 2008). However, there are no published data on foraging behavior of bats in response to fires or on the effects of fire on the prey base of bats (Carter et al. 2002; Loeb and Waldrop

2008).

Historically, fire played a significant role in the ecology of forests in eastern North America by creating disturbance regimes that altered forest species composition and structure (Brose et al. 2001; Delcourt and Delcourt 1998; Waldrop et al. 1992). The use of prescribed fire is increasing in eastern forests to produce stand conditions typical of those believed to exist before fire suppression (Brose et al. 1999; Hutchinson et al. 2005; Van Lear et al. 2000; Waldrop et al. 1992), to control populations of insect pests (Martin and Mitchell 1980; Miller 1979; Mitchell 1990), and to reduce fuel loads that may contribute to wildfires (Fettig et al. 2007; McCullough et al. 1998; Van Lear et al. 2004).

Declines in insect abundance can be substantial in the hours immediately following fire (Paquin and Coderre 1997; Siemann et al. 1997); however, long-term numeric responses are more variable (Swengel 2001). Orthopterans and coleopterans increase in abundance following fires (Galley and Flowers 1998; Pippin and Nichols 1996; Reed 1997), potentially a positive outcome for bats. Some moths are attracted to fires causing direct mortality, which suggests that the seasonality of fires relative to the timing of insect life stages is an important consideration when examining the effects of fire on nocturnal lepidopterans (Gerson and Kelsey 1997; Miller 1979). In general, examination of data demonstrates that composition of insect communities remains altered for up to 16 years following fires (Buddle et al. 2006; Moretti et al. 2006; Warren et al. 1987). Therefore, data on bat responses to insect communities altered by prescribed fire are needed to determine the implications of prescribed fire in forested areas occupied by bats.

The northern bat (Myotis septentrionalis) is ubiquitous in eastern North American forests (Broders and Forbes 2004; Carter and Feldhamer 2005; Lacki and Schwierjohann 2001; Menzel et al. 2002), so it is a good model to assess the use of prescribed fire. Northern bats form maternity colonies in dead and living trees during the summer (Carter and Feldhamer 2005; Foster and Kurta 1999), and forage in areas close to roosts (Henderson and Broders 2008).

The northern bat is a gleaner, that is, it captures prey directly from the surface of objects, and uses echolocation calls that enable it to successfully catch moths (Faure et al. 1993). The northern bat also is hypothesized to use aerial- hawking to capture prey (Ratcliffe and Dawson 2003; Whitaker 2004), because the diet of these bats consists of numerous other arthropod groups typical of bats that are generalist feeders (Brack and Whitaker 2001; Griffith and Gates 1985; Whitaker 2004). Two insect groups commonly eaten by northern bats, coleopterans and dipterans, exhibit population-level increases with changes in available resources resulting from fire, smoke, and freshly burned wood, with the latter used for oviposition sites (Frost 1984; Gerson and Kelsey 1997; Miller 1979; Reed 1997; Warren et al. 1987). This suggests that abundance of some prey of northern bats may increase following fire. We tested the response of adult female northern bats to prescribed fire by comparing diet, foraging behavior, habitat selection, and roosting behavior of bats before and after prescribed fires on the Daniel Boone National Forest, Kentucky. We evaluated these data in relation to habitat available and abundance of nocturnal insects before and after fires.

MATERIALS AND METHODS

Study area.—The study took place in the Red River Gorge Geological Area, Daniel Boone National Forest, Kentucky (37°51’N, 83°39’W). The forest community and topography are typical of the Cumberland Plateau physiographic region in eastern Kentucky. The area was covered in 2nd-growth forest, comprised mainly of mixed mesophytic tree species including American beech (*Fagus grandifolia*), cucumber magnolia (*Magnolia acuminata*), oaks (*Quercus*), maples (*Acer*), tulip poplar (*Liriodendron tulipifera*), white ash (*Fraxinus americana*), eastern hemlock (*Tsuga canadensis*), and various pines and other conifers (Jones 2005). The terrain is characterized by dissected valleys, steep slopes, cliffs, and rocky outcrops, with elevations ranging from 200 to 365 m above sea level (McGrain 1983). The climate is moderate with average temperatures ranging from 16.6uC to 22.9uC from May to August and an average annual precipitation of 101 cm; rainfall events are common in all months except for August and September.

The study area was organized into 3 experimental units. Two units, Powder Mill and Bear Waller, were exposed to independent prescribed burns, whereas the 3rd unit remained unburned. The burn units were selected in collaboration with United States Forest Service personnel to meet both research and management needs. The burn units were within 0.53 km of each other, separated by a single ridgeline. Neither burn unit had a history of prescribed burning; however, there are reports of ‘‘numerous fires having burned’’ within the original

Cumberland purchase area before 1930 (Collins 1975:195). The ignition pattern for both burn units consisted of firing ridgelines and burn-unit boundaries with a drip torch and allowing the fire to burn down the slope. This produced a mosaic of burned habitats mixed with unburned habitats, especially where moisture conditions were higher. The Powder Mill burn occurred on 10 April 2007 and covered 435 ha, with 53.8% of the area burned. The Bear Waller burn occurred on 30 April 2007 and covered 185 ha, with 54.1% of the area burned. Flame height during both burns ranged from 0.2 to 2.5 m, but was typically <1m. General fire behavior was similar for both burns. Fire spread over most of the ridges and upper slopes, whereas much of the lower slopes and drainages remained un-burned as did some areas below cliffs. In 2007, we added a 3rd study unit, that is, unburned unit, which was approximately 2,400 ha in size, due to the spatial arrangement and number of roosts discovered in this area during pre-burn sampling. This unit bordered the southwestern edge of the 2 burned units.

Capture and tracking of bats.—We captured bats from 14 June to 20 July 2006 and 22 April to 9 September 2007 using nylon mist nets (Avinet Inc., Dryden, New York) of varying lengths. Nets were placed over deep pools in drainages, and upland wildlife ponds in the interior of burned and unburned units. We recorded sex, reproductive condition, body mass, and forearm length of each northern bat captured. We affixed 0.36- or 0.42-g transmitters (LB-2N; Holohil Systems Ltd., Carp, Ontario, Canada) to 18 adult female northern bats between the shoulder blades using Skinbond adhesive cement (Smith and Nephew United, Largo, Florida). Transmitter mass ranged from 3.9% to 8.0% of bat body mass. All protocols followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

We tracked bats daily while foraging and to roost trees using TRX-1000S receivers and 3-element yagi antennas (Wildlife Materials Inc., Murphysboro, Illinois). Tracking of bats continued until the transmitter battery failed or the transmitter was shed. Bats were followed for an average of 6.33 days 6 0.46 SE. Nighttime telemetry began each night after bats left their roosts and continued until at least midnight, terminating when all tracked bats night-roosted. Two or 3 observers were stationed at high-elevation locations and their position recorded with a global positioning system. Contact among observers was maintained using handheld radios permitting simultaneous azimuths to be obtained, because the direction of bat positions was sustained by each observer up to the moment that bearings were requested from the data-recording station. This permitted azimuths to be recorded at 3- to 5-min intervals. When a 3rd observer was used, the 3rd tracking station helped in identifying signal bounce and ensuring correct crosses. Further, vehicles were used to shift among tracking stations, depending on the landscape position of bats, to facilitate detection and tracking of bats and, when a 3rd observer was available, ensure that bats were in the areas determined from the intersection of azimuths. An approach similar to ours was successfully used by Johnson et al. (2007) in radio-tracking long-legged myotis (*Myotis volans*) in Idaho. We tracked individuals in alternating 30-min time periods and, on most nights, tracked </= 3 bats. This sampling scheme likely resulted in some autocorrelation in the foraging data (White and Garrott 1990), possibly resulting in underestimates of the actual home range and core-area sizes used by bats. Regardless, because our purpose was to evaluate spatial use parameters of bats before and after experimental treatment, we suggest that autocorrelation likely affected pre- and post-burn foraging data sets similarly, and, thus, did not influence outcomes of the experimental design.

Home range and characterization of foraging habitat.—We used triangulation to determine the locations of radio-tagged bats during nightly foraging (White and Garrott 1990). We entered azimuths into the Locate 3.19 program to determine exact crossings in order to estimate bat locations (Nams 2006). We used 2 azimuths to determine each bat location. Other studies have shown that the use of > 2 azimuths does not necessarily increase accuracy or precision (Nams and Boutin 1991). We used ArcGIS version 9.2 (ESRI, Redlands, California) to calculate 95% home ranges and 50% core-area estimates using Hawth's Tools extension version 3.27 (Beyer 2004). We generated pre- and post-burn estimates of home- range and core-area sizes of bats captured and radio-tagged on the burn units for which we had > 20 locations. We compared the size of home ranges and core areas before and after prescribed burns using Kruskal–Wallis tests (Hollander and Wolfe 1973).

We analyzed habitat use with the Euclidian distance method (Conner and Plowman 2001; Conner et al. 2003). This method compares distances of animal locations and random locations to each habitat type. We performed 2nd-order (location of home ranges relative to habitat types on the landscape—sensu Johnson 1980), and 3rd-order (use of habitat types within a home range) habitat analyses. We extended each burn-unit boundary outward by the maximum distance a bat moved in a single night within its burn unit, 1.3 km and 0.7 km for the Powder Mill and Bear Waller burn units, respectively. We merged the extended burn units to create an area for use in distance analyses totaling 2,670 ha. We combined bats into pre-burn and post-burn groupings to assess the effects of burning on use of foraging habitat.

We evaluated 4 habitat variables using 2nd- and 3rd-order analyses. Habitat variables were aspect, stand type, slope position, and whether areas had burned or not burned during prescribed fires. We derived data for aspect from digital elevation models based on geographic information system coverage available from the Kentucky Geospatial Data Clearinghouse Web site (http://kygeonet.ky.gov/). We defined slope aspects as north (315°–45°), east (45°–135°), south (135°–225°), and west (225°–315°) facing. We obtained data on stand availability in the study area from the United States Forest Service, and categorized stands into 4 types. We defined pine and hardwood stands as having >/= 70% of the dominant and co-dominant basal area as pine or hardwoods, respectively. We defined pine–hardwood and hardwood–pine stands as having 51–69% of the dominant and co-dominant basal areas as pine or hardwoods, respectively. We used a geographic information system to create slope position classes using the Topographic Position Index extension version 1.2 (Jenness 2006). We based the classification system used for defining the slope position index on the 6-Class scheme (Jenness 2006). We classified location as ridge, mid-slope, and lower slope. United States Forest Service personnel delineated burned area coverage on a topographic map and we digitized the areas burned into a geographic information system. Analysis of distance data for burn condition (i.e., burned versus unburned) was restricted to the post-burn bat grouping.

We measured distances of observed and random (expected) locations to available habitat types in a geographic information system using the Nearest Features 3.8b extension (Jenness 2004). To determine 2nd-order habitat selection, we generated 5,000 random points within the study area and calculated the minimum distances to each available habitat type. For 3rd- order habitat selection, we generated 1,000 random points within each bat's 95% home range and calculated the minimum distances to each available habitat type. Under the null hypothesis, habitat use should be occurring at random and the ratio of bat locations to random distances should equal 1.0 (Conner and Plowman 2001). We analyzed distance ratios to available habitat types using multivariate analysis of variance (MANOVA). When MANOVAs were significant, we used t- tests to rank habitat types in order of closest to farthest from bat locations or home ranges (Conner and Plowman 2001; Conner et al. 2003).

Characteristics of roost trees.—For all roost trees and random snags we recorded geographic position and tree or stand characteristics in a tree-centered 20-m-radius plot. We identified tree species, decay class (Hunter 1990), and estimated the number of cavity openings. We measured diameter at breast height (DBH; cm), tree height (m), and canopy height (m), and visually estimated canopy cover (%), bark coverage (%), and exfoliating bark coverage (%). We counted the number of snags and live trees ≥ 16 cm DBH within 20 m of the focal tree. At roost trees we estimated roost height (m) and diameter at roost height (cm) and compared these values for roosts selected before and after the burn using t-tests. We determined roost position as above, below, or within the canopy, and the roost structure as crevice, cavity, or bark. We counted the number of bats exiting a roost the night after it was 1st discovered and sporadically thereafter when logistics permitted. For all roost trees and random snags found after burning, we estimated the percentage of the 20-m plot that burned and recorded char (i.e., fire scar) height on the tree (m).

We sampled random snags by taking a random azimuth and locating the 1st suitable snag that was between 40 and 100m from the roost tree. If none was found, we randomly selected new azimuths until a random snag was located. We chose 40m as the minimum distance to ensure no overlap in circular plots between random snags and roost trees, and chose random snags to ensure no overlap of circular plots among random snags. A suitable random snag had to have a decay class of 3–7 (Hunter 1990), and a minimum diameter of 16cm based on the mean diameter for roost trees of northern bats recorded elsewhere in Kentucky (Lacki and Schwierjohann 2001). We compared tree and stand characteristics using Kruskal–Wallis tests (Hollander and Wolfe 1973) between roosts and random snags measured pre-burn, and between roosts and random snags measured post-burn.

Insect sampling and food habits.—In 2006 and 2007, we sampled insect communities with blacklight traps (Universal Light Trap; Bioquip Products, Gardena, California). Black- light traps preferentially attract lepidopterans and are a commonly used trap type for assessing insect abundance (Lacki et al. 2007a).

Regardless, traps are effective in elucidating patterns as long as only relative comparisons (e.g., pre-burn versus post-burn) of prey taxa are made. We activated black-lights within 1h of sunset and operated the traps until sunrise. Insects captured were killed with ethyl acetate. We established 4 trap locations in each of the 2 burn units; 2 traps were positioned on north-facing (mesic) slopes and 2 on south-facing (xeric) slopes. Trap sites ranged from 294 to 387m in elevation and were situated on slopes ranging from 18% to 40%. We sampled all trap locations within a burn unit on the same nights, and trapping occurred at 10-day intervals. This scheme resulted in 68% of trap nights occurring during radio-tracking sessions, with the remainder occurring before or after tracking sessions. Trapping of insects took place from 10 July to 25 September 2006 (pre-burn sampling) and from 22 April to 1 October 2007 (post-burn sampling). We identified insects that were ≥10 mm in size to the ordinal level. Smaller insects were often in too poor a condition to identify to order.

We analyzed responses of the insect community using 2-factor analyses of variance (ANOVAs), with the main effects being aspect and burn condition (pre-burn versus post-burn). Response variables included abundance of all insects combined (i.e., number of individuals ≥10 mm in size), and abundance of Lepidoptera, abundance of Coleoptera, and abundance of Diptera because these groups are known to be eaten by northern bats (Faure et al. 1993; Whitaker 1972, 2004). We tested homogeneity of variance using a variance ratio F-max test, with ANOVAs based on log-transformed values when variances were heterogeneous to ensure that data were homoscedastic (Sokal and Rohlf 1969).

Fecal samples collected from bats captured and radio-tagged were frozen until analysis. Pellets were dissected following Whitaker (1988) and prey remains identified to order. In our identification of insects the order Hemiptera included the suborder Auchenorrhyncha, previously recognized as the order Homoptera (Triplehorn and Johnson 2005). We determined the frequency of occurrence of prey items (i.e., present or not present in a pellet) and also estimated percent volume of prey items in pellets from each bat to the nearest 5%. Up to 3 pellets from each bat were dissected and values were averaged across pellets to determine the percent values for each prey item for each bat (Lacki et al. 2007b). Percent volume of insect orders in pellets of bats radio-tracked before the burn were compared to values for bats radio-tracked after the burn using Kruskal–Wallis tests (Hollander and Wolfe 1973).

RESULTS

In 2006 and 2007, we captured and radio-tagged pregnant females (n = 6) from 29 April until 10 June, lactating females (n = 3) in mid-June (19–22 June), post-lactating females (n 5 2) from 20 July to 2 September, and non-reproductive females (n = 7) in early spring from 22 to 29 April and in late summer from 6 to 8 August. Body mass of female northern bats, irrespective of reproductive condition, averaged 6.6 g ± 0.25 *SE*.

Maternity colonies began forming as early as 29 April and persisted through 26 June. Large colonies (i.e., > 15 bats exiting a roost) were recorded at 18 different trees with the largest exit counts of 56 and 52 observed on 15 June and 26 May 2007, respectively. Both roosts with the largest exit counts were in tall (> 25m in height) and large (> 45cm DBH) tulip poplar snags. Bats used multiple roosts (3.8 roosts per bat ± 0.42 *SE*) and switched roosts frequently, as demonstrated by a pregnant female (B 11), which over 6 nights used 3 different roosts holding 18–39 bats.

Foraging behavior.—Mean home-range size of female northern bats was no larger after burning (72.3ha ± 6.2 SE; n = 9 bats) than before (60.2 ± 14.1ha; n = 5 bats; Kruskal– Wallis = 0.54, *P* = 0.46). The largest home range recorded was 172ha for a pregnant female captured on 10 June 2007, and the smallest was 18.6ha for a post-lactating female captured on 20 July 2006. Mean core-area size was no larger after burning (13.5 ± 0.8ha) than before (11.4 ± 6.1ha; Kruskal–Wallis = 0.36, *P* = 0.55).

Female northern bats foraged closer to pine stands than pine–hardwood stands before burning (Wilks' lambda = 0.0007, *d.f.* = 4, 1, *P* < 0.04), and located their home ranges closer to pine stands than to hardwood or hardwood–pine stands (Wilks' lambda = 0.035, *d.f.* = 4, 5, *P* < 0.001; Table 1) after the burns. Home ranges of bats were closer to mid-slope positions than to lower slope positions before burning (Wilks' lambda = 0.049, *d.f.* = 3, 2, P < 0.07), and closer to mid-slope positions than to either ridge or lower slope positions after burning (Wilks' lambda = 0.044, *d.f.* = 3, 6, P < 0.001). Home ranges of bats were closer to burned than to unburned habitats after burning (Wilks' lambda = 0.042, *d.f.* = 2, 7, P < 0.001). There was no difference in use of aspects by bats either before or after burning.

Data on insect abundance (≥10 mm in size) showed increases for coleopterans, dipterans, and all insects combined following burning (Table 2). The abundance of moths did not change. Fecal pellet analysis showed that bats consumed members of 7 orders of insects, with lepidopterans, coleopterans, and dipterans being the 3 most important prey groups (Table 3). Percent frequency and percent volume of dipterans increased in the diet of female northern bats after burning. Percent volume of all other orders of insects did not change following burning, although hymenopertans were only found in pellets before burning and neuropterans only in pellets after burning.

Roosting behavior.—We tracked female northern bats to 54 tree roosts, with 29.6% located before burning and 70.4% after. Bats roosted in 11 species and 3 additional genera of trees including chestnut oak (*Quercus prinus*; n = 13), red maple (*Acer rubrum*; n = 8), hickories (*Carya*; n = 7), tulip poplar (n = 6), pines (*Pinus*; n = 4), scarlet oak (*Q. coccinea*; n = 3), white oak (*Q. alba*; n = 3), black oak (*Q. velutina*; n = 3), sassafras (*Sassafras albidum*; n = 2), and 1 each of elm (*Ulmus*), cucumber magnolia, black walnut (*Juglans nigra*), black gum (*Nyssa sylvatica*), and flowering dogwood (*Cornus florida).*

All but 2 roost trees were in hardwood stands, with 74.3% of roost trees located in burned habitats and 25.7% in unburned habitats following burning. Distribution of roost trees by aspect shifted after burning from predominantly south- and west-facing aspects to south- and east-facing aspects (Table 4). Roost trees were most often found on mid-slope and ridge positions regardless of burn condition. Fire burned 80% of the area on 67.6% of sample plots surrounding roost trees with charred surfaces reaching 14.6m in height, with charring caused by smoldering combustion. Fire burned 80% of the area on 54.4% of sample plots surrounding random snags with char reaching 17.6m. The structural integrity of 2 roosts trees appeared to have been compromised from extensive smoldering combustion.

Comparisons of roost trees with random snags before burning indicate that female northern bats selected trees that were in an earlier stage of decay and taller (Table 5). After burning, bats continued to select trees in earlier stages of decay than random snags, but also chose trees as roosts with a greater number of cavities and higher percentages of bark coverage and exfoliating bark coverage than random snags. We found no difference between stand characteristics measured around roost trees and random snags.

Roost height (t = 0.45, *d.f.* = 28, P > 0.2) and stem diameter at roost (t = 0.54, *d.f.* = 28, P > 0.2) were not different between roosting sites of female northern bats before and after burning (Table 6). The majority of roosts were situated below the canopy and none was found above the canopy. Only type of structure used for roosting changed after burning with an increased selection for cavities and fewer roosts located under bark. This is consistent with comparisons made with random snags that showed number of cavities to be associated with selection of roost trees following burning.

TABLE 1.—Second- and 3rd-order habitat use by stand type, slope position, and burn condition for female northern bats (Myotis septentrionalis) on the Daniel Boone National Forest, Kentucky, in 2006 and 2007. Habitats are ranked from closest to farthest from bat locations. Only comparisons where differences were found are shown. Within rows, different letters (A, B, C) indicate habitats that differ significantly (P < 0.1) from each other in their distances from bat locations.

	Closest			Farthest
Stand type				
Pre-burn, 3rd order	Pine^{A}	Hardwood^{A,B}	Hardwood-pine^{A,B}	Pine-hardwood^{B}
Post-burn, 2nd order	Pine^{A}	Pine-hardwood^{A,B}	Hardwood^{B,C}	Hardwood-pine^{C}
Slope position				
Pre-burn, 3rd order	Mid-slope^{A}	Ridge^{A}		Lower slope^{B}
Post-burn, 2nd order	Mid-slope^{A}	Ridge^{B}		Lower slope^{C}
Burn condition				
Post-burn, 2nd order	Burned^{A}			Unburned^{B}

TABLE 2.—Means 6 SE for abundance of insects (≥10 mm in size) captured per trap night in black-light traps before and after prescribed burning on the Daniel Boone National Forest, Kentucky, in 2006 and 2007. ANOVA test outcomes are included.

	All insects combined	Coleoptera	Lepidoptera	Diptera
Pre-burn (n = 43)	140 ± 14	8.0 ± 1.47	126 ± 13	1.0 ± 0.25
Post-burn (n = 84)	188 ± 14	24.3 ± 3.24	154 ± 13	2.4 ± 0.34
F-statistic (P-value)	4.1 (0.04)	20.3 (0.001)	0.3 (0.6)	12.2 (0.001)

TABLE 3.—Mean percent volume 6 SE and frequency of occurrence (%) of insect prey in fecal samples of northern bats (Myotis septentrionalis) radio-tracked before (n = 6 bats) and after (n = 8 bats) prescribed burning on the Daniel Boone National Forest, Kentucky, in 2006 and 2007.

	Percent volume		Percent frequency	
Taxon	Pre-burn	Post-burn	Pre-burn	Post-burn
Coleoptera	27.8 ± 2.8	35.5 ± 8.6	100.0	100.0
Diptera[a]	1.4 ± 1.1	11.0 ± 3.6	50.0	100.0
Hemiptera	6.1 ± 3.5	5.6 ± 1.9	83.3	75.0
Hymenoptera	1.4 ± 1.4	0.0	16.7	0.0
Lepidoptera	62.6 ± 5.2	46.4 ± 8.3	100.0	100.0
Neuroptera	0.0	0.2 ± 0.2	0.0	12.5
Trichoptera	0.4 ± 0.4	0.2 ± 0.2	16.7	12.5
Othera[b]	0.8 ± 0.6	1.0 ± 1.0	33.3	62.5

[a] Between burn conditions, average percent volume for Diptera is different in fecal samples of radiotracked bats at P , 0.01.

[b] Represents unidentified materials, hair, or vegetation.

TABLE 4.—Percentage of tree roosts (n 5 51) of female northern bats (Myotis septentrionalis) by aspect and slope position before and after prescribed burning on the Daniel Boone National Forest, Kentucky, in 2006 and 2007.

Habitat Characteristic	Pre-burn	Post-burn
Aspect		
North	13.0	17.0
East	6.0	23.0
South	43.0	51.0
West	38.0	9.0
Slope position		
Ridge-top	44.0	54.0
Mid-slope	50.0	40.0
Lower slope	6.0	6.0

TABLE 5.—Means (*SE*) of tree- and stand-level habitat characteristics for roosts of female northern bats (Myotis septentrionalis) and random snags before and after prescribed burning on the Daniel Boone National Forest, Kentucky, in 2006 and 2007. Asterisks indicate that within burn condition, characteristic is different between roosts and random snags; * P < 0.05; ** P < 0.01.

	Pre-burn		Post-burn	
Habitat Characteristic	Roosts (n = 16)	Random (n = 11)	Roosts (n = 35)	Random (n = 57)
Decay class (1-9)	3.62 (0.4)*	5.27 (0.4)	2.43 (0.2)**	4.46 (0.2)
Tree diameter (cm)	44.2 (4.0)	41.6 (6.6)	34.6 (3.4)	32.0 (1.8)
Tree height (m)	20.6 (2.5)*	12.1 (2.1)	19.7 (1.4)	17.8 (1.0)
No. cavities (n)	1.44 (0.7)	1.27 (0.6)	1.54 (0.5)*	0.82 (0.2)
Bark coverage (%)	62.0 (9.0)	40.0 (10.2)	83.0 (4.4)**	46.0 (4.9)
Exfoliating bark coverage (%)	16.0 (4.0)	25.0 (6.0)	7.0 (2.4)*	13.0 (2.1)
Canopy height (m)	21.3 (1.5)	16.9 (1.2)	27.8 (0.8)	30.5 (1.2)
Canopy cover (%)	47.0 (5.0)	51.0 (7.2)	65.0 (4.4)	61.0 (3.0)
Snag density (stems/ha)	40.5 (6.7)	27.5 (8.7)	25.2 (3.1)	33.9 (5.2)
Live tree density (stems/ha)	363 (50)	280 (27)	272 (10)	252 (10)

TABLE 6.—Characteristics of roosting sites of female northern bats (Myotis septentrionalis) before and after prescribed burning on the Daniel Boone National Forest, Kentucky, in 2006 and 2007. Data are presented as percent of total or as mean 6 SE. Sample sizes reflect our inability at times to locate the specific roosting site of the bats on the tree or snag.

Roost characteristic	Pre-burn (n = 6)	Post-burn (n = 24)
Roost height (m)	10.6 ± 3.6	9.1 ± 1.4
Diameter of stem at roost (cm)	20.3 ± 6.8	24.0 ± 3.0
Roost position		
Above canopy (%)	0.0	0.0
Within canopy (%)	33.3	20.8
Below canopy (%)	66.7	79.2
Roost structure		
Crevice (%)	16.7	17.4
Cavity (%)	33.3	60.9
Bark (%)	50.0	21.7

DISCUSSION

We found size of home ranges and core areas of female northern bats was unaffected by changes in habitat caused by prescribed fire, suggesting populations of insect prey likely remained available in proximity to roosting sites. The higher abundance of coleopterans, dipterans, and all insects combined captured in black-light traps post-fire compared to pre-fire conditions supports this contention, because the former 2 insect groups were the 2nd and 3rd most important prey of these bats. The importance of these 2 insect groups is consistent with data for other populations of northern bats (Griffith and Gates 1985; Whitaker 2004).

The home-range sizes we measured for female northern bats are likely minimum estimates because we limited our radio-tracking to the early evening foraging period. Northern bats use a biphasic activity pattern when foraging (Owen et al. 2003), so our approach omitted the predawn foraging period. However, we argue that this influence likely affected both pre-burn and post-burn estimates equally. Foraging behavior of adult female bats also is known to vary by reproductive condition, with lactating females using habitats where they can drink more frequently (Adams and Hayes 2008) and foraging earlier and for longer periods than pregnant, post-lactating, or non-reproductive females (Barclay 1989). We radio-tracked only 3 lactating females, 2 in the pre-burn period and 1 post-burn, so it is unlikely that differences associated with foraging behavior of lactating females affected the outcome of our analyses. Moreover, the mean home-range size of lactating females (93.6ha ± 4.8 *SE*) was comparable to that of pregnant females (95.5 ± 21.9ha) in our study, so the influence of radio-tagged lactating females was likely not significant on pre-burn versus post-burn estimates of home- range size.

The home-range sizes we estimated were small compared to those reported for bats elsewhere in North America (Lacki et al. 2007a), but comparable to those measured for other populations of northern bats (Broders et al. 2006; Owen et al. 2003). Northern bats radio-tracked in a heavily fragmented, forest–agricultural landscape used foraging areas an order of magnitude smaller than we found (Henderson and Broders 2008). These authors suggested that the possible behavioral differences in use of available foraging space by northern bats were associated with the available local landscape resulting from forest fragmentation. Thus, northern bats likely exhibit plasticity in foraging behavior with the magnitude of movements being related to the local landscape structure.

The preference of northern bats for foraging at heavily forested mid-slope positions, regardless of burn condition, suggests these bats feed in and around closed canopies and are likely cluttered-adapted (Aldridge and Rautenbach 1987; Crome and Richards 1988; Norberg and Rayner 1987); however, we do not know the extent to which they may have foraged above the canopy. The extensive use of forested habitats for foraging by northern bats in other landscapes with varying amounts of fragmentation is consistent with our findings (Broders et al. 2006; Caire et al. 1979; Henderson and Broders 2008; LaVal et al. 1977; Owen et al. 2003). Nevertheless, we found northern bats also foraged in or near pine-dominated stands more often than hardwood-dominated stands, regardless of burn condition, and in burned habitats more than unburned habitats. We argue that within forests bats used microhabitats with less clutter as our observations indicated pine stands and burned habitats possessed less- cluttered canopies than hardwood stands and unburned habitats, respectively. The behavior we observed is not consistent with activity by assemblages of bats in southern pine forests, where the use of burned habitats was no different from activity levels recorded in unburned habitats (Loeb and Waldrop 2008). However, northern bats were not among the suite of species examined.

Northern bats use a wide range of tree species as roosts (e.g., Broders and Forbes 2004; Carter and Feldhamer 2005; Foster and Kurta 1999; Menzel et al. 2002), and the pattern we observed for adult females was no different, with ≥ 11 species of trees used as roosts. On occasion we had difficulty classifying the species of tree beyond genus due to the state of decay, so it is likely that more species of trees were actually used. The majority of roosts (92.6%) were in hardwood species and only 7.4% of roosts occurred in pines. This contrasts with other data for northern bats where shortleaf pine (*Pinus echinata*) was the species of tree used most frequently (Lacki and Schwierjohann 2001; Perry and Thill 2007). Our data may partly reflect the extensive damage to and loss of pine snags that resulted from burning. Regardless, northern bats can use both hardwoods (Foster and Kurta 1999; Menzel et al. 2002) and conifers as roosts (Broders and Forbes 2004; Carter and Feldhamer 2005). Examination of our data shows that females preferentially chose roost trees in burned compared to unburned habitats, similar to evening bats in Missouri, which used snags in burned stands more frequently than in unburned stands (Boyles and Aubrey 2006).

Regardless of burn condition, the roosts of female northern bats were situated on ridge and mid-slope positions but rarely in lower slope positions. This is consistent with roost use by northern bats elsewhere in eastern Kentucky, where the majority chose roosts in upper slope positions (Lacki and Schwierjohann 2001). The aspect of roosts changed from south- and west-facing aspects to south- and east-facing aspects, likely due to the extent of forested stands on east- facing aspects that were burned. We found female northern bats chose live trees, and snags in earlier stages of decay than random snags; a common trait of cavity-roosting bats (Barclay and Kurta 2007). This pattern also is consistent with studies showing that northern bats use live trees more frequently than syntopic populations of Indiana bats (Myotis sodalis), a species that also roosts beneath bark and inside crevices of trees and snags (Carter and Feldhamer 2005; Foster and Kurta 1999).

Before burning, female northern bats roosted in tall trees and snags, but after burning the condition of the bole (i.e., main stem) was more important in regards to the selection of trees and snags. Bats still used trees in an early decay class; however, post-burn roost trees had a higher percent cover of bark compared to those randomly available on the landscape after fires. Although not statistically compared, post-burn roost trees on average had higher bark coverage compared to pre-burn roost trees. Overall, female northern bats used bark, crevices, and cavities as roosting structures, but roosts were situated more often beneath bark before burning and inside cavities after burning. The use of cavities as roosting structures after burning is consistent with our result that post-burn selection was based on bole condition (i.e., number of cavities and bark coverage).

The importance of bole surface for roost choice by northern bats following fire was unexpected and its significance needs to be addressed. We propose 2 hypotheses. First, stems possessing more cavities and a higher percentage of exfoliating bark provide a wider range of choices for roosting, which may provide longer-term roosting sites. Second, stems possessing more cavities and a higher percentage of exfoliating bark provide a greater density of roosting sites within a tree in case bats need to relocate on the same roost tree to avoid smoke and heat effects during fire. Dickinson et al. (2009) suggested that both female and male northern bats emerge from roosting sites during prescribed burns and avoid smoke and heat by temporarily relocating to alternate roosts away from the fire. This is not consistent with our 2nd hypothesis.

The extent to which roosts are limiting in forested habitats remains unclear (Crampton and Barclay 1998; Kunz and Lumsden 2003). Although there is evidence for competition among syntopic species of tree-roosting bats (Boonman 2000; Lumsden et al. 2002), other authors conclude the opposite based on use of available roosting structures (Sedgeley and O’Donnell 1999). There are few quantitative estimates of suitable roosting trees for bats inhabiting forests in eastern North America. Based on data from roosts with >15 bats exiting, or large flyouts, we estimated 30.8 ha per large-flyout roost at the Bear Waller burn unit, 87ha per large fly-out roost at the Powder Mill burn unit, and 343ha per large fly-out roost at the unburned control. The latter estimate is likely biased upward given the lower sampling effort, meaning important roosts likely went undiscovered relative to the 2 burn units.

We believe female northern bats exhibit behaviors consistent with being fire-tolerant as they foraged and roosted extensively in burned habitats after prescribed burning. Moreover, the use of both live trees and snags as roosts (Carter and Feldhamer 2005; Foster and Kurta 1999; Lacki and Schwierjohann 2001; Perry and Thill 2007; this study), the range of roosting structures (Carter and Feldhamer 2005; Foster and Kurta 1999; Lacki and Schwierjohann 2001; Perry and Thill 2007; this study), and the ability to arouse and move during fires (Dickinson et al. 2009) is strong evidence that northern bats adjust to changed habitats resulting from fires.

The heavily forested regions of eastern Kentucky have a long history of burning, and although the majority of forested habitats burn infrequently, some autumn fires can be large and their impact is likely severe on the resources needed by forest- dwelling bats (Maingi and Henry 2007). Knowledge of fire history is reflected in the long-term plan of the Daniel Boone National Forest, Kentucky, to prescribe-burn approximately 22,700 ha per year in the next decade (Mann 2006). Although the consequences of this policy are unknown for the majority of species our results suggest that there will be no negative effects on populations of northern bats. We argue that the bats will likely benefit from the proposed burning program, but monitoring is recommended.

Trends in the use of prescribed fire in national forests in the eastern United States suggests that early growing season (i.e., spring) burns will increase in frequency and extent because of their utility in vegetation management (Dickinson et al. 2009). Formation of northern bat colonies occurred from 29 April, about the time of the Bear Waller burn, and extended to the last week in June. Thus, increased spring burning (Dickinson et al. 2009) has the potential to disturb bats during the period when maternity colonies of northern and other bark- and cavity-roosting bat species are being established. Bats are capable of exiting tree and ground roosts before they experience extensive exposure to heat and gases during fires (Dickinson et al. 2009; Rodrigue et al. 2001; Saugey et al. 1989); however, adult females are more likely to use daytime torpor following nights of poor foraging success due to rainfall events or cooler nighttime temperatures that lower prey abundance (Audet and Thomas 1997; Kurta 1991). These are conditions that can be typical of early spring weather patterns in eastern North America, although prescribed burning would not occur during wet periods. Moreover, peak burning conditions occur during the daytime when ambient temperatures are highest and arousal times of bats likely the shortest (Chruszcz and Barclay 2002; Ruczyński 2006), further reducing the risk of bats to prescribed fire. Growing-season burns have the potential to be detrimental to non-volant young, because these bats are not capable of escaping. Because of concern for the endangered Indiana bat, however, there are no proposals on National Forests for burning during the lactation period where Indiana bats are known to be present (Dickinson et al. 2009); this region overlaps a large portion of the range of the northern bat and other species.

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1174 JOURNAL OF MAMMALOGY Vol. 90, No. 5

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October 2009 LACKI ET AL.—NORTHERN BATS AND PRESCRIBED FIRE 1175

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Cave Conservation: Special Problems of Bats

by Gary F. McCracken

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Ignorance as to the real status of populations of almost all bat species is a major problem for their conservation. This ignorance is reflected in the IUCN “red list” of threatened species, which is both minimalist and biased. The recent proposition that we should construct “green lists” of species known to be secure, rather than red lists, is extended to bats. Available information regarding the status of the five species of North American bats listed as endangered is reviewed, and these species are used to illustrate major problems encountered by bat populations. All of these species rely on cave roosts. Their habit of roosting in large aggregations during hibernation and/or reproduction make these and other cave dwelling bats particularly vulnerable to disturbances which can reduce populations. Types of disturbances and their likely effects are discussed. The long life spans and low reproductive rates of bats mandate that they will recover slowly following population reductions. Habitat alteration and destruction outside of roosts and poisoning from pesticides also have impacted negatively on bat populations; however, roost site disturbance and habitat destruction have probably had much greater negative effects than has pesticide poisoning. Because disturbance within their cave roosts is a major problem in bat conservation, constructing lists of “green caves” (those which can be visited) and “red caves” (those which must be avoided) is encouraged. Criteria for constructing these lists of caves are discussed.

Red Books, Green Lists, And a Lack of Information

Each year the International Union for the Conservation of Nature (IUCN) updates the Red Data Book which lists plant and animal species known to be endangered, vulnerable, or rare. The 1988 Red Data Book places 33 bat species in these categories. As there are approximately 900 species of bats in the world (nearly one-fourth of all mammal species), this “red list” of threatened species includes less than 4% of the world’s bats. This disproportionately small number should lead anyone with even remote awareness of the worldwide extinction crisis to question whether this list reflects reality with regard to bat species that are threatened. In reality, the red list does not come close to giving an accurate picture of the problem.

First, consider that the red list has a substantial geographical bias toward North American species. The standard reference on North America bats (Barbour and Davis, 1969) lists 39 species of bats in North America, north of Mexico. These 39 species comprise about 5% of the worldwide bat species diversity. However, of the 33 threatened bat species on the IUCN list, 5 are native to North America. So, a fauna comprising 5% of total bat species diversity, accounts for 15% of the species considered as threatened. I argue that this bias does not reflect reality with regard to species endangerment. Rather, this bias reflects our ignorance regarding the status of most bat populations. We simply know the status of bats in North America better than for most other parts of the world. I also argue that our degree of ignorance is even more frightening when you recognize that we are not even certain how accurate the IUCN red list is for bat species in North America. This is so because for most bat species in North America, much less for those elsewhere (particularly in the tropics), we simply do not have the information to determine whether overall population sizes are stable, decreasing, or if they are decreasing, at what rates? So our ignorance on the status of bats is extreme. Given this ignorance, the IUCN red list gives a highly inaccurate and minimal assessment of our current extinction crisis.

Recognizing this, prominent conservation biologists recently have suggested that the construction of red lists has been a major tactical error by those who wish to preserve the world’s biota (Imboden, 1987; Diamond, 1988). Red lists are thought to be a tactical error because the existence of such a list may lead to the assumption that if a species is not on the list that species is not in jeopardy. This, of course, is not how the list should be interpreted. Many species that are not on the list should be, but are not, simply because we don’t know enough about them. To correct this tactical error, it has been suggested that rather than constructing red lists we should construct “green lists.” Green lists would include species that we know are secure. To be on the green list a species should meet the criterion of “known not to be declining in numbers now, and unlikely to decline in the next decade” (Diamond, 1988). With a green list, it is argued, the burden of proof is shifted to those who wish to maintain that all is well with a species.

Those proposing green lists have been concerned with birds, not with bats. Certainly, much more is known about the status of birds than of bats. However, it is estimated that fewer than 1/3 of the world's bird species would qualify for inclusion on a green list. This being the case with birds, I also suspect that fewer than 1/3 of the world's bats likewise would qualify for such a list.

Some Things That We Do Know

With our ignorance as a perspective, I wish to consider some of what we do know about the status of bats, particularly cave bats. This requires going back to the red list. Of the 39 bat species in North America, north of Mexico, 18 rely substantially on caves for roosting sites. Some of the remaining 21 species also are occasionally found in caves, but caves evidently are not absolutely essential to them. Of the 18 species for which caves are essential, 13 species utilize caves year-round; both for reproduction and as winter roosts. The remaining 5 species rely on caves as hibernating sites, but roost elsewhere during reproduction. Four of the 5 North American species on the red list require caves year round (Table 1), and one species (the Indiana bat) requires caves for hibernation, but roosts elsewhere during the summer. So all North American bats listed as threatened are cave-dwelling; there appears to be a correlation with cave-dwelling and species jeopardy. However, to hearken briefly back to our ignorance, it is easier (not easy, just easier) to assess the status of cave-dwelling bats than the status of bats that are more dispersed in their roosting habits, and thus more difficult to find and monitor. The bias toward cave-dwelling bats being on the threatened list may in part be a result of relative ease of censussing.

Life History Traits Predisposing Bats to Extinction

Unlike most small mammals, bats have extremely long life spans. Even the smallest bat typically has a life expectancy on the order of 10 years, and individuals are known to live much longer than this. Wild little brown bats, for example, are known to survive as long as 30 years (Keen and Hitchcock, 1980). In addition to long life expectancies, bats have very low rates of reproduction. Many female bats do not reproduce until their second year and, after reaching maturity, females usually produce only a single pup each year. Consequently, bats have far lower potential rates of population growth than are typical of most small mammals. Although bats are often perceived of as similar to rats or mice, the reproductive rates of bats are, in contrast, more similar to those of antelopes or primates. If a bat population is decreased in size, it can recover only slowly.

Bats have other characteristics, which contribute to their vulnerability. Among the most significant is their habit of roosting together in large aggregations. The fact that large numbers of individuals often are concentrated into only a few specific roost sites results in high potential for disturbance. Because of their aggregative roosting habits, species that are very common actually can be vulnerable because they are in only a limited number of roosts. Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) are an excellent example. Single cave roosts of these bats can contain 10's of millions of individuals and the loss of even one such roost would mean the loss of a significant portion of the entire species population.

Table 1. Officially endangered North American bats* and their use of cave roosts.

Species	**Roost Requirements**
Indiana Bat *Myotis sodalis*	Winter Hibernacula
Gray Bat *Myotis grisescens*	Year-Round
Big-Eared Bat§ *Plecotus townsendii*	Year-Round
Sanborn's Long-Nosed Bat *Leptonycteris sanborni*	Year-Round
Mexican Long-Nosed Bat *Leptonycteris nivalis*	Year-Round

*These species are listed on both the IUCN Red List and the U.S. Fish and Wildlife Service Endangered Species List.

§Two subspecies of big-eared bats are listed: Ozark big-eared bat (*P. t. ingens*) and Virginia big-eared bat (*P. t. virginianus*)

Disturbance of Roosts by Humans

Aggregations of bats are vulnerable to a variety of human-caused disturbances. At least 3 North American endangered species (Indiana, gray, and Sanborn's long-nosed bats) are known to have abandoned traditional roost sites because of commercial cave development (Humphrey, 1978; Tuttle, 1979; Wilson, 1985a). An important hibernaculum for endangered big-eared bats has been threatened by quarrying (Hall and Harvey, 1976), and I personally have observed numerous examples of vandalism such as burning old tires, or shooting guns inside bat cave roosts. Although intentional disturbance of roosts is well documented, unintentional disturbance often poses an even greater threat. In the temperate zone, aggregations of bats which cavers typically encounter are either hibernating groups that occur in late fall, winter, and early spring, or maternity colonies that occur in late spring or summer. There is no question that disturbances as seemingly trivial as merely entering a roost area, or shining a light on hibernating bats or on a maternity group of females and their pups, can result in decreased survival, perhaps outright death, and possible abandonment of the roost site. Although there is some controversy about the significance of this apparently "innocent" disturbance, my own experience and reading of the literature lead me to the opinion that it can be extremely significant. However, there is no question that the impact of such disturbances are somewhat species-specific, and that the timing of the disturbance is very important.

The results of "innocent" disturbance of a maternity colony can include the following. (1) It can cause individuals to abandon roost sites, particularly early in the reproductive season when females are pregnant. This may result in females moving to other, perhaps less ideal, roosts where their success at reproducing is reduced. (2) Disturbance raises the general level of activity within roosts. This may result in greater expenditure of energy and less efficient transfer of energy to nursing young. This, in turn, may cause slower growth of young and increase the foraging demands on females, thus increasing the time females are outside of the roost and vulnerable to predation. (3) Disturbance can cause outright death of young that lose their roost-hold and fall to the cave floor. (4) Maternity aggregations often result in thermoregulatory benefits. Clustering bats gain thermal benefits from being surrounded by other warm bodies. However, individuals also may receive thermal benefit because the accumulated body heat of all individuals present serves to raise temperatures within the roost area. Therefore, if the size of a colony decreases, the accumulated thermal advantages to the individuals in that colony may likewise decrease, and it may become energetically less advantageous, or perhaps even energetically impossible for females to raise pups in that roost. Thus, there may be a "threshold," where after a population reaches a certain lower size, roost temperatures cannot be raised sufficiently for rearing young and that roost must be abandoned as a maternity site.

Problems caused by disturbing hibernating bats also relate to their energy requirements. During winter, temperate zone bats go long periods without eating, and allow their body temperatures to drop, often to near freezing. The energy reserves that bats accumulate prior to hibernation are often close to what is needed to survive the winter. Disturbance during hibernation may cause bats to arouse prematurely, elevating their body temperatures and utilizing stored energy reserves, which should not be spared. The bats may go back into torpor after the disturbance, but then they may not have sufficient energy to survive the rest of winter. This may not be apparent to the person causing the disturbance.

Roost site disturbance also can seriously impact bats, which do not form large aggregations. This is undoubtedly so for many tropical bats, which roost in mature, hollow trees, which are being cut as more tropical forest goes into cultivation. To my knowledge, we don't know the trajectories of populations of any of these tree-roosting bats. As an example closer to home, it seems probable that the decline of the Indiana bat may be attributed in part to the loss of roost sites other than caves. Indiana bats hibernate in caves and there is no question that disturbance of hibernacula has contributed to their decline. However, in the midwestern United States, several large hibernacula of Indiana bats are protected from disturbance, yet these cave populations continue to decline (Clawson, 1987). We can only speculate on the reasons for this continued decline, and this again points to our ignorance. However, while Indiana bats hibernate in caves, in summer they roost and give birth in tree hollows and under the loose bark of trees. The loss of tree roosts may very well be a serious factor in the continuing decline of the Indiana bat in the Midwest. That the decline of the Indiana bat may be due in part to factors outside of their hibernacula in no way implies that disturbances at hibernacula are unimportant. Rather, it emphasizes the importance of protecting hibernacula so as not to add additional stresses to these populations.

Habitat Degradation Outside of Roosts

Man also has impacted negatively on bat populations by causing habitat alteration and degradation outside of their roost sites. For example, two species of North American bats on the red list are endangered, in large part, because man's activities have decreased their food resources. Both species of long-nosed bats inhabit desert regions of the Southwestern U.S. and Mexico, and both feed on the nectar and pollen of desert flowers (Wilson, 1985a,b; Anonymous, 1988). Wild agave is a major food source of both species. Wild agaves have been severely reduced because they interfere with cattle grazing and because they are harvested by moonshiners for making tequila. Although long-nosed bat populations also have been affected by interference with their cave roosts (Wilson, 1985a, Anonymous, 1988), the reduction in agaves is clearly important in their decline. Long-nosed bats also are major pollinators of both organ pipe and giant Saguaro cacti. The well-known decline of these cacti also is evidently directly attributable to the decline of long-nosed bats (Wilson, 1985a,b; Anonymous, 1988).

The Role of Pesticides

Pesticides used to control insect populations have negatively impacted populations of many bats (Clark, 1981). Two effects seem likely; (1) direct poisoning of bats, and (2) reduction in the resource base of bats which eat insects. At present, we know little regarding the effects caused by pesticides reducing the insect prey of bats. However, direct poisoning by DDT (now banned for use in the U.S.) and other organochlorine pesticides has been widely implicated in the decline of many bats (reviewed in Clark, 1981). While pesticide poisoning clearly has caused the decline of local populations of many bats, there has been a tendency to over-emphasize the importance of pesticide poisoning as one of the major factors in the decline of bats (Clark, 1981; McCracken, 1986). In fact, I question whether the general decline of any bat species can be attributed solely or even largely to the toxic effects of pesticides. This is not to exonerate pesticides, but rather to point more strongly at what are the major causes of bat population declines: i.e., roost site interference and the reduction of resources. I suspect that overemphasis of the importance of pesticide poisoning serves to draw attention away from these other causes.

How do I justify these statements? First, the belief that bats are unusually sensitive to pesticides dates from an early paper which purported to document their extreme susceptibility to DDT poisoning (Luckens and Davis, 1964). It is now established that the susceptibility of bats to DDT is in general no greater than that of other similar sized animals (Clark, 1981). Second, there have been many observed, dramatic declines of bat populations that have been attributed to DDT poisoning, without strong data to support these attributions. The most spectacular of these occurred in Eagle Creek Cave, Arizona, where the population of Mexican free-tailed bats declined from an estimated 30 million to an estimated 30 thousand individuals. While other toxins, such as methyl parathion (Clark, 1986), may have contributed to this decline, and human disturbance also seems a likely culprit, there is no evidence that DDT poisoning was a major cause of the loss of this population (Clark, 198 1; McCracken, 1986). Again, this is not to say that DDT or other toxins have not directly killed bats. It is well documented, for example, that young Mexican free-tailed bats from Carlsbad Caverns have had potentially lethal pesticide concentrations. However, this is evidently a local problem that has not been reported in other colonies of this species (Geluso et al., 1981). Finally, a natural "experiment" on DDT poisoning has been done for us. In the early 1960's, Cave Springs Cave in Alabama housed a major maternity colony of gray bats. This cave was heavily disturbed by humans and by the early 1970's all its gray bats were gone. However, Cave Springs Cave was then protected by fencing and its gray bat population began recovering to the point that it now houses an estimated 50,000 individuals. Cave Springs Cave is near a former DDT processing plant which also was a major toxic waste dumping site. At present, the bats and bat guano within this cave are substantially polluted with a variety of toxic chemicals including DDE (derived from DDT) and PCB's. Although, this bat colony experiences occasional dieoffs resulting from these toxins, the colony has nonetheless continued to recover in the face of these pollutants; this recovery dating from when the cave was protected (Tuttle, 1986).

Red Caves/Green Caves

From what we know about human-caused impacts on bat populations, there is little question that roost-site disturbance, vandalism, and habitat destruction have had severe effects. This is particularly so for cave-dwelling bats. My opinion that these impacts are likely to have had greater negative effects than pesticide poisoning is shared by other researchers (Clark, 1981; Tuttle, 1985). People who visit caves, both professionally or for sport, must be acutely aware of the potential damage they can do to resident bats. To minimize such damage, we should recognize that there are caves ("Red Caves") which should not be visited by humans at any time, or only visited during certain times of the year, and other caves ("Green Caves") which are not important to bats or other threatened species and can be open to visitation. Bats select caves as hibernacula or as maternity sites because they fulfill very specific requirements. Fulfilling these requirements depends on cave structure, air circulation patterns, temperature profiles, and the cave's location relative to foraging sites (Tuttle and Stevenson, 1978; Tuttle, 1979). Because the requirements of bats are highly specific, those caves which do fulfill them will be relatively rare and may be absolutely essential to the bats. There may simply be no acceptable, alternative roost sites available. These caves must be placed on our red list. Conversely, most caves will not satisfy these requirements and will not be important as bat roosts. These can be placed on a green list. It seems likely that the vast majority of caves would go on the green list. For example, less than 5% of caves surveyed in the southeastern U.S. were found to be physically suitable as gray bat maternity or hibernating roost sites (Tuttle, 1979).

A major problem, of course, will be deciding whether a cave belongs on the green versus the red list. One obvious criterion is that major hibernacula and maternity roosts of threatened or declining bats should be red-listed, at least during the seasons when bats are present. Conversely, caves which are not occupied by bats and for which there is no evidence of prior occupancy should be green-listed. But, obviously, judgments will have to be made, often with only limited information. For example, it can be argued that historically important roosting sites that are now abandoned should be red-listed, at least temporarily, in the hope that they will be reoccupied. It also can be argued that caves with only small colonies should be red-listed, possibly for gene pool conservation, or that caves important to transients during seasonal movements should be red-listed during the relevant seasons. On the other hand, there may be no harm in green-listing some cave roosts of abundant, widely dispersed species (e.g., those of eastern pipistrelles), particularly if those caves have inherent interest to cavers.

Although listing caves for no or restricted access because of their use by roosting bats is likely to be controversial, these listings are necessary to preserve bat populations. Individuals who explore caves for sport or scientific study have a high probability of encountering roosting bats. The NSS as the largest single organization of cavers has the opportunity to provide education regarding potential impacts on bat populations to large numbers of people who are likely to encounter bats. In addition, cavers often have knowledge of bat roosting sites, and this knowledge is essential to informed and responsible listing of caves on red or green lists. Opportunities are abundant for cavers to cooperate with state, national, and private conservation agencies in identifying and preserving sensitive cave habitat. Several NSS grottos have taken the initiative themselves to construct, or are in the process of constructing, red and green lists of caves. These people should be supported in their efforts. Efforts to construct these lists should be expanded.

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Thermal Requirements During Hibernation

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Abstract

We monitored temperatures for up to 2 years at 15 of the most important sites for hibernation of Indiana bats (*Myotis sodalis*). Comparison of temperatures at successful and unsuccessful sites revealed that populations occupying roosts with midwinter (December–February) temperatures of 3.0–7.2°C increased by 97,339 bats over the past 20 years, whereas populations hibernating at temperatures outside this range decreased by 185,117 animals. In all but the northernmost range of Indiana bats, caves and mines required for successful hibernation must provide chimney-effect air flow between at least two entrances, store sufficient cold air to meet the bats' hibernation needs, and buffer the internal environment to minimize risk of freezing. Protection of caves and mines providing these exceptional characteristics and restoration of appropriate temperatures in altered sites is essential for recovery of the Indiana bat.

Key words: caves, hibernation, Indiana bat, management, mines, *Myotis sodalis*, population, temperature

Introduction

In the early 1800s, the Indiana bat (*Myotis sodalis*) ranked as one of North America's most abundant mammals, with possibly millions occurring in single caves (Silliman et al. 1851, Tuttle 1997). Nonetheless, by 1980, fewer than 700,000 bats remained, and size of the population fell to 382,000 bats by 2001 (Clawson 2002). The greatest losses occurred in discrete, unrelated episodes that rendered overwintering caves no longer suitable for hibernation, mostly due to reductions in size of a cave's entrance, which ultimately raised internal temperatures (Humphrey 1978). Increases of as little as 2°C resulted in severe reduction of a cave's population (Tuttle 1977). Humphrey (1978), however, concluded that such losses were reversible, because restoration of acceptable temperatures led to prompt recovery at some sites.

Nevertheless, specific temperatures required by Indiana bats during hibernation are not understood completely. Our purpose is to compare annual patterns of temperature in hibernacula where populations of Indiana bats have been successful with temperatures in hibernacula where populations are declining. In addition, we indicate correctable deficiencies at important sites of current and past use and suggest characteristics for evaluating roosts for protection or restoration.

Methods

We evaluated patterns of temperature at 15 of the most important, current and past, hibernating sites of Indiana bats, in caves and mines of Illinois, Indiana, Kentucky, Missouri, Tennessee, and Virginia (Fig. 1). To monitor temperature, we used 60 dataloggers (Model Hobo Pro Temp–RH, Onset Computer Corporation, Pocasset, Massachusetts) in 1998 and 58 instruments in 1999. A datalogger was installed within each hibernaculum, at each site that was favored by hibernating Indiana bats, either currently or in the past. Another datalogger was positioned outside each cave or mine to monitor external conditions, except at the Magazine Mine. All instruments recorded data at 3-h intervals. Although dataloggers recorded temperature and relative humidity, we found no evidence of an effect of humidity beyond that indicated by temperature, so humidity was not included in our analyses.

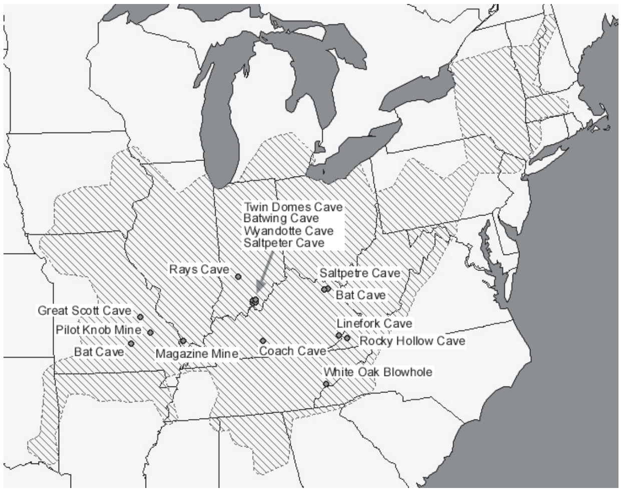

Figure 1. Range of the Indiana bat and location of hibernacula in which we monitored temperature.

Most dataloggers were installed in July 1998 and downloaded in July, August, or September 1999 and again in 2000. When dataloggers were installed in 1998 (except at the Magazine Mine), temperatures of the air and wall of the cave also were measured at each roosting site, using a portable digital thermometer (Model 2300-PNC5, IMC Instruments, Inc., Menomonee Falls, Wisconsin) that was recalibrated prior to each field trip. Temperatures indicated by the dataloggers at time of installation differed, on average, by less than 0.3 °C (range = 0.0–0.4°C; *n* = 31 sites) from wall At time of downloading in 1999, a sample of 10 dataloggers from five caves provided readings that again averaged within 0.3°C (0.0–0.7°C) of those obtained with the digital thermometer. In addition, controlled tests of random batches of dataloggers yielded similar average variation (0.3°C).

We also evaluated ability of each hibernaculum to buffer the internal environment against changes in the external environment, using an index of temperature variability:

$$V = (T_{\text{max-roost}} - T_{\text{min-roost}})/(T_{\text{max-surface}} - T_{\text{min-surface}}),$$

where T represents maximum or minimum temperature recorded at the roost or outside the hibernaculum, as indicated by the subscripts. A small value of *V* indicates a stable internal environment that varies little with changing external conditions; a large value of *V* indicates a less stable, more variable, internal environment.

Results

In both 1998–1999 and 1999–2000, 43 dataloggers recorded temperatures year-round. Although 17 loggers failed the 1st year and 15 malfunctioned during the 2nd year, only two of 32 malfunctions were caused by operator error. The others were due to problems such as moisture bypassing past dirty seals, moisture entering through cracked housings, or an increased internal

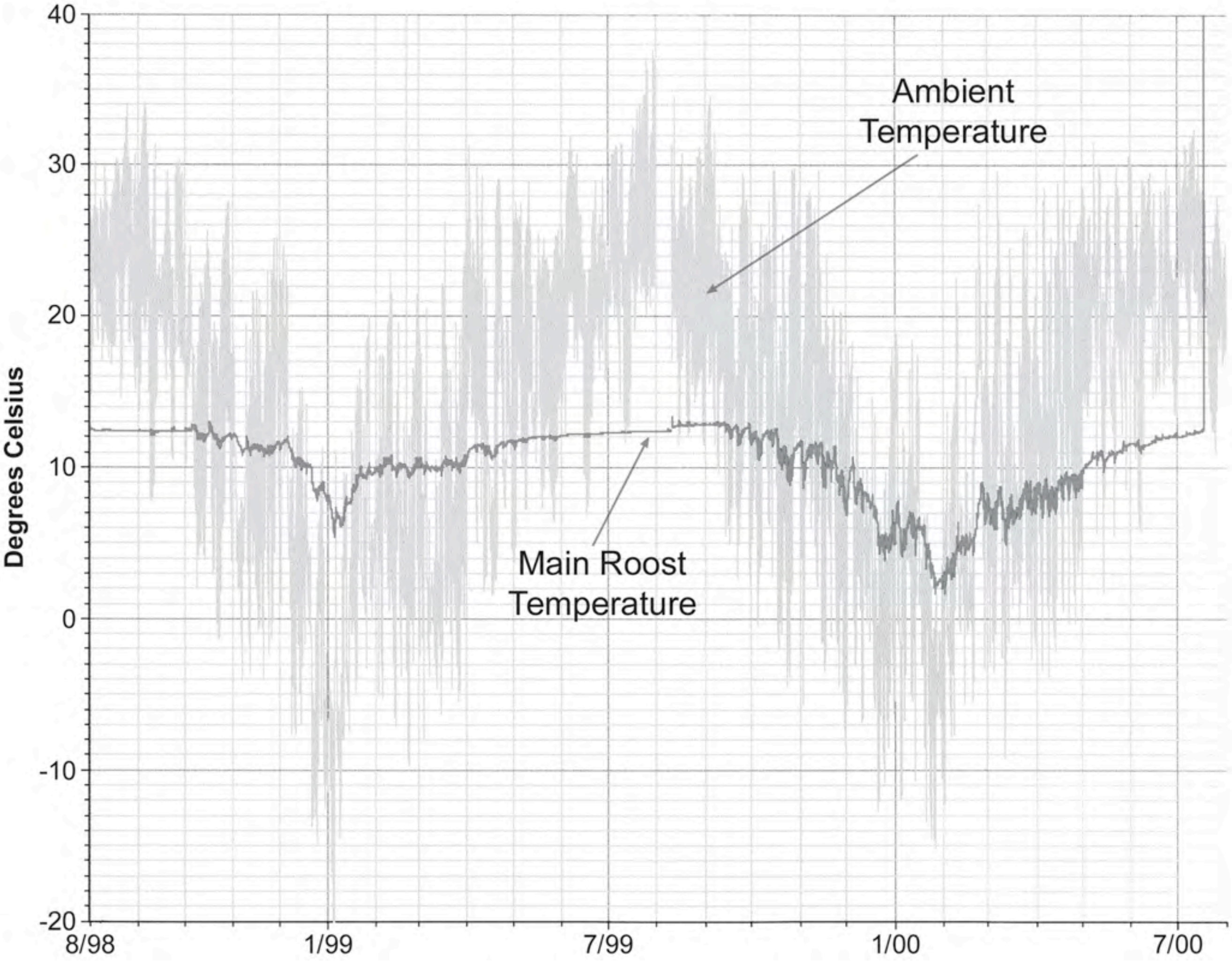

Figure 2. External ambient temperatures and tempearature at the main hibernation site in Great Scott Cave, Missouri before and after opening a blocked entrance in September 1999.

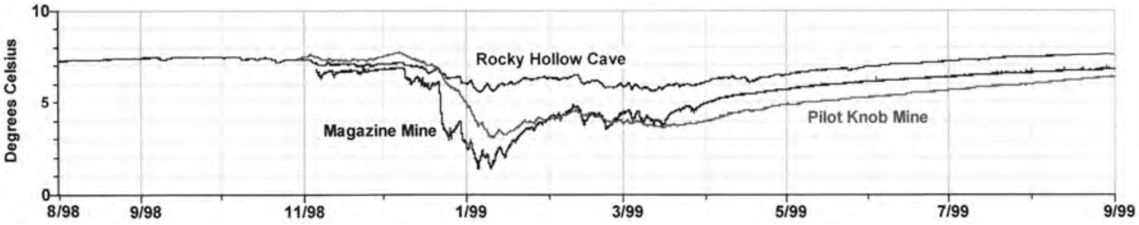

Figure 3. Annual profiles of temperature for unusually successful hibernacula of the Indiana bat.

resistance that developed within the lithium batteries initially supplied by the manufacturer. Nevertheless, most failures occurred after the hibernation season, thus minimizing loss of data.

Overall, temperatures at the 15 hibernacula in midwinter (December–February) were similar between years (Tables 1–4). Average mean temperature within hibernacula was 6.8°C in 1998–1999 and 6.5°C in 1999– 2000, while average mean surface temperatures were 3.5°C and 3.0°C for the same periods. Midwinter means at individual hibernacula varied by less than 1°C between years at all locations, except Great Scott Cave. In addition, changes between years in mean midwinter temperature inside hibernacula always were in the same direction as changes on the surface, again with the exception of Great Scott Cave. Temperature in Great Scott Cave decreased by 3.6°C between years, despite an increase of 0.4°C in surface temperature, following reopening of a previously blocked entrance (Fig. 2). Given the similarity in temperatures between years, we typically restrict further discussion to data obtained in the 1st year for simplicity.

Individual caves differed by almost a factor of eight in ability to buffer changes in external temperature, as indicated by the index of variability. In December–February 1998–1999, the index of variability for Rocky Hollow and Wyandotte caves was 0.05; White Oak Blowhole, 0.06; Saltpeter Cave, 0.08; Saltpetre Cave, 0.09; Bat Cave, Kentucky, 0.10; Pilot Knob Mine, 0.11; Linefork Cave, 0.12; Great Scott Cave, 0.13; Twin Domes Cave, 0.15; Ray's Cave, 0.16; Coach Cave, 0.17; and Bat Cave, Missouri, 0.38. Dataloggers failed during the first winter at Batwing Cave, but the comparable index in 2000 was 0.02. External temperatures were not monitored at the Magazine Mine, so we could not calculate an index for it. Annual temperature profiles for some caves of low-to-medium variability (medium-to-high stability) are shown in Figure 3.

We also examined roost temperatures and changes in population size at seven caves and mines that we monitored, using data on temperature and population provided by the Indiana Bat Recovery Team (Table 5). Hibernacula where populations grew provided roost temperatures of 3.0–7.2°C, whereas populations fell at hibernacula with temperatures outside that range. At Great Scott Cave, the population increased by 22,800 bats between 1976 and 1979, when internal temperatures averaged 4.8°C, but declined by 46,625 bats between 1980 and 1997, when temperatures averaged 8.1°C, following closure of an entrance.

Discussion

The ideal situation—Caves that historically sheltered the largest populations of hibernating Indiana bats, without exception, were those that provided the largest volumes and structural diversity, ensuring the most stable internal temperatures, over the widest ranges of external temperature, with the least likelihood of freezing. Such caves also provide chimney-effect airflow, typically through multiple entrances, and trap and store cool winter air in low areas (Tuttle and Stevenson 1978). Within such caves, hibernating Indiana bats prefer temperatures of 3–6°C in midwinter (Hall 1962, Henshaw and Folk 1966). Although metabolism of hibernating bats is lowest at temperatures slightly above 0°C, Indiana bats are forced to increase production of metabolic heat or arouse from torpor as temperatures fall to 0°C and below. They also arouse in response to abrupt changes in ambient temperature (Davis and Reite 1967, Henshaw and Folk 1966). Thus, roosts with the most stable temperatures should result in fewest arousals, thereby minimizing energy expenditure (Thomas et al. 1990).

Recent and historic populations of hibernating Indiana bats support these conclusions. For example, Mammoth Cave is the world's largest and most complex cave system, with a length of 571 km. Staining left on walls and ceilings of Mammoth Cave (Toomey et al. 2002) suggests that this cave once sheltered the largest hibernating population of Indiana bats, conservatively estimated at ca. 10 million animals (Tuttle 1997). In addition, comparison of other populations of Indiana bats that remained stable or increased with those that declined over the past 20 years (Table 5) strongly implies that inappropriate temperatures at hibernating sites are a primary cause of decline, as suggested by Humphrey (1978).

We believe that temperature profiles documented for Rocky Hollow Cave, Magazine Mine, and Pilot Knob Mine (Fig. 3) most closely approximate ideal hibernating conditions for the Indiana bat. Through the entire annual cycle (not just midwinter) of 1998–1999, Rocky Hollow Cave remained at 5.6–7.6°C; Magazine Mine, at 1.4– 6.9°C; and Pilot Knob Mine, at 3.1–7.7°C. Such stability within the Indiana bat's preferred range of hibernating temperatures is achieved through the buffering effects of very large volume.

Not surprisingly, these three sites have histories of extraordinary success at supporting hibernating populations of Indiana bats. Rocky Hollow Cave contained one of North America's largest populations prior to the onset of intense human disturbance, and the population of Indiana bats at the Magazine Mine grew to nearly 15,000 bats in only a few years after the mine closed (Kath 2002). Pilot Knob Mine also rapidly attracted a hibernating population of at least 100,000 Indiana bats soon after it became available, though subsequent collapse has prevented further censuses (Clawson 2002).

Effects of restoring airflow—Comparison of annual cycles before and after reopening a blocked entrance illustrates that management efforts can restore unacceptably altered roost temperatures. The population at Great Scott Cave (Fig. 2, Tables 1, 3, and 5) was growing prior to blockage of its second entrance in summer 1978, after which roost temperature rose by at least 3.3°C and the population decreased by 80%. After the entrance was reopened in September 1999, average internal temperatures decreased by 3.6°C, even though outside temperatures averaged 0.4°C higher in winter 1999–2000 than in the previous winter. Consequently, temperatures at the roost were within the ideal, 3–6°C range on 61 days during 1999–2000, greatly improving from only 1 day in the entire previous hibernating season.

We anticipate that the population at Great Scott Cave, with return of more appropriate hibernating temperatures, will again begin to grow, as happened at Wyandotte Cave. The entrance to this cave was mostly blocked by a masonry wall that was removed in 1977 (see fig. 4 in Currie 2002). Afterwards, temperatures in Wyandotte Cave decreased, and the population grew by 90% (Johnson et al. 2002, Richter et al. 1993). Nevertheless, temperatures in Wyandotte Cave (Tables 1 and 3) remain too high, in our opinion, to permit reestablishment of a historic-sized population of Indiana bats.

Staining on the walls and ceiling in Wyandotte Cave suggest a much larger past population that possibly numbered in the millions. The current population, despite encouraging recovery, is no more than a small fraction of its presumed former size. Results of temperature monitoring strongly suggest that this population could be expanded substantially with further lowering of internal temperature. Stability of internal temperature in Wyandotte Cave already is similar to that of Rocky Hollow Cave ($V = 0.05$ for both; Tables 1 and 3), probably contributing greatly to the level of recovery already achieved at Wyandotte Cave. An additional decrease of 5°C would further enable large numbers of bats to hibernate in traditional roosts beyond areas now disturbed by commercial tours in winter (Johnson et al. 2002), probably permitting even greater recovery.

Are we protecting marginal sites?—Knowledge of energetics during hibernation, historical conditions chosen by the largest hibernating populations, and temperature profiles that we provide, strongly suggest that a large proportion of currently protected sites are marginal, at best, in terms of long-term survival of the Indiana bat. To understand better what is required to rebuild historically large populations, one must consider the impact of known factors on the species' annual energy budget. When inappropriate temperatures or rapid fluctuations in temperature cause arousal and increase the cost of hibernation, less energy remains for surviving unusually stressful winters or unpredictable weather during spring migration.

Summer nursery roosts that provide marginally warm temperatures or that are distant from good feeding habitat result in extra energy expenditure and slower growth of young in insectivorous bats (Tuttle 1975, 1976a). Late fledging leads to low body mass in autumn (Humphrey et al. 1977), and this can make the cost of long-distance migration, already an important mortality factor, prohibitive (Tuttle 1975, 1976b; Tuttle and Stevenson 1977). Hibernation sites sheltering the largest populations of Indiana bats require the longest average migrations from suitable summer habitats, because these hibernacula serve animals from the largest geographic areas. Also, long autumn migrations may require as much energy as an entire winter of hibernation (Tuttle 1976b), so it seems that the very substantial costs of marginal hibernating conditions cannot be borne by bats having to make long migrations.

When hibernating conditions deteriorate and large populations decline due to significant disturbance and/or altered roost temperatures, a small proportion of the population usually survives in the now-marginal hibernaculum. Size of this proportion undoubtedly is determined by the amount of added costs that are imposed by the disturbance or altered microclimate during hibernation. In contrast, the relatively few bats that summer in more ideal conditions near the hibernaculum avoid the costs of autumn and spring migration, thereby conserving substantial energy that can be spent on hibernation, as well as on surviving unpredictable spring weather. Those that use less-than optimal summer habitat or migrate long distances may not have sufficient energy available to meet the new demands and may succumb over winter.

Also, some small populations that continue using marginal caves appear stable only because of annual immigration of bats from more successful populations at more ideal hibernacula. For example, ca. 1,000–2,000 Indiana bats hibernated in Wyandotte Cave each winter before 1978, i.e., before removal of the wall that elevated winter temperatures. Richter et al. (1993), based on body-mass dynamics, estimated that survivorship of hibernating individuals at this time was not high enough to sustain the population and that apparent stability of the population at Wyandotte Cave actually was due to an influx of bats each year from other hibernacula. Their data suggested annual mortality rates of 45% during hibernation in Wyandotte Cave, compared with 1% in a cooler hibernaculum, Twin Domes Cave, which was located nearby.

Buffering climatic extremes—Although suitable roost-temperature profiles are important, a roost's ability to buffer climatic extremes is also critical. For example, our temperature profiles from Bat Cave, in Missouri, illustrate that it is a mortality trap. Although Bat Cave provides ideal temperatures in autumn, it often falls well below freezing in winter, and Indiana bats attracted to this cave in autumn risk freezing to death before spring (Tables 1 and 3).

Our data suggest that some caves with currently stable or growing populations also are mortality traps that more seriously threaten survival of the species than do sites like Bat Cave, Missouri. Small, simple sites, such as Ray's Cave and Twin Domes Cave, may provide ideal internal temperatures over long-enough periods that a large population develops between lethal, external extremes in temperature. Range of internal temperatures at these two caves, during December– February 1998–1999, was 7.8 and 6.7°C, respectively, compared with nearby Wyandotte Cave, with a range of 2.3°C (Table 1). By comparing indices of temperature variability at these sites, we see that Ray's (V = 0.16) and Twin Domes (0.15) caves are 3.2 and 3.0 times less stable than Wyandotte Cave (0.05), which probably was the traditional, primary hibernaculum for the region.

Differences in stability were even more pronounced during January, when temperatures within Ray's and Twin Domes caves were 4.3 and 5.0 times less stable, respectively. Average surface temperature for January 1999 at Ray's Cave was 0.8°C higher than in 2000, and consequently, internal temperatures were 0.7°C higher. In contrast, a 1.3°C external rise at Wyandotte Cave raised roost temperatures only 0.2°C. Mean temperatures for January over the past 100 years in that area of Indiana ranged from 4.9°C, in 1950, to -10.2°C, in 1977, a difference of 15.1°C (http://www.wrcc.dri.edu/spi/divplot2map.html, South Central Indiana Division). This large difference among years suggests that sites like Ray's and Twin Domes caves are extremely vulnerable over several decades, and emphasizes the importance of restoration efforts at former key bastions of survival, such as Wyandotte, Rocky Hollow, and Mammoth caves (e.g., Toomey et al. 2002), that are more stable.

Comments on other hibernacula—Efforts to restore temperature are also in progress at Coach Cave, the former home of at least 100,000 Indiana bats. Internal temperatures appear suitable, but fluctuations in December–February 1999–2000 (Table 3) are still 3.2 and 3.5 times greater than those at Wyandotte and Rocky Hollow caves, respectively. Such instability, along with rapid airflow through roosting areas, may explain current failures to restore the population at this site (Currie 2002). Cooler temperatures and airflow may be due to an artificial entrance that remains open, although past enlargement of passages for use by tourists also may be a factor. This is definitely a correctable problem that should receive high priority.

Linefork Cave is another site of a large past population, and it appears to have an adequate temperature profile to justify a population larger than it currently has. We suspect that disturbance remains an issue here. The cave is popular with cavers, and an entrance (Dungeon Entrance) that leads through the primary area of past use by bats, remains unprotected.

Our data suggest that Bat Cave, Kentucky, is a site of secondary importance, compared with nearby Saltpetre Cave, which is another apparently essential hibernaculum of the past. Staining indicates a historic population of perhaps a million Indiana bats at Saltpetre Cave prior to extensive mining of nitrate during the War of 1812, followed by use of the cave for commercial tours. Remnants of its population of Indiana bats apparently reside in Bat Cave. Physical alterations resulting from mining and commercialization probably cause temperatures to be slightly higher than the optimum for Indiana bats (Tables 1 and 3), but Indiana bats still should prefer Saltpetre Cave to Bat Cave because of Saltpetre's lower and more stable internal temperatures ($V = 0.08$ for Saltpetre Cave and $V = 0.10$ for Bat Cave; Tables 1 and 3). A cessation of commercial tours during hibernation, beginning in winter 1998–1999, likely is responsible for an increase in population, from 475 bats in 1999 to 1,225 bats in 2001. Research on how best to restore ideal temperatures is underway, and we believe this site offers excellent potential for further recovery.

Conclusions

Available evidence strongly suggests that protection of hibernacula from disturbance by humans is critically important, yet it is insufficient if not accompanied by restoration of appropriate temperatures. All populations of which we are aware, which are not jeopardized by inappropriate temperatures, disturbance, or flooding, are stable or growing, indicating that problems during hibernation likely are a key factor in the species' overall decline. Degradation of summer feeding and roosting habitats is probably a contributing factor in decline of Indiana bats. Nevertheless, restoration of required temperatures and protection of essential hibernating sites is vital to recovery, and we agree with Humphrey (1978) that losses are reversible through restoration.

We suggest that resource managers make immediate efforts to identify and correct deficiencies in temperature at major caves of past or current use. In addition, we suggest that abandoned mines now provide some of the best options for large-scale restoration of the population, due to the enormous size of some mines, the resulting stability of temperature, and the multiple entrances to many mines that cause chimney-effect airflow (e.g., Kath 2002). Furthermore, we emphasize that significant hibernacula of the past may not be occupied currently and that other sites of historic use remain undiscovered. Such sites easily are identified by a combination of temperature, roost staining, and a structure that traps cold air; these caves may need nothing more than protection from disturbance or removal of material blocking the entrance to restore large populations of Indiana bats. Finally, all cave entrances essential to proper cooling of key hibernating sites must be identified and protected from inadvertent closures, including those that may occur naturally. Most caves that once served as bastions of survival for Indiana bats already have been lost to commercialization or closure, and those that remain require careful management if this species is to recover.

Acknowledgments

We congratulate the U.S. Forest Service and Kentucky's Carter Caves State Resort Park on their recent leadership in protecting Rocky Hollow and Saltpetre caves, respectively. We also recognize Indiana's Wyandotte Caves State Recreation Area for substantial progress at restoration of Wyandotte Cave. Primary funding for this project was provided by the U.S. Fish and Wildlife Service, U.S. Forest Service, U.S. Environmental Protection Agency, National Fish and Wildlife Foundation, Bass Foundation, and David and Lucile Packard Foundation. We are deeply indebted to the following individuals for assistance in the past 3 years: S. Amelon, S. Beam, V. Brack, E. Britzke, R. Clawson, R. Currie, Ja. DePew, Je. DePew, K. Dunlap, W. Elliott, R. Gleitz, M. Gumbert, C. Hobson, F. Johnson, S. Johnson, J. Kath, D. Kemper, J. MacGregor, N. Michie, P. Moosman, L. Nutt, B. Palmer-Ball, S. Plummer, S. Reis, R. Reynolds, B. Schwartz, M. Spanel, J. Thomison, N. Thomison, J. Tierney, T. Wethington, and S. Widowski. Additional dataloggers and field support were provided by George Washington–Jefferson National Forests, Great Smoky Mountains National Park, Illinois Department of Natural Resources, Indiana Department of Natural Resources, Kentucky Nature Preserves, Kentucky State Parks, Missouri Department of Conservation, Park Mammoth Resort, Shawnee National Forest, and Wyandotte Caves State Recreation Area. We also thank numerous private landowners and agencies for allowing access to their caves and mines and for supporting recovery efforts for the Indiana bat.

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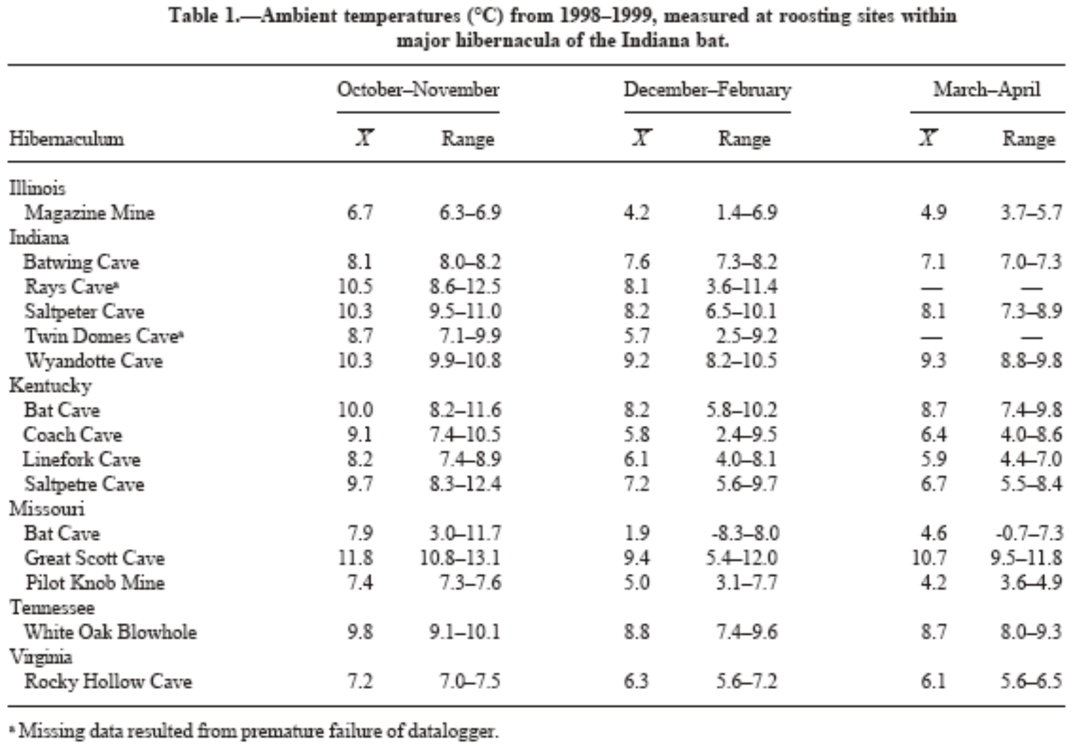

Table 1.—Ambient temperatures (°C) from 1998–1999, measured at roosting sites within major hibernacula of the Indiana bat.

	October–November		December–February		March–April	
Hibernaculum	$\overline{X}$	Range	$\overline{X}$	Range	$\overline{X}$	Range
Illinois						
Magazine Mine	6.7	6.3–6.9	4.2	1.4–6.9	4.9	3.7–5.7
Indiana						
Batwing Cave	8.1	8.0–8.2	7.6	7.3–8.2	7.1	7.0–7.3
Rays Cave[a]	10.5	8.6–12.5	8.1	3.6–11.4	—	—
Saltpeter Cave	10.3	9.5–11.0	8.2	6.5–10.1	8.1	7.3–8.9
Twin Domes Cave[a]	8.7	7.1–9.9	5.7	2.5–9.2	—	—
Wyandotte Cave	10.3	9.9–10.8	9.2	8.2–10.5	9.3	8.8–9.8
Kentucky						
Bat Cave	10.0	8.2–11.6	8.2	5.8–10.2	8.7	7.4–9.8
Coach Cave	9.1	7.4–10.5	5.8	2.4–9.5	6.4	4.0–8.6
Linefork Cave	8.2	7.4–8.9	6.1	4.0–8.1	5.9	4.4–7.0
Saltpetre Cave	9.7	8.3–12.4	7.2	5.6–9.7	6.7	5.5–8.4
Missouri						
Bat Cave	7.9	3.0–11.7	1.9	-8.3–8.0	4.6	-0.7–7.3
Great Scott Cave	11.8	10.8–13.1	9.4	5.4–12.0	10.7	9.5–11.8
Pilot Knob Mine	7.4	7.3–7.6	5.0	3.1–7.7	4.2	3.6–4.9
Tennessee						
White Oak Blowhole	9.8	9.1–10.1	8.8	7.4–9.6	8.7	8.0–9.3
Virginia						
Rocky Hollow Cave	7.2	7.0–7.5	6.3	5.6–7.2	6.1	5.6–6.5

[a] Missing data resulted from premature failure of datalogger.

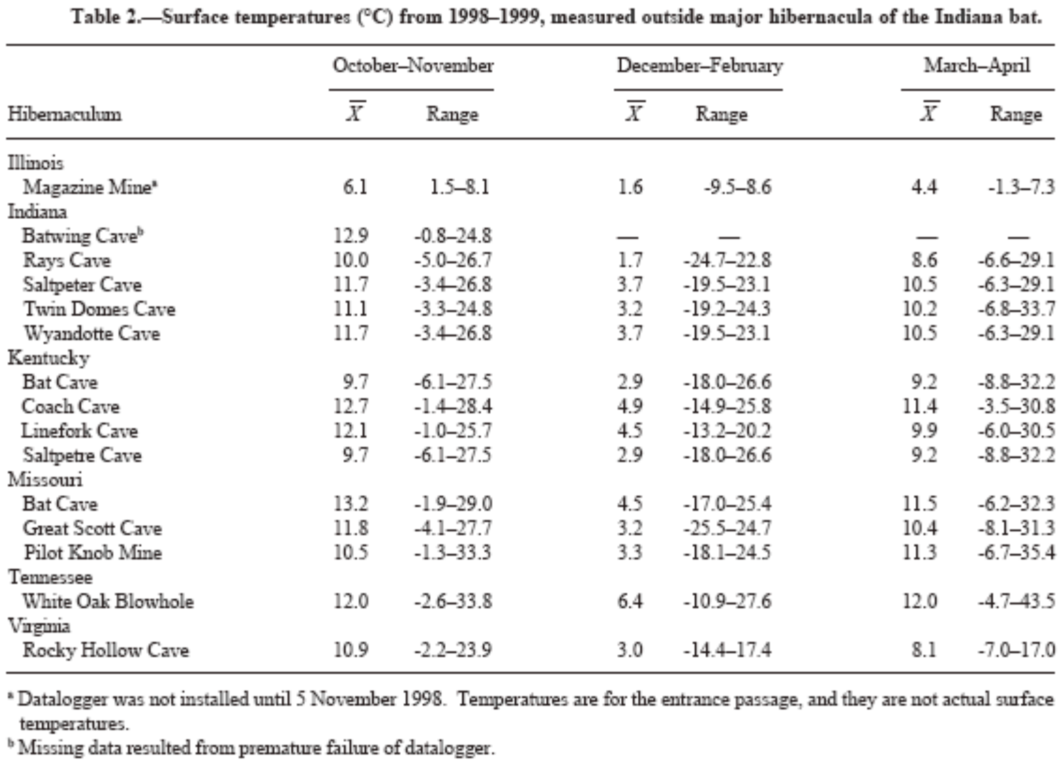

Table 2.—Surface temperatures (°C) from 1998–1999, measured outside major hibernacula of the Indiana bat.

	October–November		December–February		March–April	
Hibernaculum	$\overline{X}$	Range	$\overline{X}$	Range	$\overline{X}$	Range
Illinois						
Magazine Mine[a]	6.1	1.5–8.1	1.6	-9.5–8.6	4.4	-1.3–7.3
Indiana						
Batwing Cave[b]	12.9	-0.8–24.8	—	—	—	—
Rays Cave	10.0	-5.0–26.7	1.7	-24.7–22.8	8.6	-6.6–29.1
Saltpeter Cave	11.7	-3.4–26.8	3.7	-19.5–23.1	10.5	-6.3–29.1
Twin Domes Cave	11.1	-3.3–24.8	3.2	-19.2–24.3	10.2	-6.8–33.7
Wyandotte Cave	11.7	-3.4–26.8	3.7	-19.5–23.1	10.5	-6.3–29.1
Kentucky						
Bat Cave	9.7	-6.1–27.5	2.9	-18.0–26.6	9.2	-8.8–32.2
Coach Cave	12.7	-1.4–28.4	4.9	-14.9–25.8	11.4	-3.5–30.8
Linefork Cave	12.1	-1.0–25.7	4.5	-13.2–20.2	9.9	-6.0–30.5
Saltpetre Cave	9.7	-6.1–27.5	2.9	-18.0–26.6	9.2	-8.8–32.2
Missouri						
Bat Cave	13.2	-1.9–29.0	4.5	-17.0–25.4	11.5	-6.2–32.3
Great Scott Cave	11.8	-4.1–27.7	3.2	-25.5–24.7	10.4	-8.1–31.3
Pilot Knob Mine	10.5	-1.3–33.3	3.3	-18.1–24.5	11.3	-6.7–35.4
Tennessee						
White Oak Blowhole	12.0	-2.6–33.8	6.4	-10.9–27.6	12.0	-4.7–43.5
Virginia						
Rocky Hollow Cave	10.9	-2.2–23.9	3.0	-14.4–17.4	8.1	-7.0–17.0

[a] Datalogger was not installed until 5 November 1998. Temperatures are for the entrance passage, and they are not actual surface temperatures.

[b] Missing data resulted from premature failure of datalogger.

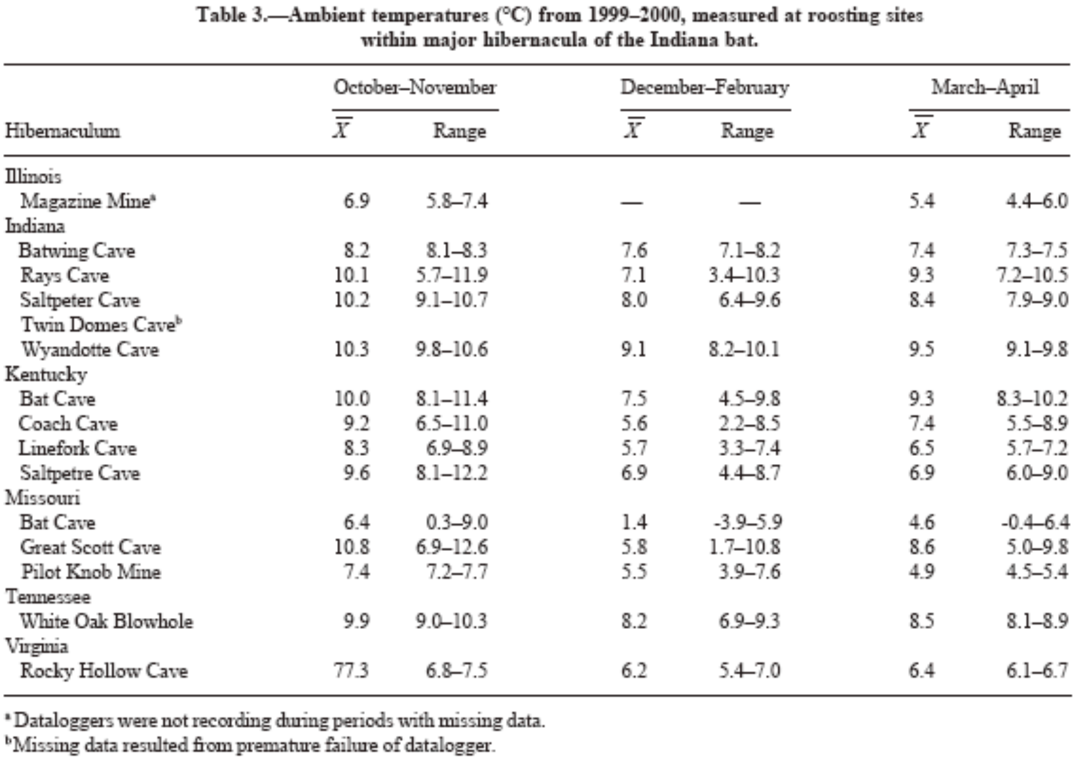

Table 3.—Ambient temperatures (°C) from 1999–2000, measured at roosting sites within major hibernacula of the Indiana bat.

Hibernaculum	October–November $\overline{X}$	October–November Range	December–February $\overline{X}$	December–February Range	March–April $\overline{X}$	March–April Range
Illinois						
Magazine Mine[a]	6.9	5.8–7.4	—	—	5.4	4.4–6.0
Indiana						
Batwing Cave	8.2	8.1–8.3	7.6	7.1–8.2	7.4	7.3–7.5
Rays Cave	10.1	5.7–11.9	7.1	3.4–10.3	9.3	7.2–10.5
Saltpeter Cave	10.2	9.1–10.7	8.0	6.4–9.6	8.4	7.9–9.0
Twin Domes Cave[b]						
Wyandotte Cave	10.3	9.8–10.6	9.1	8.2–10.1	9.5	9.1–9.8
Kentucky						
Bat Cave	10.0	8.1–11.4	7.5	4.5–9.8	9.3	8.3–10.2
Coach Cave	9.2	6.5–11.0	5.6	2.2–8.5	7.4	5.5–8.9
Linefork Cave	8.3	6.9–8.9	5.7	3.3–7.4	6.5	5.7–7.2
Saltpetre Cave	9.6	8.1–12.2	6.9	4.4–8.7	6.9	6.0–9.0
Missouri						
Bat Cave	6.4	0.3–9.0	1.4	-3.9–5.9	4.6	-0.4–6.4
Great Scott Cave	10.8	6.9–12.6	5.8	1.7–10.8	8.6	5.0–9.8
Pilot Knob Mine	7.4	7.2–7.7	5.5	3.9–7.6	4.9	4.5–5.4
Tennessee						
White Oak Blowhole	9.9	9.0–10.3	8.2	6.9–9.3	8.5	8.1–8.9
Virginia						
Rocky Hollow Cave	77.3	6.8–7.5	6.2	5.4–7.0	6.4	6.1–6.7

[a] Dataloggers were not recording during periods with missing data.

[b] Missing data resulted from premature failure of datalogger.

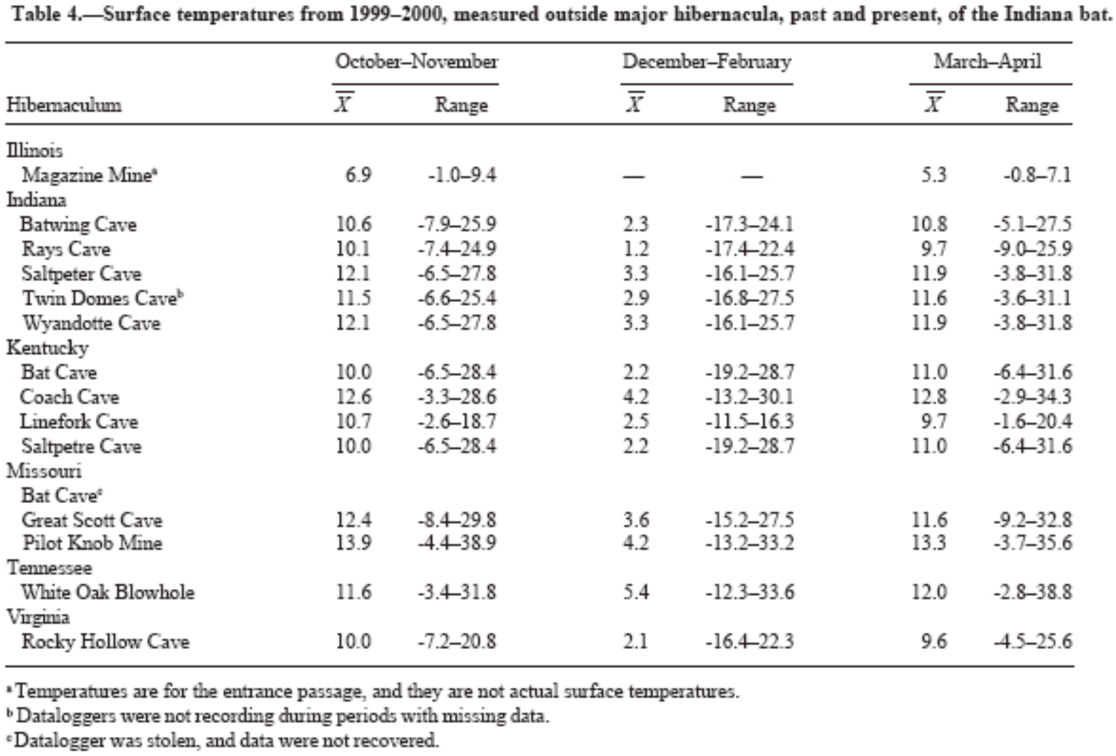

Table 4.—Surface temperatures from 1999–2000, measured outside major hibernacula, past and present, of the Indiana bat.

Hibernaculum	October–November $\overline{X}$	October–November Range	December–February $\overline{X}$	December–February Range	March–April $\overline{X}$	March–April Range
Illinois						
Magazine Mine[a]	6.9	-1.0–9.4	—	—	5.3	-0.8–7.1
Indiana						
Batwing Cave	10.6	-7.9–25.9	2.3	-17.3–24.1	10.8	-5.1–27.5
Rays Cave	10.1	-7.4–24.9	1.2	-17.4–22.4	9.7	-9.0–25.9
Saltpeter Cave	12.1	-6.5–27.8	3.3	-16.1–25.7	11.9	-3.8–31.8
Twin Domes Cave[b]	11.5	-6.6–25.4	2.9	-16.8–27.5	11.6	-3.6–31.1
Wyandotte Cave	12.1	-6.5–27.8	3.3	-16.1–25.7	11.9	-3.8–31.8
Kentucky						
Bat Cave	10.0	-6.5–28.4	2.2	-19.2–28.7	11.0	-6.4–31.6
Coach Cave	12.6	-3.3–28.6	4.2	-13.2–30.1	12.8	-2.9–34.3
Linefork Cave	10.7	-2.6–18.7	2.5	-11.5–16.3	9.7	-1.6–20.4
Saltpetre Cave	10.0	-6.5–28.4	2.2	-19.2–28.7	11.0	-6.4–31.6
Missouri						
Bat Cave[c]						
Great Scott Cave	12.4	-8.4–29.8	3.6	-15.2–27.5	11.6	-9.2–32.8
Pilot Knob Mine	13.9	-4.4–38.9	4.2	-13.2–33.2	13.3	-3.7–35.6
Tennessee						
White Oak Blowhole	11.6	-3.4–31.8	5.4	-12.3–33.6	12.0	-2.8–38.8
Virginia						
Rocky Hollow Cave	10.0	-7.2–20.8	2.1	-16.4–22.3	9.6	-4.5–25.6

[a] Temperatures are for the entrance passage, and they are not actual surface temperatures.

[b] Dataloggers were not recording during periods with missing data.

[c] Datalogger was stolen, and data were not recovered.

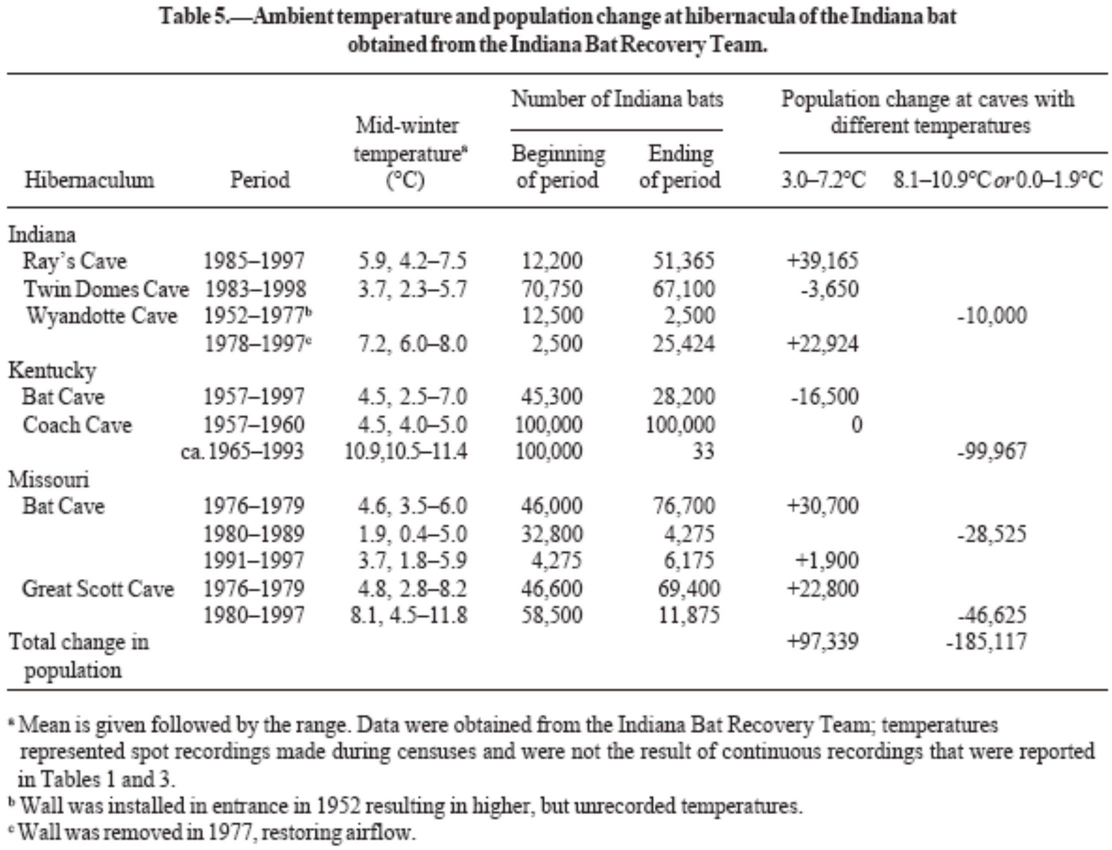

Table 5.—Ambient temperature and population change at hibernacula of the Indiana bat obtained from the Indiana Bat Recovery Team.

Hibernaculum	Period	Mid-winter temperature[a] (°C)	Number of Indiana bats: Beginning of period	Number of Indiana bats: Ending of period	Population change at caves with different temperatures: 3.0–7.2°C	Population change at caves with different temperatures: 8.1–10.9°C *or* 0.0–1.9°C
Indiana						
Ray's Cave	1985–1997	5.9, 4.2–7.5	12,200	51,365	+39,165	
Twin Domes Cave	1983–1998	3.7, 2.3–5.7	70,750	67,100	-3,650	
Wyandotte Cave	1952–1977[b]		12,500	2,500		-10,000
	1978–1997[c]	7.2, 6.0–8.0	2,500	25,424	+22,924	
Kentucky						
Bat Cave	1957–1997	4.5, 2.5–7.0	45,300	28,200	-16,500	
Coach Cave	1957–1960	4.5, 4.0–5.0	100,000	100,000	0	
	ca. 1965–1993	10.9,10.5–11.4	100,000	33		-99,967
Missouri						
Bat Cave	1976–1979	4.6, 3.5–6.0	46,000	76,700	+30,700	
	1980–1989	1.9, 0.4–5.0	32,800	4,275		-28,525
	1991–1997	3.7, 1.8–5.9	4,275	6,175	+1,900	
Great Scott Cave	1976–1979	4.8, 2.8–8.2	46,600	69,400	+22,800	
	1980–1997	8.1, 4.5–11.8	58,500	11,875		-46,625
Total change in population					+97,339	-185,117

[a] Mean is given followed by the range. Data were obtained from the Indiana Bat Recovery Team; temperatures represented spot recordings made during censuses and were not the result of continuous recordings that were reported in Tables 1 and 3.

[b] Wall was installed in entrance in 1952 resulting in higher, but unrecorded temperatures.

[c] Wall was removed in 1977, restoring airflow.

Ecological Impacts of Wind Energy on Bats: Questions, Research Needs, & Hypotheses

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Abstract

At a time of growing concern over the rising costs and long-term environmental impacts of the use of fossil fuels and nuclear energy, wind energy has become an increasingly important sector of the electrical power industry, largely because it has been promoted as being emission-free and is supported by government subsidies and tax credits. However, large numbers of bats are killed at utility-scale wind energy facilities, especially along forested ridge-tops in the eastern United States. These fatalities raise important concerns about cumulative impacts of proposed wind energy development on bat populations. This paper summarizes evidence of bat fatalities at wind energy facilities in the US, makes projections of cumulative fatalities of bats in the Mid-Atlantic Highlands, identifies research needs, and proposes hypotheses to better inform researchers, developers, decision makers, and other stakeholders, and to help minimize adverse effects of wind energy development.

Wind energy has become an increasingly important sector of the renewable energy industry, and may help to satisfy a growing worldwide demand for electricity (Pasqualetti *et al*. 2004; GAO 2005; Manville 2005). Environmental benefits of wind energy accrue from the replacement of energy generated by other means (e.g., fossil fuels, nuclear fuels), reducing some adverse environmental effects from those industries (Keith *et al*. 2003). However, development of the wind energy industry has led to some unexpected environmental costs (Morrison and Sinclair 2004). For example, soaring and feeding raptors have been killed in relatively large numbers in areas of high raptor abundance in the United States and Europe (Barrios and Rodriquez 2004; Hoover and Morrison 2005). More recently, large numbers of bat fatalities have been observed at utility-scale wind energy facilities, especially along forested ridge-tops in the eastern US (Arnett 2005; GOA 2005; Johnson 2005; Fiedler *et al*. 2007), and in agricultural regions of southwestern Alberta, Canada (RMR Barclay and E Baerwald pers comm). Similar fatalities have been reported at wind energy facilities in Europe (UNEP/Eurobats 2005; Brinkmann *et al*. 2006). As such facilities continue to develop in other parts of the world, especially in Australia, China, and India (National Wind Watch Inc 2006), increased numbers of bat and bird fatalities can be expected.

In this paper, we highlight ongoing development of wind energy facilities in the US, summarize evidence of bat fatalities at these sites, make projections of cumulative fatalities of bats for the Mid-Atlantic Highlands (MD, PA, VA, and WV), identify research needs to help reduce or mitigate adverse environmental impacts at these facilities, and propose hypotheses to evaluate where, when, how, and why bats are being killed.

Utility-scale wind energy development in the US

In 2005, utility-scale wind energy facilities in the US accounted for approximately 9616 MW of installed capacity (also called name plate capacity or the potential generating capacity of turbines; EIA 2006). The number and size of wind energy facilities have continued to increase, with taller and larger turbines being constructed. Available estimates of installed capacity in the US by 2020 range up to 72 000 MW, or the equivalent 48 000 1.5 MW wind turbines. This is enough, according to some projections, to account for 5% of the country's electrical generating capacity. Most existing wind energy facilities in the US include turbines with installed capacity ranging from 600 kW to 2 MW per turbine. Wind turbines up to about 3 MW of installed capacity for onshore applications are currently being tested. However, owing to seasonally variable wind speeds, the generating capacity of most existing wind turbines is less than 30% of installed capacity.

Utility-scale wind turbines (> 1 MW) installed in, or planned for, the US since the 1990s are designed with a single monopole (tubular tower), ranging in height from 45 to 100 m, with rotor blades up to 50 m in length. At their greatest height, blade tips of typical 1.5 MW turbines may extend to 137 m (as tall as a 40-story building with a rotor diameter the size of a 747 jumbo jet). The nacelle, located at the top of the monopole, houses a gearbox that is connected to an electric generator and associated electronic converters and controls. Three rotor blades are attached to a drive shaft that extends outward from the nacelle. The pitch or angular orientation of the three blades can be adjusted to control turbine output and rotation speed of the rotor. Typically, wind turbines are arranged in one or more arrays, linked by underground cables that provide energy to a local power grid (WebFigure 1). Some modern turbines (e.g., GAMESA G87 2.0 MW turbine) rotate up to 19 rpm, driving blade tips at 86 m s–1 (193 mph) or more. Since utility-scale wind turbines were first deployed in the US in the 1980s, the height and rotor-swept area has steadily increased with each new generation of turbines.

To date, most utility-scale wind turbines in the US have been installed in grassland, agricultural, and desert landscapes in western and mid-western regions. More recently, however, wind turbines have been installed along forested ridge tops in eastern states (Figure 1). More are proposed in this and other regions, including the Gulf Coast and along coastal areas of the Great Lakes. Large wind energy facilities off the coastline of the northeastern US have also been proposed.

In a nutshell:

- Bat species that migrate long distances are those most commonly killed at utility-scale wind energy facilities in the US
- Future research and monitoring should emphasize regions and sites with the highest potential for adverse environmental impacts on bats
- Multi-year monitoring and hypothesis-based research are needed to address these concerns
- A policy framework that requires owners and developers to provide full access to publicly-supported wind energy facilities should be implemented, and should include funds for research and monitoring at these sites

Bat fatalities

Relatively small numbers of bat fatalities were reported at wind energy facilities in the US before 2001 (Johnson 2005), largely because most monitoring studies were designed to assess bird fatalities (Anderson *et al*. 1999). Thus, it is quite likely that bat fatalities were underestimated in previous research. Recent monitoring studies indicate that some utility-scale wind energy facilities have killed large numbers of bats (Kerns and Kerlinger 2004; Arnett 2005; Johnson 2005). Of the 45 species of bats found in North America, 11 have been identified in ground searches at wind energy facilities (Table 1). Of these, nearly 75% were foliage-roosting, eastern red bats (*Lasiurus borealis*), hoary bats (*Lasiurus cinereus*), and tree cavity- dwelling silver-haired bats (*Lasionycteris noctivagans*), each of which migrate long distances (Figure 2). Other bat species killed by wind turbines in the US include the western red bat (*Lasiurus blossivilli*), Seminole bat (*Lasiurus seminolus*), eastern pipistrelle (*Perimyotis [=Pipistrellus] subflavus*), little brown myotis (*Myotis lucifugus*), northern long-eared myotis (*Myotis septentrionalis*), long-eared myotis (*Myotis evotis*), big brown bat (*Eptesicus fuscus*), and Brazilian free-tailed bat (*Tadarida brasiliensis*). A consistent theme in most of the monitoring studies conducted to date has been the predominance of migratory, tree-roosting species among the fatalities.

For several reasons (eg cryptic coloration, small body size, steep topography, overgrown vegetation), bats may have been overlooked during previous carcass searches. Based on recent evaluations of searcher efficiency, on average, only about half of test subjects (fresh and frozen bats or birds) are recovered by human observers (Arnett *et al*. in press; WebTable 1). In these studies, bats were nearly twice as likely to be found in grassland areas as in agricultural landscapes and along forested ridge tops. Moreover, scavengers often remove carcasses before researchers are able to recover them (Arnett *et al*. in press).

To date, no fatalities of state or federally listed bat species have been reported; however, the large number of fatalities of other North American species has raised concerns among scientists and the general public about the environmental friendliness of utility-scale wind energy facilities. For example, the number of bats killed in the eastern US at wind energy facilities installed along forested ridge tops has ranged from 15.3 to 41.1 bats per MW of installed capacity per year (WebTable 1). Bat fatalities reported from other regions of the western and mid-western US have been lower, ranging from 0.8 to 8.6 bats MW–1yr–1, although many of these studies were designed only to assess bird fatalities (Anderson *et al*. 1999). Nonetheless, in a recent study designed to assess bat fatalities in southwestern Alberta, Canada, observed fatalities were comparable to those

found at wind energy facilities located in forested regions of the eastern US (RMR Barclay and E Baerwald pers comm).

Figure 1. Partial view of the Mountaineer Wind Energy Center, Tucker County, WV, located along a forested ridge top, where large numbers of bats have been killed

While the seasonal duration of reported studies, corrections for searcher efficiency, and scavenging rates vary geographically, fatality rates have been among the highest reported in the eastern US (Table 1). As research protocols for bats shift toward improved monitoring studies, more bat species are likely to be affected and greater measured fatality rates at wind energy facilities are expected.

Locations of bat fatalities

Bat fatalities at wind energy facilities appear to be highest along forested ridge tops in the eastern US and lowest in relatively open landscapes in the mid-western and western states (Johnson 2005; Arnett *et al*. in press), although relatively large numbers of fatalities have been reported in agricultural regions from northern Iowa (Jain 2005) and southwestern Alberta, Canada (RMR Barclay and E Baerwald pers comm). Additionally, in a recent study conducted in mixed-grass prairie in Woodward County, north-central Oklahoma, Piorkowski (2006) found 111 dead bats beneath wind turbines, 86% of which were pregnant or lactating Brazilian free-tailed bats. Western red bats, hoary bats, silver-haired bats, and Brazilian free-tailed bats have also been reported at wind energy facilities in northern California (Kerlinger *et al.* 2006). To date, no assessments of bat fatalities have been reported at wind energy facilities in the southwestern US, a region where large numbers of migratory Brazilian free-tailed bats are resident during the warm months (McCracken 2003), and where this species provides important ecosystems services to agriculture (Cleveland *et al*. 2006). High fatality rates can also be expected for other species in the southwestern US and at wind energy facilities in western states, where rigorous monitoring for bat fatalities has been limited.

Seasonal timing of bat fatalities

Most bat fatalities in North America have been reported in late summer and early autumn (Johnson 2005; Arnett *et al*. in press; RMR Barclay and E Baerwald pers comm), and similar seasonal trends have been reported for bats in northern Europe (Bach and Rahmel 2004; Dürr and Bach 2004). Migration of tree bats in North America is known to occur from March through May and again from August through November (Cryan 2003). The few bat fatalities reported during spring migration and early summer may reflect the fact that less intensive fatality searches were conducted during this period, but it may also be due to bats migrating at higher altitudes during spring. Many, if not most, of the bat species that have been killed by wind turbines in the US (Table 1 and WebTable 1) are resident during summer months (Barbour and Davis 1969). A study by Piorkowski (2006) provided evidence that bats are at risk of being killed by wind turbines during summer, and, thus, more rigorous fatality assessment is warranted during this season. In addition to being at risk during migration, the large colonies of Brazilian free-tailed bats that disperse nightly across vast landscapes in the southwestern US (McCracken 2003; Kunz 2004) may be at risk during the period of summer residency. Uncertainty with respect to the seasonality of bat fatalities in North America may, in part, reflect the lack of full-season, multi-year monitoring studies that include spring and autumn migratory periods as well as summer months, when bats are in residence (Arnett *et al*. in press).

How and why are bats being killed?

It is clear that bats are being struck and killed by the turning rotor blades of wind turbines (Horn *et al*. in press). It is unclear, however, why wind turbines are killing bats, although existing studies offer some clues. Are bats in species are known to seek the nearest available trees as daylight approaches (Cryan and Brown in press), and thus could mistake large monopoles for roost trees (Ahlén 2003; Hensen 2004). Tree-roosting bats, in particular, often seek refuge in tall trees (Pierson 1998; Kunz and Lumsden 2003; Barclay and Kurta 2007). As wind turbines continue to increase in height, bats that migrate or forage at higher altitudes may be at increased risk (Barclay *et al*. 2007).

Figure 2. The three species of migratory tree bats most frequently killed at wind turbine facilities in North America. (a) hoary bat (*Lasiurus cinereus*), (b) reastern red bat (*L. borealis*), and (c) silver-haireed bat (*Lasionyctyeris noctivagans*).

Are bats attracted to sites that provide rich foraging habitats? Modifications of landscapes during installation of wind energy facilities, including the construction of roads and power-line corridors, and removal of trees to create clearings (usually 0.5–2.0 ha) around each turbine site may create favorable conditions for the aerial insects upon which most insectivorous bats feed (Grindal and Brigham 1998; Hensen 2004). Thus, bats that migrate, commute, or forage along linear landscapes (Limpens and Kapteyn 1991; Verboom and Spoelstra 1999; Hensen 2004; Menzel *et al*. 2005) may be at increased risk of encountering and being killed by wind turbines.

Are bats attracted to the sounds produced by wind turbines? Some bat species are known to orient toward distant audible sounds (Buchler and Childs 1981), so it is possible that they are attracted to the swishing sounds produced by the rotating blades. Alternatively, bats may become acoustically disoriented upon encountering these structures during migration or feeding. Bats may also be attracted to the ultrasonic noise produced by turbines (Schmidt and Jermann 1986). Observations using thermal infrared imaging of flight activity of bats at wind energy facilities suggest that they do fly (and feed) in close proximity to wind turbines (Ahlén 2003; Horn *et al*. 2007; Figure 3).

What other factors might contribute to bat fatalities? Wind turbines are also known to produce complex electromagnetic fields in the vicinity of nacelles. Given that some bats have receptors that are sensitive to magnetic fields (Buchler and Wasilewski 1985; Holland *et al*. 2006), interference with perception in these receptors may increase the risk of being killed by rotating turbine blades. Bats flying in the vicinity of turbines may also become trapped in blade-tip vortices (Figure 4) and experience rapid decompression due to changes in atmospheric pressure as the turbine blades rotate downward. Some bats killed at wind turbines have shown no sign of external injury, but evidence of internal tissue damage is consistent with decompression (Dürr and Bach 2004; Hensen 2004). Additionally, some flying insects are reportedly attracted to the heat produced by nacelles (Ahlén 2003; Hensen 2004). Preliminary evidence suggests that bats are not attracted to the lighting attached to wind turbines (Arnett 2005; Kerlinger *et al*. 2006; Horn *et al*. in press).

Do some weather conditions place bats at increased risk of being killed by wind turbines? Preliminary observations suggest an association between bat fatalities and thermal inversions following storm fronts or during low cloud cover that force the animals to fly at low altitudes (Dürr and Bach 2004; Arnett 2005). Thermal inversions create cool, foggy conditions in valleys, with warmer air masses rising to ridget ops. If both insects and bats respond to these conditions by concentrating their activities along ridge tops instead of at lower altitudes, their risk of being struck by the moving turbine blades would increase (Dürr and Bach 2004). Interestingly, the highest bat fatalities occur on nights when wind speed is low (< 6 m s–1), which is when aerial insects are most active (Ahlén 2003; Fiedler 2004; Hensen 2004; Arnett 2005).

Are bats at risk because they are unable to acoustically detect the moving rotor blades? Current evidence is inconclusive as to whether bats echolocate during

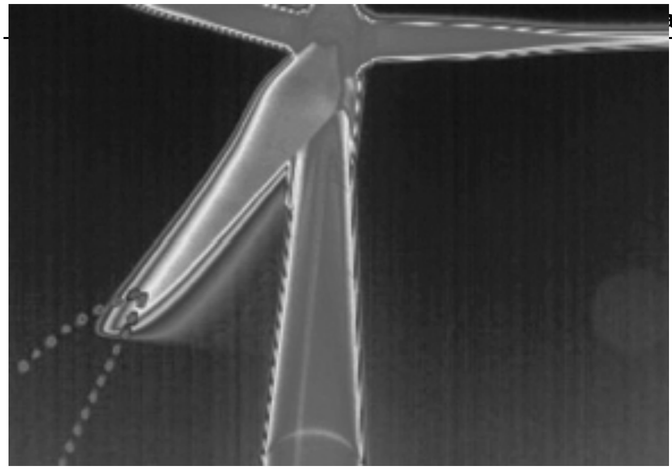

Figure 3. Thermal infrared image of a modern wind turbine

migration, independent of time spent searching for and capturing insects. Bats less likely to make long-distant migrations in North America (e.g., members of the genera *Myotis, Eptesicus, Perimyotis*) and others that engage in long-distance migrations (e.g., *Lasiurus, Lasionycteris*, *Tadarida*) typically rely on echolocation to capture aerial insects and to avoid objects in their flight paths. However, for most bat species, echolocation is ineffective at distances greater than 10 m (Fenton 2004), so bats foraging in the vicinity of wind turbines may miscalculate rotor velocity or fail to detect the large, rapidly moving turbine blades (Ahlén 2003; Bach and Rachmel 2004; Dürr and Bach 2004). Given the speed at which the tips of turbine blades rotate, even in relatively low-wind conditions, some bats may not be able to detect blades soon enough to avoid being struck as they navigate.

Projected cumulative fatalities

We have projected cumulative fatalities of bats at wind energy facilities for the Mid-Atlantic Highlands using data on current fatality rates (Table 1) and projections of installed capacity for wind energy facilities in the Highlands for the year 2020 (see WebTable 2 for supporting data, assumptions, and calculations). Projections of installed capacity range from 2158 MW (based on the National Renewable Energy Laboratory [NREL] WinDS model [nd]) to 3856 MW (based on the PJM electricity grid operator interconnection queue; see PJM [2006]). Although the estimated number of bat fatalities reported for each study (WebTable 1) were not consistently corrected for search efficiency or for potential bias associated with carcass removal by scavengers, we have nonetheless used these estimates to project cumulative impacts on bats because they are the only fatality rates available for bats in this region.

In making our projections of cumulative fatalities, we have assumed that: (1) current variation in fatality rates is representative of the Mid-Atlantic Highlands, (2) future changes in design or placement of turbines (e.g., more and larger installed turbines) will not cause deviations from current fatality estimates, (3) abundance of affected bat species will not decrease due to turbine-related fatalities or other factors (e.g., habitat loss), and (4) projections of cumulative fatalities for other geographic regions differ from those in the Mid-Atlantic Highlands.

The projected number of annual fatalities in the year 2020 (rounded to the nearest 500) range from 33 000 to 62 000 individuals, based on the NREL's WinDS Model, and 59 000 to 111 000 bats based on the PJM grid operator interconnection queue. For the three migratory, tree roosting species from the Mid-Atlantic Highlands, the projected cumulative fatalities in the year 2020 based on the WinDS model and PJM grid operator queue, respectively, would include 9500 to 32 000 hoary bats, 11 500 to 38 000 eastern red bats, and 1500 to 6 000 silver-haired bats. Given the uncertainty in estimated installed wind turbine capacity for the Mid-Atlantic Highlands and existing data on bat fatalities reported for this region, the above projections of cumulative fatalities should be considered provisional and thus viewed as hypotheses to be tested as improved estimates (or enumerations) of installed capacity and additional data on bat life histories and fatalities become available for this region.

Nonetheless, these provisional projections suggest substantial fatality rates in the future. At this time, we have avoided making projections of cumulative fatalities for the entire period from 2006–2020, because of uncertainty with respect to population sizes and the demographics of bat species being killed in this region.

If these and other species-specific projections are realized for the Mid-Atlantic Highlands, there may be a substantial impact on both migratory and local bat populations. Migratory tree-roosting species are of particular concern because these bats have experienced the highest fatality rates at wind energy facilities in North America. Risk assessments of ecological impacts typically require knowledge of baseline population estimates and demographics (Munns 2006). However, virtually no such data exist for any foliage-roosting species (Carter *et al*. 2003; O'Shea *et al*. 2003), on either regional or continental scales, that would make it possible to conduct a meaningful risk assessment. However, given the limitations noted above, the projected numbers of bat fatalities in the Mid- Atlantic Highlands are very troubling.

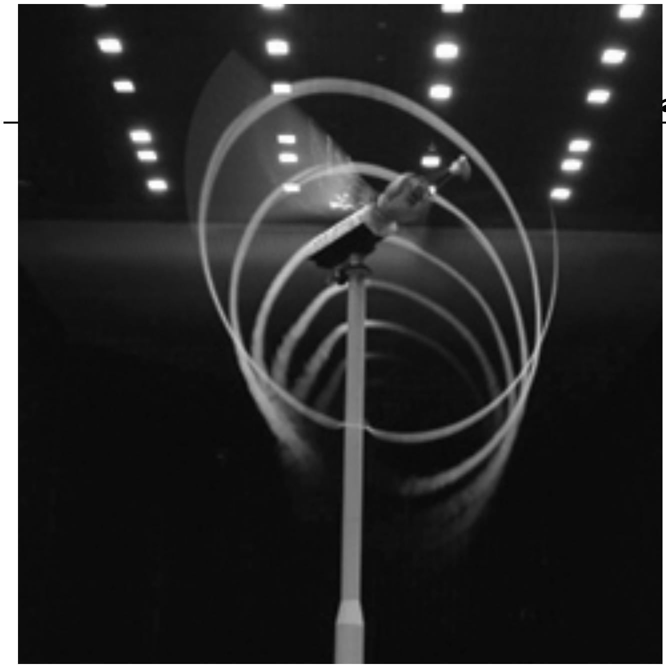

Figure 4. Blade-tip vortices created by moving rotor blades in a wind tunnel illustrate the swirling wake that trails

Our current knowledge and the projected future development of wind energy facilities in the US suggest the potential for a substantial population impact to bats. For example, it is unlikely that the eastern red bat (*Lasiurus borealis*) could sustain cumulative fatality rates associated with wind energy development as projected, given that this species already appears to be in decline throughout much of its range (Whitaker et al. 2002; Carter *et al*. 2003; Winhold and Kurta 2006). There are major gaps in knowledge regarding the timing, magnitude, and patterns of bat migration, and the underlying evolutionary forces that have shaped this seasonal behavior (Fleming and Eby 2003). When lack of knowledge is combined with the fact that bats generally have low reproductive rates (Barclay and Harder 2003), significant cumulative impacts of wind energy development on bat populations are likely.

Much of the existing data on bat fatalities at wind energy facilities are based on monitoring studies designed primarily for the detection and estimation of bird fatalities. Results from these studies vary considerably with respect to geographic location, landscape conditions, search frequency, season of monitoring, and potential biases based on searcher efficiency and carcass removal by scavengers. In addition, search intervals have ranged from 1 to 28 days (WebTable 1). Because some studies have shown that bats can be scavenged within hours of being killed, there is considerable uncertainty in reported fatality estimates when search intervals longer than 24 hrs are used (Fiedler *et al*. 2007; Arnett *et al*. in press).

Moreover, because only six monitoring studies have routinely used bat carcasses to correct for observer bias, the number of reported fatalities provides, at best, a minimum estimate (WebTable 1).

Research needs

The unexpectedly large number of migratory tree bats being killed by wind turbines and the projected cumulative fatalities in the Mid-Atlantic Highlands should be a wake-up call for those who promote wind energy as being “green” or environmentally friendly. Uncertainties with respect to the projected fatalities, as noted above, invite comprehensive, multi-year surveys and hypothesis-based research to advance our understanding of where, when, how, and why bats are killed at wind energy facilities (Panel 1). Research is needed to develop solutions at existing facilities and to aid in assessing risk at proposed facility sites, particularly in landscapes where high bat fatalities have been reported and in regions where little is known about the migratory and foraging habits of bats.

To advance our knowledge about the causes of bat fatalities at wind energy facilities and to help guide the establishment of mitigating solutions, we propose the following research directions:

- Employ scientifically valid, pre- and post-construction monitoring protocols to ensure comparable results across different sites.
- Conduct full-season (April–November in the continental US, for example), multi-year pre- and post-construction monitoring studies to assess species composition, species abundance, local population variability, and temporal and spatial patterns of bat activity at facilities that encompass diverse landscapes.
- Conduct pre- and post-construction studies that simultaneously employ different methods and tools (e.g., mist netting, horizontal and vertical radar, NEXRAD [WSR-88D] Doppler radar, thermal infrared imaging, radio telemetry, and acoustic monitoring) to improve understanding of bat activity, migration, nightly dispersal patterns, and interactions with moving turbine blades at different wind speeds.
- Conduct local-, regional-, and continental-scale population estimates of North American bat species. In particular, use of molecular methods to estimate effective population size of species most at risk should be a high priority.
- Quantify geographic patterns of bat activity and migration with respect to topography and land cover.
- Quantify relationships between bat abundance and fatality risks and the relationship between fatalities and bat demography at local, regional, and continental scales.

•Conduct quantitative studies of bat activity at existing wind energy facilities to evaluate how variations in weather and operating conditions of turbines affect bat activity and fatalities. Variables to be evaluated should include air temperature, wind speed and direction, cloud cover, moon phase, barometric pressure, precipitation, and turbine operating status such as rotation rate and cut-in speeds.

• Quantify effects of wind turbine design on bat fatalities with respect to height and rotor diameter, base and tip height of rotor-swept areas, distance between adjacent turbine rotor swept areas, and the scale (size) of wind power facilities.

• Quantify effects of feathered (i.e., turbine blades pitched parallel to the wind, making them essentially stationary) versus not feathered (ie turbine blades pitched angularly to the wind, causing rotation) turbines at different wind speeds and at multiple sites, especially during high-risk, migratory periods.

• Evaluate and quantify sources of potential attraction of bats to turbines (e.g., sound emissions, lighting, blade movement, prey availability, potential roosting sites).

• Develop predictive and risk assessment models, with appropriate confidence intervals, on local, regional, and continental scales to evaluate impacts of wind energy development on bat populations.

• Evaluate possible deterrents under controlled conditions and under different operating conditions and turbine characteristics at multiple sites.

A call for full cooperation and research support from the wind industry

As part of the permitting process, owners and developers should be required to provide full access to proposed and existing wind energy facilities and to fund research and monitoring studies by qualified researchers. Research and monitoring protocols should be designed and conducted to ensure unbiased data collection and should be held to the highest peer-review and legal standards.

Panel 1. *Hypotheses for bat fatalities at wind energy facilities*

We propose 11 hypotheses to explain where, when, how, and why insectivorous bats are killed at wind energy facilities. These hypotheses are not mutually exclusive, given that several causes may act synergistically to cause fatalities. Nevertheless, testing these and other hypotheses promises to provide science-based answers to inform researchers, developers, decision makers, and other stakeholders of the observed and projected impacts of wind energy development on bat populations.

1. Linear corridor hypothesis. Wind energy facilities constructed along forested ridge tops create clearings with linear landscapes that are attractive to bats.
2. Roost attraction hypothesis. Wind turbines attract bats because they are perceived as potential roosts.
3. Landscape attraction hypothesis. Bats feed on insects that are attracted to the altered landscapes that commonly surround wind turbines.
4. Low wind velocity hypothesis. Fatalities of feeding and migrating bats are highest during periods of low wind velocity.
5. Heat attraction hypothesis. Flying insects upon which bats feed are attracted to the heat produced by nacelles of wind turbines.
6. Acoustic attraction hypothesis. Bats are attracted to audible and/or ultrasonic sound produced by wind turbines.
7. Visual attraction hypothesis. Nocturnal insects are visually attracted to wind turbines.
8. Echolocation failure hypothesis. Bats cannot acoustically detect moving turbine blades or miscalculate rotor velocity.
9. Electromagnetic field disorientation hypothesis. Wind turbines produce complex electromagnetic fields, causing bats to become disoriented.
10. Decompression hypothesis. Rapid pressure changes cause internal injuries and/or disorient bats while foraging or migrating in proximity to wind turbines.
11. Thermal inversion hypothesis. Thermal inversions create dense fog in cool valleys, concentrating both bats and insects on ridge tops.

Conclusions

To date, bat fatalities reported in the US have been highest at wind energy facilities along forested ridge tops in the East. While the lowest fatality rates have been observed in western states, few of these studies were designed to monitor bat fatalities, and thus may represent substantial underestimates. The highest fatality rate for bats (41.6 bat fatalities MW–1yr–1) was reported at the Buffalo Mountain Wind Energy Center, TN, where estimates were consistently corrected for both search efficiency and scavenging. A recent study conducted at wind energy facilities in an agricultural region in southwestern Alberta, Canada, unexpectedly found fatality rates comparable to those observed in some forested ridge tops in the eastern US. Given that previous monitoring studies in western agricultural and grassland regions reported relatively low fatality rates of bats, high fatality rates in regions with similar landscapes should receive increased attention. High fatality rates can also be expected at wind energy facilities located in the southwestern US, where, to date, no monitoring studies have been conducted.

Future research should focus on regions and at sites with the greatest potential for adverse effects. Improved documentation, with emphasis on evaluation of causes and cumulative impacts, should be a high priority. There is an urgent need to estimate population sizes of bat species most at risk, especially migrating, tree-roosting species. Moreover, additional data are needed for assessing fatalities caused by other human activities (eg agricultural pesticides, heavy metals released from the burning of fossil towers) to place impacts of wind energy development on bats into a broader context. However, these latter studies should not take priority over research to find solutions for fatalities caused by wind turbines. An important challenge for policy makers is to ensure that owners and developers of wind energy and other energy-generating facilities are required, as part of the permitting process, to fund qualified research designed to assess impacts of these facilities on bats and other wildlife.

Results of scientifically sound research and monitoring studies are needed to inform policy makers during the siting, permitting, and operation of renewable energy sources. Although bat fatalities at wind turbines have been reported at nearly every wind energy facility where post-construction surveys have been conducted, few of these studies were designed to estimate bat fatalities and only a few included a full season or more of monitoring.

Rigorous protocols should include reliable estimates of searcher efficiency and scavenger removal to correct fatality estimates for potential biases.

Future development of wind energy facilities, and expected impacts on bats, depend upon complex interactions among economic factors, technological development, regulatory changes, political forces, and other factors that cannot be easily or accurately predicted at this time. Our preliminary projections of cumulative fatalities of bats for the Mid-Atlantic Highlands are likely to be unrealistically low, especially as larger and increasing numbers of wind turbines are installed. Reliable data on bat fatalities and estimates of demographic and effective population sizes for species at risk are needed from all regions of North America, to fully understand the continental- scale impacts of wind energy development. Until then, current and projected cumulative fatalities should provide an important wake-up call to developers and decision makers. Additional monitoring and hypothesis-based research is needed to address a growing concern of national and international importance.

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WebPanel 1. Additional acknowledgements

This paper evolved as an outgrowth of several state, regional, and national wind-energy and wildlife workshops, including:

- Bats and wind power generation technical workshop (Juno Beach, FL; 19–20 February 2004; sponsored by the US Fish and Wildlife Service [USFWS], Bat Conservation International, National Renewable Energy Laboratory, and American Wind Energy Association)
- Wind energy and birds/bats workshop: understanding and resolving bird and bat impacts (Washington, DC; 18–19 May 2004; sponsored by the National Wind Coordinating Committee [NWCC])
- Research meeting V: onshore wildlife interactions with wind development (Lansdowne, VA; 3–4 Nov 2004; sponsored by NWCC)
- Wind power and wildlife in Colorado (Fort Collins,CO;23–25 Jan 2006; sponsored by the Colorado Department of Natural Resources)
- Toward wildlife friendly wind power: a focus on the Great Lakes (Toledo, OH; 27–29 Jun 2006; sponsored by US Environmental Protection Agency, USFWS Great Lakes Basin Ecosystem Team, Illinois Natural History Survey, and US Geological Survey)
- New York wind/wildlife technical workshop (Albany, NY; 2–3 Aug 2006; sponsored by the New York State Energy Research and Development Authority, and New York Department of Environmental Conservation)

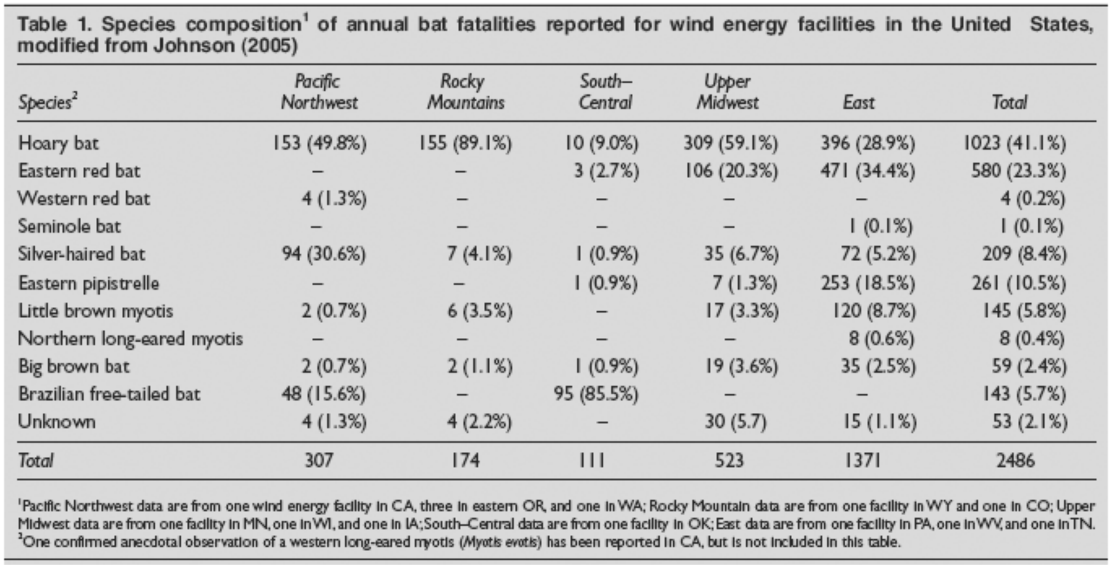
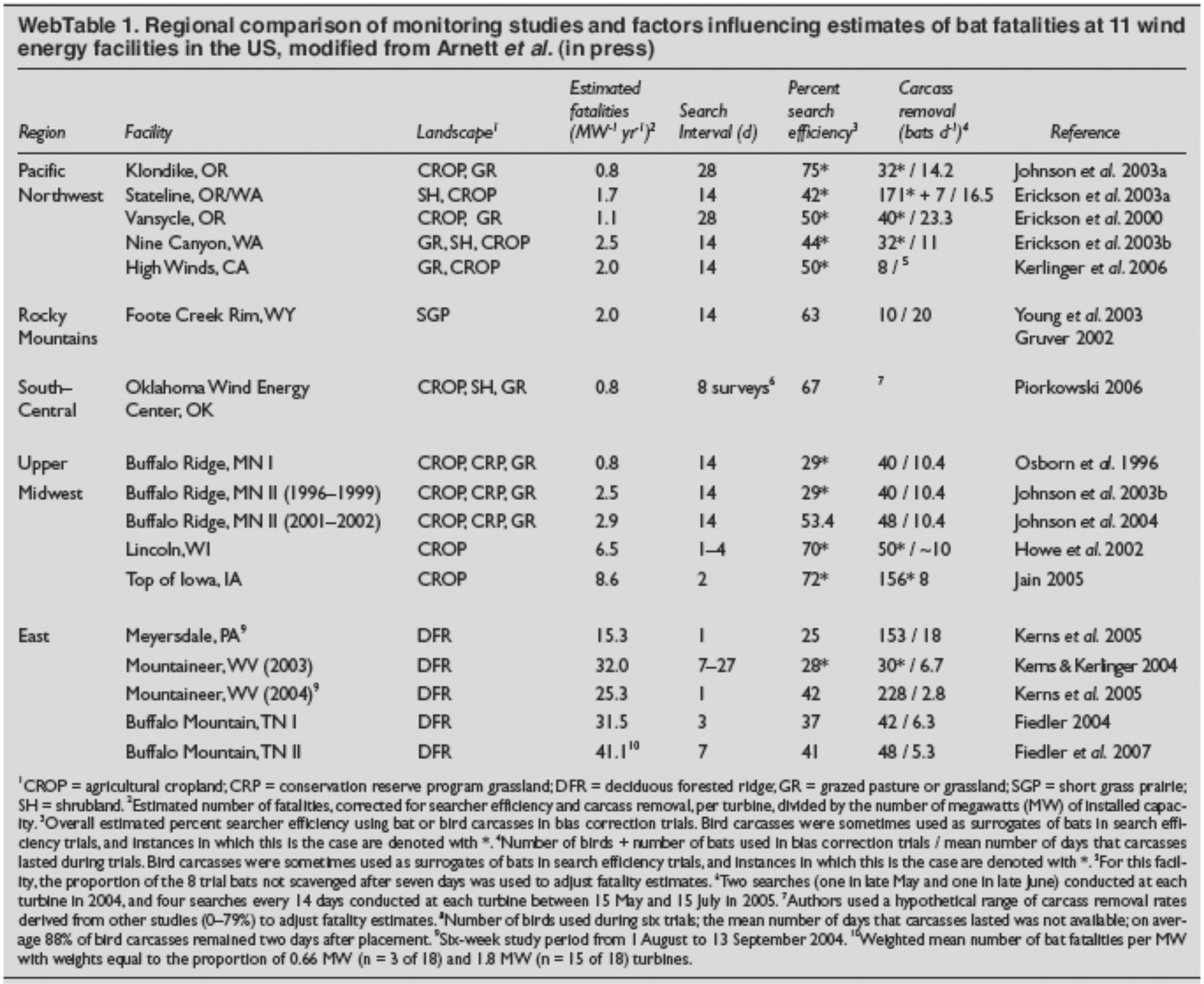


Table 1. Species composition[1] of annual bat fatalities reported for wind energy facilities in the United States, modified from Johnson (2005)

Species[2]	*Pacific Northwest*	*Rocky Mountains*	*South–Central*	*Upper Midwest*	*East*	*Total*
Hoary bat	153 (49.8%)	155 (89.1%)	10 (9.0%)	309 (59.1%)	396 (28.9%)	1023 (41.1%)
Eastern red bat	–	–	3 (2.7%)	106 (20.3%)	471 (34.4%)	580 (23.3%)
Western red bat	4 (1.3%)	–	–	–	–	4 (0.2%)
Seminole bat	–	–	–	–	1 (0.1%)	1 (0.1%)
Silver-haired bat	94 (30.6%)	7 (4.1%)	1 (0.9%)	35 (6.7%)	72 (5.2%)	209 (8.4%)
Eastern pipistrelle	–	–	1 (0.9%)	7 (1.3%)	253 (18.5%)	261 (10.5%)
Little brown myotis	2 (0.7%)	6 (3.5%)	–	17 (3.3%)	120 (8.7%)	145 (5.8%)
Northern long-eared myotis	–	–	–	–	8 (0.6%)	8 (0.4%)
Big brown bat	2 (0.7%)	2 (1.1%)	1 (0.9%)	19 (3.6%)	35 (2.5%)	59 (2.4%)
Brazilian free-tailed bat	48 (15.6%)	–	95 (85.5%)	–	–	143 (5.7%)
Unknown	4 (1.3%)	4 (2.2%)	–	30 (5.7)	15 (1.1%)	53 (2.1%)
Total	307	174	111	523	1371	2486

[1] Pacific Northwest data are from one wind energy facility in CA, three in eastern OR, and one in WA; Rocky Mountain data are from one facility in WY and one in CO; Upper Midwest data are from one facility in MN, one in WI, and one in IA; South–Central data are from one facility in OK; East data are from one facility in PA, one in WV, and one in TN.

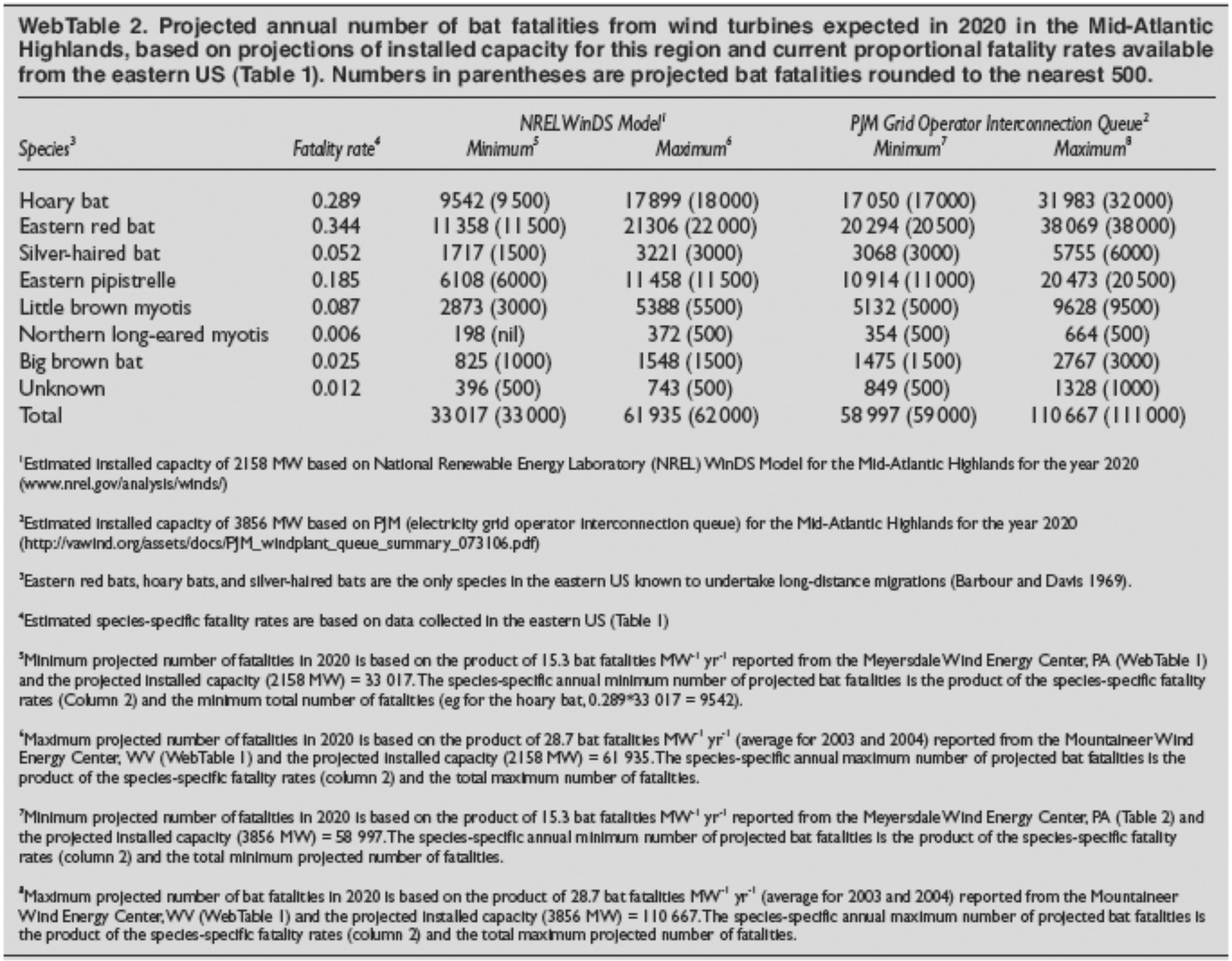
[2] One confirmed anecdotal observation of a western long-eared myotis (*Myotis evotis*) has been reported in CA, but is not included in this table.



WebTable 1. Regional comparison of monitoring studies and factors influencing estimates of bat fatalities at 11 wind energy facilities in the US, modified from Arnett *et al.* (in press)

Region	*Facility*	*Landscape*[1]	*Estimated fatalities* $(MW^{-1}\ yr^{-1})$[2]	*Search Interval (d)*	*Percent search efficiency*[3]	*Carcass removal (bats d⁻¹)*[4]	*Reference*
Pacific Northwest	Klondike, OR	CROP, GR	0.8	28	75*	32* / 14.2	Johnson *et al.* 2003a
	Stateline, OR/WA	SH, CROP	1.7	14	42*	171* + 7 / 16.5	Erickson *et al.* 2003a
	Vansycle, OR	CROP, GR	1.1	28	50*	40* / 23.3	Erickson *et al.* 2000
	Nine Canyon, WA	GR, SH, CROP	2.5	14	44*	32* / 11	Erickson *et al.* 2003b
	High Winds, CA	GR, CROP	2.0	14	50*	8 / [5]	Kerlinger *et al.* 2006
Rocky Mountains	Foote Creek Rim, WY	SGP	2.0	14	63	10 / 20	Young *et al.* 2003 Gruver 2002
South–Central	Oklahoma Wind Energy Center, OK	CROP, SH, GR	0.8	8 surveys[6]	67	[7]	Piorkowski 2006
Upper Midwest	Buffalo Ridge, MN I	CROP, CRP, GR	0.8	14	29*	40 / 10.4	Osborn *et al.* 1996
	Buffalo Ridge, MN II (1996–1999)	CROP, CRP, GR	2.5	14	29*	40 / 10.4	Johnson *et al.* 2003b
	Buffalo Ridge, MN II (2001–2002)	CROP, CRP, GR	2.9	14	53.4	48 / 10.4	Johnson *et al.* 2004
	Lincoln, WI	CROP	6.5	1–4	70*	50* / ~10	Howe *et al.* 2002
	Top of Iowa, IA	CROP	8.6	2	72*	156* 8	Jain 2005
East	Meyersdale, PA[9]	DFR	15.3	1	25	153 / 18	Kerns *et al.* 2005
	Mountaineer, WV (2003)	DFR	32.0	7–27	28*	30* / 6.7	Kerns & Kerlinger 2004
	Mountaineer, WV (2004)[9]	DFR	25.3	1	42	228 / 2.8	Kerns *et al.* 2005
	Buffalo Mountain, TN I	DFR	31.5	3	37	42 / 6.3	Fiedler 2004
	Buffalo Mountain, TN II	DFR	41.1[10]	7	41	48 / 5.3	Fiedler *et al.* 2007

[1] CROP = agricultural cropland; CRP = conservation reserve program grassland; DFR = deciduous forested ridge; GR = grazed pasture or grassland; SGP = short grass prairie; SH = shrubland. [2] Estimated number of fatalities, corrected for searcher efficiency and carcass removal, per turbine, divided by the number of megawatts (MW) of installed capacity. [3] Overall estimated percent searcher efficiency using bat or bird carcasses in bias correction trials. Bird carcasses were sometimes used as surrogates of bats in search efficiency trials, and instances in which this is the case are denoted with *. [4] Number of birds + number of bats used in bias correction trials / mean number of days that carcasses lasted during trials. Bird carcasses were sometimes used as surrogates of bats in search efficiency trials, and instances in which this is the case are denoted with *. [5] For this facility, the proportion of the 8 trial bats not scavenged after seven days was used to adjust fatality estimates. [6] Two searches (one in late May and one in late June) conducted at each turbine in 2004, and four searches every 14 days conducted at each turbine between 15 May and 15 July in 2005. [7] Authors used a hypothetical range of carcass removal rates derived from other studies (0–79%) to adjust fatality estimates. [8] Number of birds used during six trials; the mean number of days that carcasses lasted was not available; on average 88% of bird carcasses remained two days after placement. [9] Six-week study period from 1 August to 13 September 2004. [10] Weighted mean number of bat fatalities per MW with weights equal to the proportion of 0.66 MW (n = 3 of 18) and 1.8 MW (n = 15 of 18) turbines.



WebTable 2. Projected annual number of bat fatalities from wind turbines expected in 2020 in the Mid-Atlantic Highlands, based on projections of installed capacity for this region and current proportional fatality rates available from the eastern US (Table 1). Numbers in parentheses are projected bat fatalities rounded to the nearest 500.

		NREL WinDS Model[1]		*PJM Grid Operator Interconnection Queue*[2]	
Species[3]	*Fatality rate*[4]	*Minimum*[5]	*Maximum*[6]	*Minimum*[7]	*Maximum*[8]
Hoary bat	0.289	9542 (9 500)	17899 (18000)	17 050 (17000)	31 983 (32 000)
Eastern red bat	0.344	11 358 (11 500)	21306 (22 000)	20 294 (20 500)	38 069 (38 000)
Silver-haired bat	0.052	1717 (1500)	3221 (3000)	3068 (3000)	5755 (6000)
Eastern pipistrelle	0.185	6108 (6000)	11 458 (11 500)	10 914 (11 000)	20 473 (20 500)
Little brown myotis	0.087	2873 (3000)	5388 (5500)	5132 (5000)	9628 (9500)
Northern long-eared myotis	0.006	198 (nil)	372 (500)	354 (500)	664 (500)
Big brown bat	0.025	825 (1000)	1548 (1500)	1475 (1500)	2767 (3000)
Unknown	0.012	396 (500)	743 (500)	849 (500)	1328 (1000)
Total		33 017 (33 000)	61 935 (62 000)	58 997 (59 000)	110 667 (111 000)

[1] Estimated installed capacity of 2158 MW based on National Renewable Energy Laboratory (NREL) WinDS Model for the Mid-Atlantic Highlands for the year 2020 (www.nrel.gov/analysis/winds/)

[2] Estimated installed capacity of 3856 MW based on PJM (electricity grid operator interconnection queue) for the Mid-Atlantic Highlands for the year 2020 (http://vawind.org/assets/docs/PJM_windplant_queue_summary_073106.pdf)

[3] Eastern red bats, hoary bats, and silver-haired bats are the only species in the eastern US known to undertake long-distance migrations (Barbour and Davis 1969).

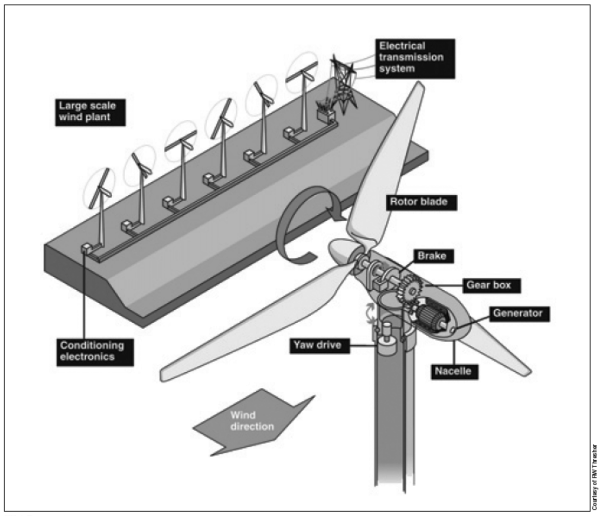
[4] Estimated species-specific fatality rates are based on data collected in the eastern US (Table 1)

[5] Minimum projected number of fatalities in 2020 is based on the product of 15.3 bat fatalities MW^{-1} yr^{-1} reported from the Meyersdale Wind Energy Center, PA (WebTable 1) and the projected installed capacity (2158 MW) = 33 017. The species-specific annual minimum number of projected bat fatalities is the product of the species-specific fatality rates (Column 2) and the minimum total number of fatalities (eg for the hoary bat, 0.289*33 017 = 9542).

[6] Maximum projected number of fatalities in 2020 is based on the product of 28.7 bat fatalities MW^{-1} yr^{-1} (average for 2003 and 2004) reported from the Mountaineer Wind Energy Center, WV (WebTable 1) and the projected installed capacity (2158 MW) = 61 935. The species-specific annual maximum number of projected bat fatalities is the product of the species-specific fatality rates (column 2) and the total maximum number of fatalities.

[7] Minimum projected number of fatalities in 2020 is based on the product of 15.3 bat fatalities MW^{-1} yr^{-1} reported from the Meyersdale Wind Energy Center, PA (Table 2) and the projected installed capacity (3856 MW) = 58 997. The species-specific annual minimum number of projected bat fatalities is the product of the species-specific fatality rates (column 2) and the total minimum projected number of fatalities.

[8] Maximum projected number of bat fatalities in 2020 is based on the product of 28.7 bat fatalities MW^{-1} yr^{-1} (average for 2003 and 2004) reported from the Mountaineer Wind Energy Center, WV (WebTable 1) and the projected installed capacity (3856 MW) = 110 667. The species-specific annual maximum number of projected bat fatalities is the product of the species-specific fatality rates (column 2) and the total maximum projected number of fatalities.



Courtesy of RW Thresher

WebFigure 1. *Model of a modern utility-scale wind turbine and wind-energy facility, showing an array of turbines with underground power lines, connected to a local grid by overhead power lines. When rotor blades are pitched into the wind, they rotate a shaft connected to a power generator, which in turn produces electricity. The nacelle is located on top of the monopole and contains the gear box, brake, and electronic control systems used to regulate the pitch of the blades, yaw of the nacelle, rpms of the rotor, and cut-in speed.*

Bat White-Nose Syndrome: An Emerging Fungal Pathogen?

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The first evidence of bat white-nose syndrome (WNS) was documented in a photograph taken at Howes Cave, 52 km west of Albany, New York, on 16 February 2006. Since emerging in the northeastern United States, WNS has been confirmed by gross and histologic examinations of bats at 33 sites in Connecticut, Massachusetts, New York, and Vermont (fig. S1). Current bat population surveys suggest a 2-year population decline in excess of 75% [see supporting on line material (SOM) text for further details].

WNS has been characterized as a condition of hibernating bats and was named for the visually strikingwhite fungal growth on muzzles, ears, and/ or wing membranes of affected bats (Fig. 1A). Detailed postmortem evaluations were completed for 97 little brown myotis (*Myotis lucifugus*; Mylu), nine northern long-eared myotis (*M. septentrionalis*; Myse), five big brown bats (*Eptesicus fuscus*; Epfu), three tricolored bats (*Perimyotis subflavus*; Pesu), and three unidentified bats from 18 sites within the WNS-affected region. Distinct cutaneous fungal infection was observed in histologic sections from 105 of the 117 necropsied bats [91 Mylu (94%), eight Myse (89%), zero Epfu (0%), three Pesu (100%), and three unidentified (100%)]. Fungal hyphae replaced hair follicles and associated sebaceous and sweat glands, breaching the basement membrane and invading regional tissue. Hyphae also eroded the epidermis of ears and wings (Fig. 1B). Additionally, 69 of the 105 bats [62 Mylu (64%), six Myse (67%), zero Epfu (0%), one Pesu (33%), and zero unidentified (0%)] with cutaneous fungal infection had little or no identifiable fat reserves, crucial for successful hibernation [see SOM text for additional mortality investigation details].

A fungus with a previously undescribed morphology was isolated from10 bats (table S1)with histologic evidence of WNS-associated cutaneous fungal infection. These bats were collected between 1 February and 1 April 2008 from all states within the confirmed WNS-affected region (fig. S1). The distinctive curved conidia (Fig. 1C) of the isolates were identical to conidia scraped directly from the muzzles of WNS-affected little brown myotis collected at Graphite Mine (New York) and to conidia observed histologically on the surface of infected bat skin (Fig. 1B, inset). Isolates were initially cultured at 3°C, grew optimally between 5°C and 10°C, but grew marginally above 15°C. The upper growth limit was about 20°C. Temperatures in WNS-affected hibernacula seasonally range between 2° and 14°C, permitting year-round growth and reservoir maintenance of the psychrophilic fungus.

Phylogenetic analysis of the identical internal transcribed spacer region (fig. S2) and small subunit (fig. S3) ribosomal RNA gene sequences from the 10 psychrophilic fungal isolates placed them within the inoperculate ascomycetes (Order Helotiales) near representatives of the anamorphic genus Geomyces (teleomorph Pseudogymnoascus) (1). In contrast to the genetic data, morphology of the psychrophilic fungal isolates differed from that known for Geomyces species. The bat isolates produced single, curved conidia (Fig. 1C)morphologically distinct from clavate and arthroconidia characteristic of Geomyces (2). Species of Geomyces are terrestrial saprophytes that grow at cold temperatures (3). Placement of the WNS fungal isolates within Geomyces, members of which colonize the skin of animals in cold climates (4), is consistent with properties predicted for a causative agent of WNS-associated cutaneous infection.

Worldwide, bats play critical ecological roles in insect control, plant pollination, and seed dissemination (5), and the decline of North American bat populations would likely have far-reaching ecological consequences. Parallels can be drawn between the threat posed by WNS and that from chytridiomycosis, a lethal fungal skin infection that has recently caused precipitous global amphibian population declines (6). A comprehensive understanding of the etiology, ecology, and epidemiology of WNS is essential to develop a strategy to manage this current devastating threat to bats of the northeastern United States.

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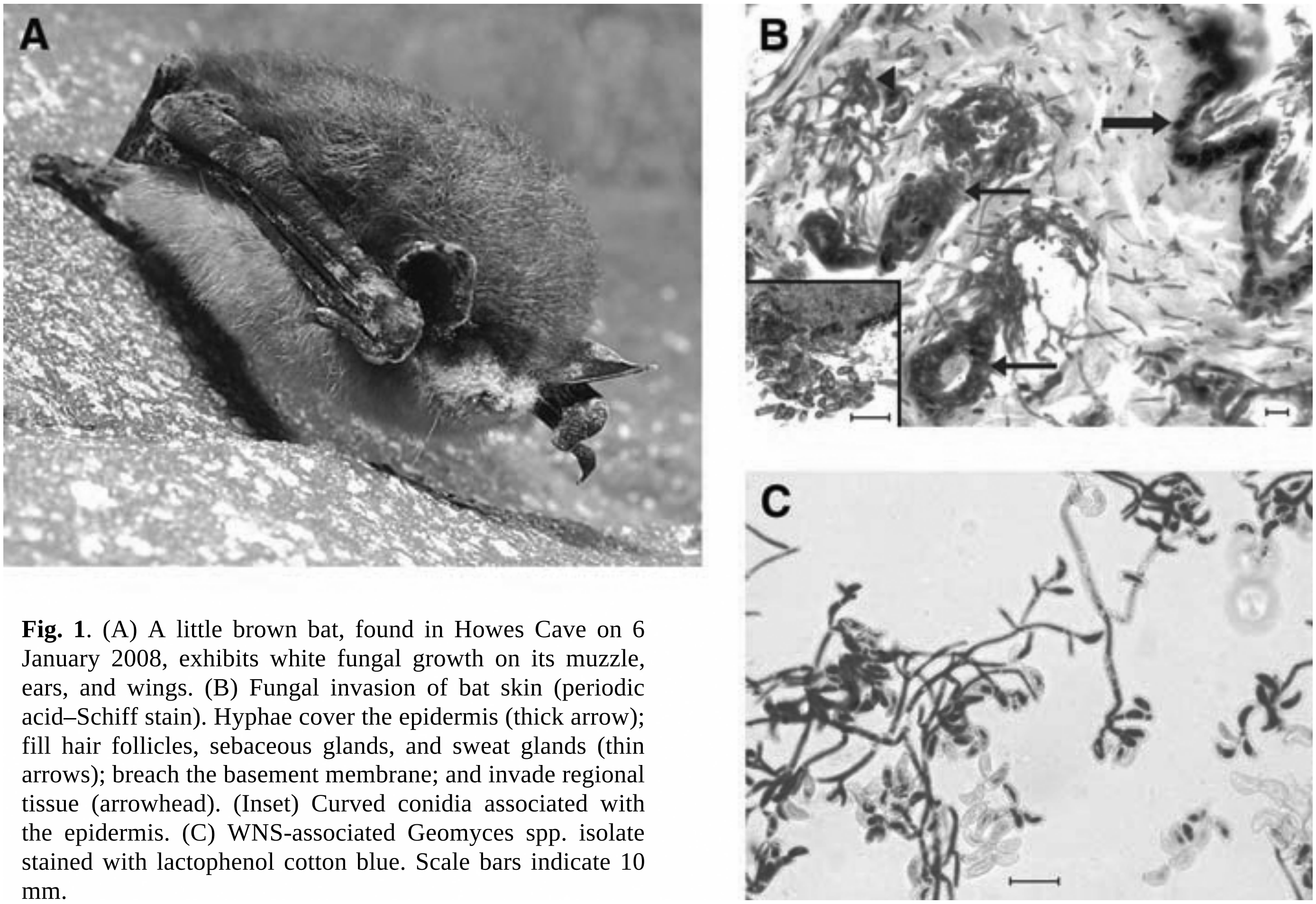

Fig. 1. (A) A little brown bat, found in Howes Cave on 6 January 2008, exhibits white fungal growth on its muzzle, ears, and wings. (B) Fungal invasion of bat skin (periodic acid–Schiff stain). Hyphae cover the epidermis (thick arrow); fill hair follicles, sebaceous glands, and sweat glands (thin arrows); breach the basement membrane; and invade regional tissue (arrowhead). (Inset) Curved conidia associated with the epidermis. (C) WNS-associated Geomyces spp. isolate stained with lactophenol cotton blue. Scale bars indicate 10 mm.

Supporting Online Material forBat White-Nose Syndrome: An Emerging Fungal Pathogen?

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Abstract: White-nose syndrome (WNS) is a condition associated with an unprecedented bat mortality event in the northeastern United States. Since the winter of 2006-2007 bat declines exceeding 75% have been observed at surveyed hibernacula. Affected bats often present with visually striking white fungal growth on their muzzles, ears, and/or wing membranes. Direct microscopy and culture analyses demonstrated that the skin of WNS-affected bats is colonized by a psychrophilic fungus that is phylogenetically related to *Geomyces spp.*, but with a conidial morphology distinct from characterized members of this genus. This report characterizes the cutaneous fungal infection associated with WNS.

Materials and Methods: Finite annual population growth rates (R) were estimated for the two caves that had at least three surveys since 2005, Hailes (R = 0.47) and Schoharie (R = 0.17). These corresponded with two-year population declines of 78% and 97%, respectively. We assumed the geometric population model Nt+I = NtRi, where Nt is the population at time t, and R is the finite annual growth rate. We estimated log(R) for each cave using the semilog regression model log(Nt+i) = log(Nt) + log(R)i, and obtained the estimate of R as R = exp(log(R)). The estimated two-year decline was obtained as 100(1-R2). Although we assumed a model of constant change, the semilog plots suggest an accelerating decline (Fig. S4).

DNA was extracted from each fungal isolate using microLYSIS-PLUS reagent (The Gel Company, San Francisco, California) following the manufacturer's instructions. rRNA gene internal transcribed spacer (ITS) region DNA (ITS1, 5.8S, and ITS2) was PCR amplified using primers ITS4 and ITS5 (S1) and ExTaq proof-reading DNA polymerase (Takara Mirus Bio, Madison, Wisconsin). Cycling parameters were an initial 2 min denaturation at 98°C followed by 30 cycles of denaturation at 98°C for 10 s, annealing at 50°C for 30 s, and extension at 72°C for 1 min, with a final extension at 72°C for 7 min. rRNA gene small subunit (SSU) DNA was PCR amplified using primers nu-SSU-0021-5' (S2) and nu-SSU-1750-3' (S3) as above, except the extension time was increased to 2 min. Sequencing primers were PCR primers with the addition of nu-SSU-0402-5' (S3), nu-SSU-1150-5' (S1), nu-SSU-0497-3' (S3), and nu-SSU- 1184-3' (S4) for the SSU. PCR products were submitted to the University of Wisconsin – Madison Biotechnology Center DNA Sequencing Facility for direct, double-stranded sequence determination using the BigDye Terminator v3.1 (Applied Biosystems, Foster City, California) DNA sequencing system. Reaction products were analyzed using an Applied Biosystems 3730xl automated DNA sequencing instrument. Complementary strand sequencing reaction results were assembled and edited for accuracy using Lasergene 5.0 (DNAStar, Madison, Wisconsin). rRNA gene ITS (EU854569-EU854572, EU884920-EU884924, and FJ170115) and SSU (FJ231093-FJ231102) sequences are archived in GenBank. As the ITS and SSU sequences from each of the ten WNS fungal isolates were identical to each other, they were represented in phylogenetic analyses by single sequences (EU854571 for ITS and FJ231093 for SSU). Although excluded from the sequences used in analysis of the ITS region, additional genetic support comes from the presence of a putative group I intron of ca 415 nt, located at small subunit position 1506 (S4) of each isolate, with 97% sequence similarity to insertions in *Geomyces spp*. AY345348 and AY345347. ITS and SSU sequences for comparison were selected from similar sequences archived in GenBank determined through BLAST search hits to query WNS isolate sequences, including only taxa with near complete gene sequences. Sequences were aligned visually using Se-AL (v2.0a11) (S5). The ITS alignment of 537 nt for 20 taxa and the SSU alignment of 1725 nt for 18 taxa are archived in TreeBase SN3954-18967. Parsimony phylograms were determined with PAUP* (4.0b10) (S6). Reliability of nodes was assessed with Bayesian posterior probabilities calculated using MCMC (MrBayes 3.1.2) (S7, S8) using the GTR model and running four chains with 1,000,000 generations, sampling each 1,000th tree and discarding as burn-in all pre-convergence trees; and bootstrap percentages based on 1,000 replicates in PAUP* (S4).

Supporting Text: Following the emergence of WNS during the winter of 2006-2007, the number of reports of day-flying bats recorded by the New York State Department of Health rabies laboratory for Schoharie County peaked in mid-March, 2007 at approximately 10 times the previous 25-year record high. This trend continued throughout the winter of 2007-2008 for Schoharie county and expanded to include Ulster County. All bats tested negative for rabies. Additional bacteriological and virological analyses of internal organs from WNS-suspect bats revealed no known pathogens. Disease-causing parasites were not found following examination of intestinal tracts. No consistent, significant lesions were observed upon gross or microscopic examination of internal organs from bats with the WNS-associated cutaneous fungal infection. Post-mortem evaluations were also completed for five little brown myotis from an unaffected mine in Wisconsin and eight little brown myotis from an unaffected cave in Kentucky, and no lesions were seen in their skin or internal organs.

Fig. S1. Hibernacula locations, including the index site Howes Cave, confirmed by survey to be positive for WNS. Fungal isolates from which ITS and SSU sequence data were generated were cultured from bats collected at sites designated with plus signs.

Fig. S2. One of 13 equally parsimonious trees for the ITS alignment (Length = 286, CI = 0.734, RI = 0.805). GenBank accession numbers precede taxa names, and the WNS fungal isolate sequence is indicated in bold with a bat image. Branch length is relative to the number of substitutions per site. Posterior probability values are shown above each supported node, and bootstrap percentages are shown below supported nodes.

Fig. S3. One of 5 equally parsimonius trees for the SSU alignment (Length = 194, CI = 0.825, RI= 0.807). GenBank accession numbers precede taxa names, and the WNS fungal isolate sequence is indicated in bold with a bat image. Branch length is relative to the number of substitutions per site. Posterior probability values are shown above each supported node, and bootstrap percentages are shown below supported nodes.

Fig. S4. Bat population trends for Hailes Cave and Schoharie Caverns.

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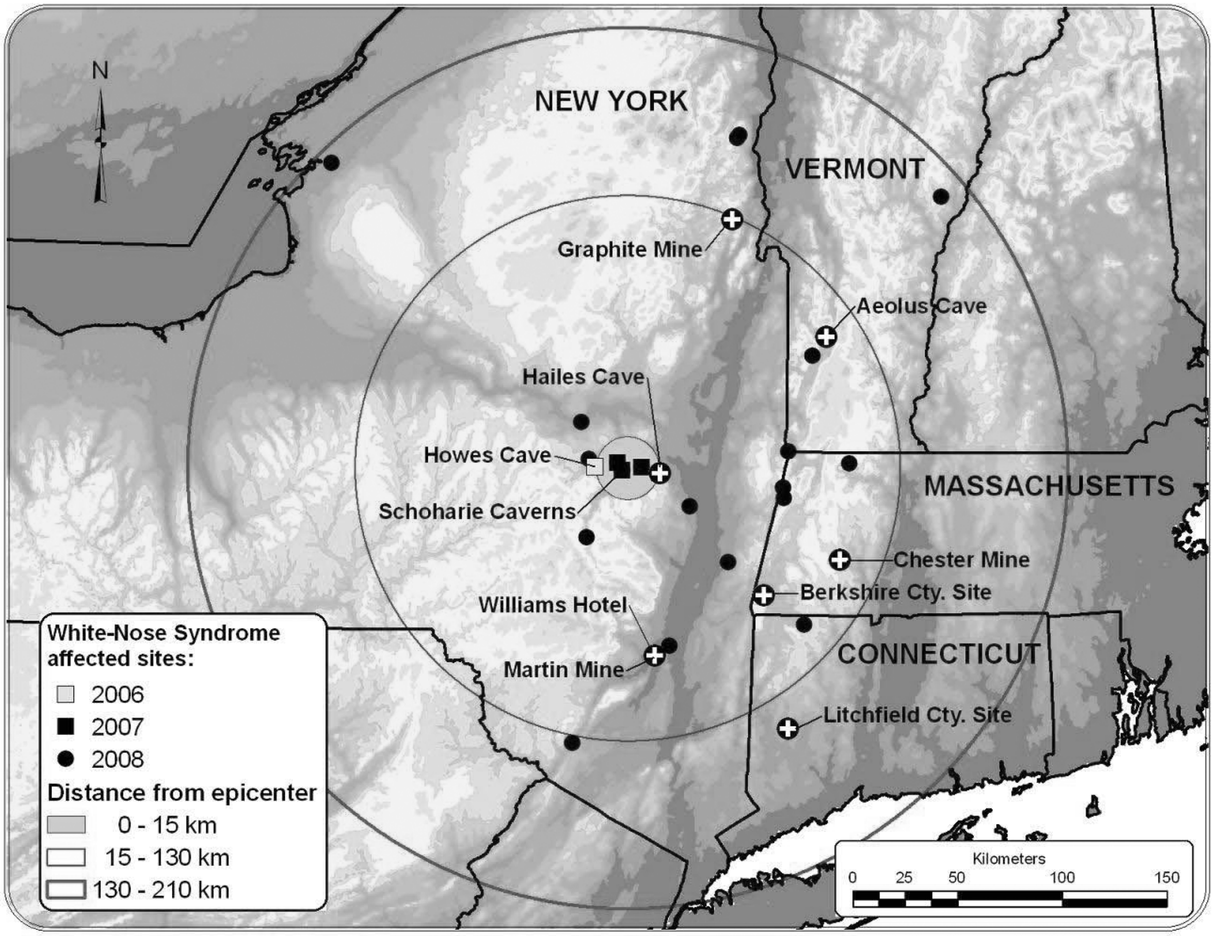
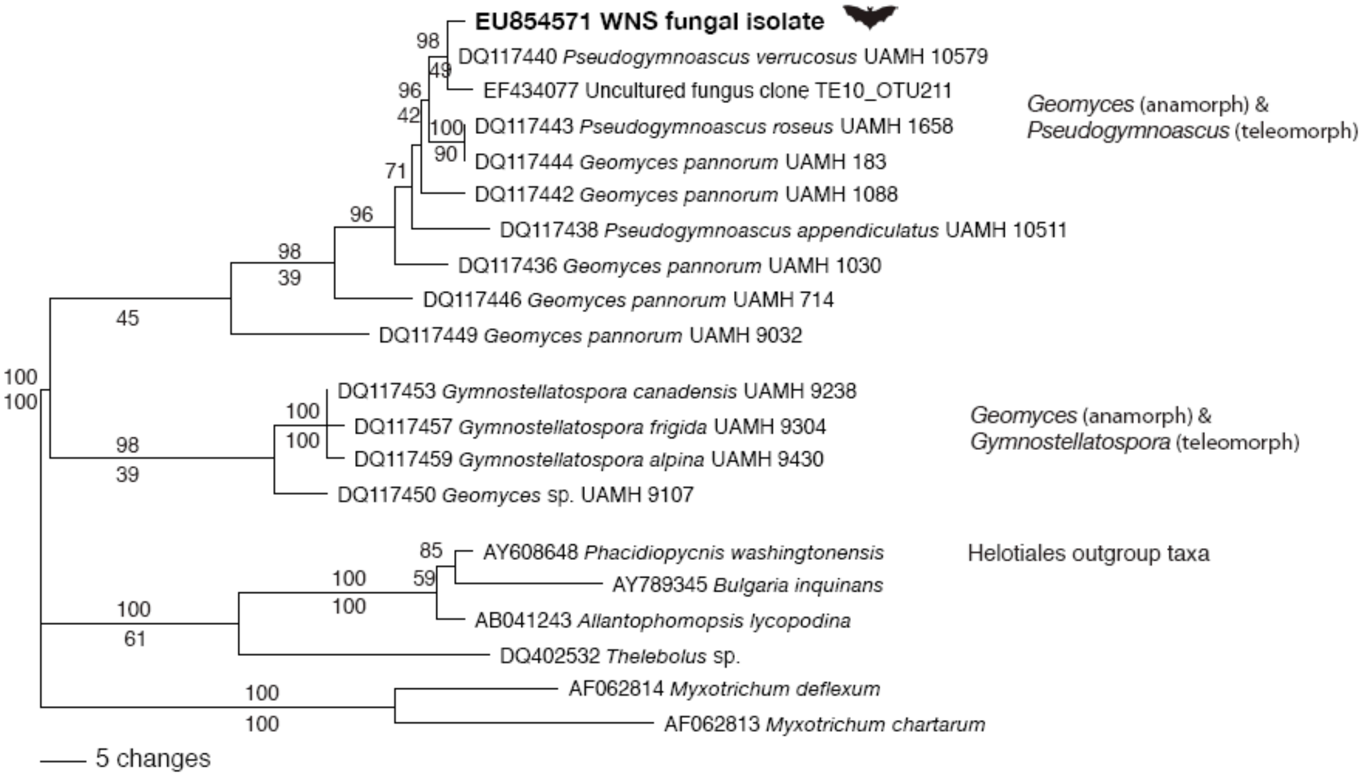
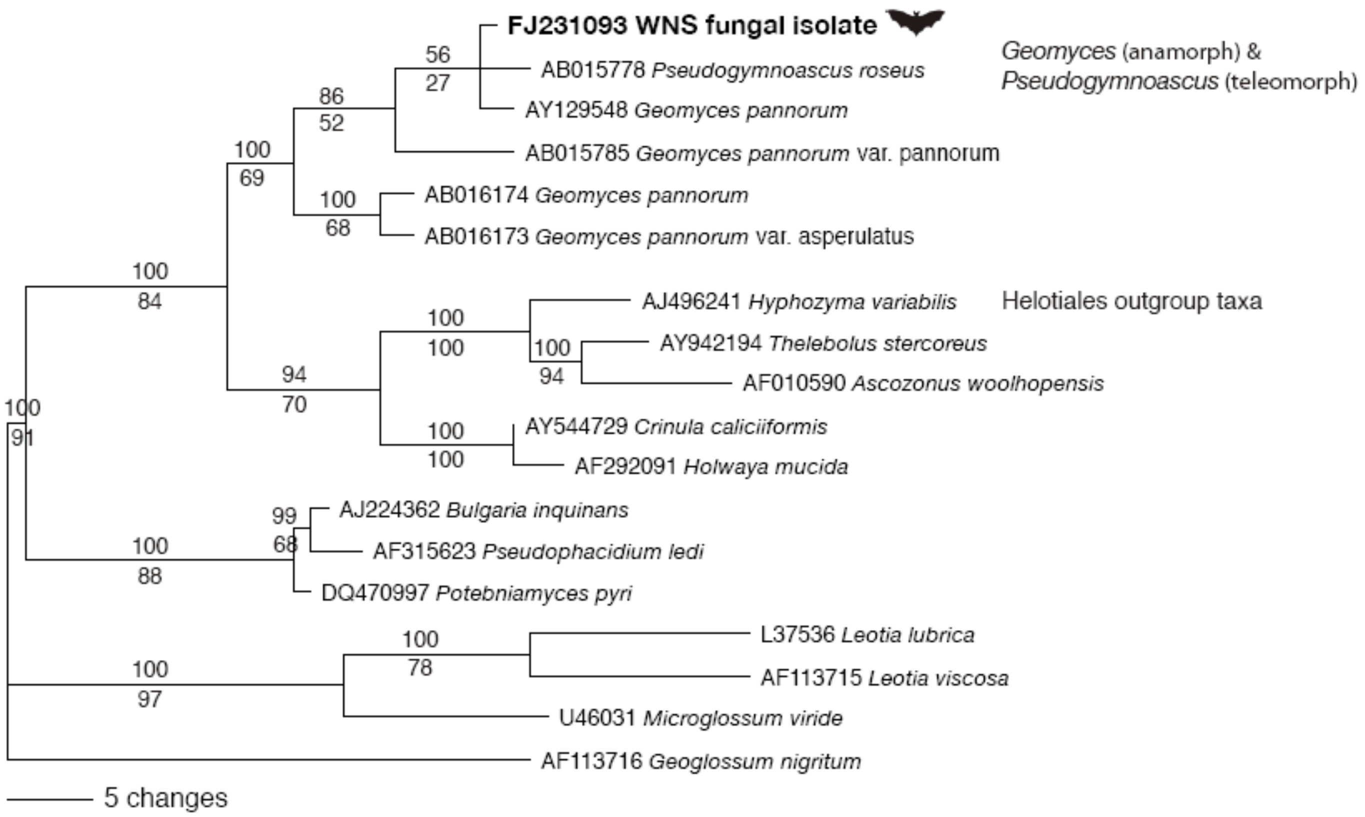
S9. We thank T. Kunz (Boston University), M. Friend (USGS-National Wildlife Health Center), and D. Constantine for manuscript suggestions. At the USGS-National Wildlife Health Center, supporting pathology was provided by D. Green, N. Thomas, and V. Shearn-Bochsler; laboratory support was contributed by H. Ip (virology), D. Berndt (microbiology), and M. Sterner (parasitology). Population trend analysis was conducted by D. Heisey. At Cornell University, we acknowledge the anatomic pathology and wildlife medicine faculty and staff; supporting pathology was provided by K. Hulme. We also thank A. Lowell (USFWS), C. Herzog (NYSDEC), A. Davis (NYSDOH), B. Wood (NYSDOH), and the many individuals who provided survey data and specimen collection assistance for hibernacula throughout the northeastern United States. Additional field support was provided by D. Redell (WI Department of Natural Resources) and T. Hemberger (KY Department for Fish and Wildlife Resources). We acknowledge Bat Conservation International for helping to bring researchers together from across North America to share data and ideas on WNS. Work reported here was supported directly by the US Geological Survey, the US Fish and Wildlife Service, the New York State Department of Environmental Conservation, and the New York State Department of Health.

Fig. S1
(top)

Fig. S2
(bottom)







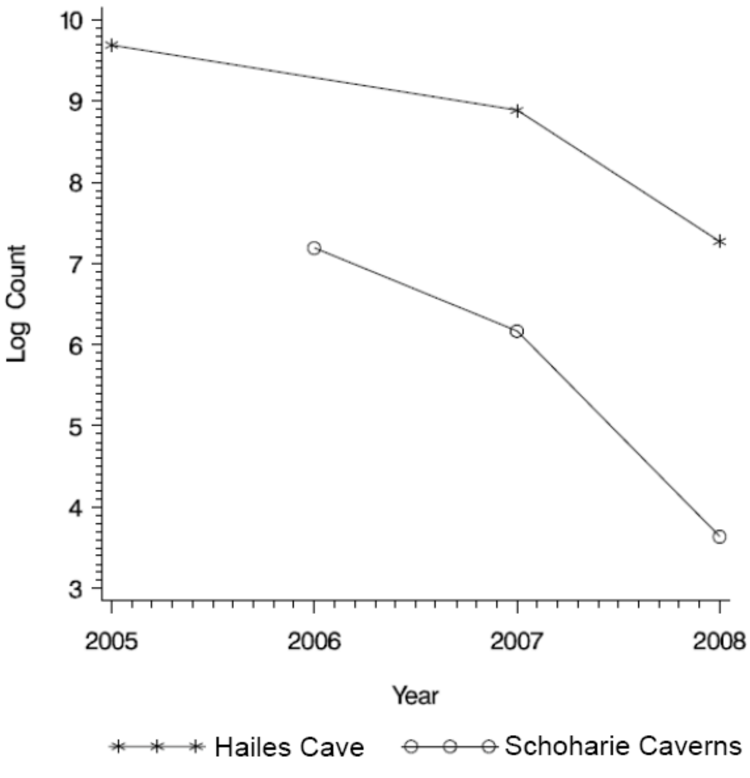


Fig. S3 (top)

Fig. S4
(bottom)

Table S1. Summary of *Geomyces spp.* isolates.

Bat Species	Collection Date	Collection Location	State	GenBank Accessions ITS[a]	GenBank Accessions SSU[b]
Myotis lucifugus	1 April, 2008	Litchfield County Site	CT	EU884924	FJ231093
Myotis septentrionalis	21 March, 2008	Berkshire County Site	MA	EU854570	FJ231094
M. septentrionalis	21 March, 2008	Berkshire County Site	MA	EU854569	FJ231095
M. lucifugus	26 March, 2008	Chester Mine	MA	EU884923	FJ231096
M. lucifugus	29 January, 2008	Hailes Cave	NY	EU884920	FJ231097
M. lucifugus	2 February, 2008	Williams Hotel	NY	EU884921	FJ231098
M. lucifugus	5 March, 2008	Martin Mine	NY	EU854571	FJ231099
M. lucifugus	6 March, 2008	Graphite Mine	NY	EU854572	FJ231100
M. septentrionalis	18 March, 2008	Aeolus Cave	VT	FJ170115	FJ231101
M. lucifugus	18 March, 2008	Aeolus Cave	VT	EU884922	FJ231102

[a] rRNA gene internal transcribed spacer
[b] rRNA gene small subunit

Food Habits of U.S. and Canadian Bat Species

Adapted with permission from: Lollar, A. and B.A.S. French. 1998. *Captive Care and Medical Reference for the Rehabilitation of Insectivorous Bats*, 2002 (2nd Ed.). Bat World Publications, Mineral Wells, TX. 340 pages.

FAMILY MORMOOPIDAE

Species Name	Common Name	Feeding Information and Food Habits
Mormoops megalophylla	Peters's ghost-faced bat	Large moths

FAMILY PHYLLOSTOMIDAE

Species Name	Common Name	Feeding Information and Food Habits
Artibeus jamaicensis	Jamaican fruit-eating bat	Fruit and nectar, including pollen and a few insects.
Choeronycteris mexicana†	Mexican long-tongued bat	Fruit, pollen, nectar, and probably insects.
Leptonycteris curasoae†	Lesser long-nosed bat	Nectar, pollen, and insects.
Leptonycteris nivalis◊	Mexican long-nosed bat	Nectar and pollen; including from the flowers of *Agave* spp.
Macrotus californicus	California leaf-nosed bat	Beetles of the families Scarabaeidae and Carabidae, grasshoppers, cicadas, noctuid moths, caterpillars, remains of sphinx moths, butterflies and dragonflies have been found beneath night-roosting sites; often feeds on the ground.

FAMILY VESPERTILIONIDAE

Species Name	Common Name	Feeding Information and Food Habits
Antrozous pallidus	Pallid bat	Ground beetles, June beetles, moths, crickets (including Jerusalem crickets) froghoppers and leafhoppers, antlions, grasshoppers, scorpions.
Corynorhinus rafinesquii	Rafinesque's big-eared bat	Moths.
Corynorhinus townsendii	Townsend's big-eared bat	Primarily moths; also flies, lacewings, dung beetles and sawflies.
Eptesicus fuscus	Big brown bat	Scrab, June beetles, spotted cucumber beetles, leaf beetles, ground beetles, termites, true bugs, leafhoppers, flying ants.
Euderma maculatum	Spotted bat	Moths.
Idionycteris phyllotis	Allen's big-eared bat	Primarily moths (microlepidopterans), soldier beetles (Cantharidae), dung beetles (Scarabaeidae), leaf beetles (Chrysomelidae), roaches (Blattidae), and flying ants (Formicidae, including Eciton)_
Lasionycteris noctivagans	Silver-haired bat	Moths, bugs, beetles, flies, and caddis flies.
Lasiurus blossevillii	Western red bat	Large moths, beetles, and grasshoppers.
Lasiurus borealis	Eastern red bat	Generalist: Moths, scarab beetles, plant-hoppers, flying ants, leafhoppers, ground beetles, and assassin bugs.
Lasiurus cinereus	Hoary bat	Primarily moths, also beetles, grasshoppers, termites, and dragonflies.
Lasiurus ega	Southern yellow bat	§
Lasiurus intermedius	Northern yellow bat	Leafhoppers, dragonflies, flies, diving beetles, Scotylidae beetles*, ants, and mosquitoes
Lasiurus seminolus	Seminole bat	Moths, true bugs, flies, beetles (including Scolytids*) and ground-dwelling crickets.
Lasiurus xanthinus	Western yellow bat	§
Myotis auriculus	Southwestern myotis	§
Myotis austroriparius	Southeastern myotis	Diptera, Coleoptera, and other flies, including some mosquitoes.
Myotis californicus	Californian myotis	Small moths, flies, and beetles that occur between, within, or below the vegetative canopy.
Myotis ciliolabrum	Western small-footed myotis	Moths, Diptera, Hemiptera, beetles, Homoptera.
Myotis evotis	Long-eared myotis	Leptdoptera, Coleoptera, Diptera, neuroptera, Hymenoptera, Hemiptera, and Homoptera (examples include a cicadellid, a chironomid, a small moth, a scarab beetle, a dragonfly, muscoid fly, Culicid species and other aquatic insects.
Myotis grisescens	Gray myotis	Coleoptera, Lepidoptera, Homoptera, mayflies (Epheneroptera: Ephemeridae), Trichopteria, Hemiptera.
Myotis keenii	Keen's myotis	§
Myotis leibii	Eastern small-footed myotis	Flies (Anthomyiidae), bugs (Jassidae), Agallia, Piesma cinerium, minute Scarabaeidae, Staphylinidae, and ants.

Species Name	Common Name	Feeding Information and Food Habits
Myotis lucifugus	Little brown myotis	Flies, moths, beetles, aquatic insects (water boatman, mayflies, chironomids), moths, midges, mosquitoes, flies, beetles, plant bugs, brown lacewings. ‡
Myotis occultus	Arizona myotis	Aquatic insects (probably mosquitoes and midges)
Myotis septentrionalis	Northern myotis	Moths, beetles, and flies.
Myotis sodalis	Indiana myotis	Lepidoptera, Coleoptera, Diptera, Trichoptera, Hymenoptera (Ichneumonidae), and Homoptera.
Myotis thysanodes	Fringed myotis	Moths, beetles, Homoptera, Diptera
Myotis velifer	Cave myotis	Small moths, weevils, ant lions, small beetles
Myotis volans	Long-legged myotis	Small moths, beetles, flies, Homoptera, Hemiptera
Myotis yumanensis	Yuma myotis	Flies, moths, beetles, frog-hoppers and leafhoppers, June beetles, ground beetles, midges, muscid flies, caddis flies, and crane flies.
Nycticeius humeralis	Evening bat	June beetles, Hemiptera, flyng ants, spittle bugs, June beetles, pomace flies, and moths.
Pipistrellus hesperus	Western pipistrelle	Moths, small beetles, flies, caddis flies, stoneflies, leaf and stilt bugs, leafhoppers, flies, mosquitoes, ants, wasps.
Pipistrellus subflavus	Eastern pipistrelle	Small beetles, small leafhoppers, ground beetles, flies, moths, and ants.

FAMILY MOLOSSIDAE

Species Name	Common Name	Feeding Information and Food Habits
Eumops glaucinus	Wagner's bonneted bat	§
Eumops perotis	Greater bonneted bat	Moths, beetles, flies, crickets, grasshoppers, bees, dragonflies, leaf-bugs, and cicadas.
Eumops underwoodi	Underwood's bonneted bat	Scarab beetles including June beetles (Scarabaeidae), short-hored grasshoppers (Acrididae) including Trimerotropis pallidipennis, leafhoppers (Cicadellidae), moths (Lepidoptera), leaf beetles (Chrysomelidae), plant-hoppers (Fulgoridae), and long-horned beetles (Cerambycidae).
Molossus molossus	Pallas's mastiff bat	§ Perhaps chiefly moths, beetles, and ants.
Nyctinomops femorosaccus	Pocketed free-tailed bat	Moths, crickets, flying ants, stink-bugs, frog-hoppers, leafhoppers, and lacewings.
Nyctinomops macrotis	Big free-tailed bat	Primarily moths, also crickets, flying ants, stink-bugs, froghoppers and leafhoppers.
Tadarida brasiliensis	Mexican free-tailed bat	Moths, flying ants, June beetles, leafhoppers, and true bugs (also midges, mosquitoes, flies, water boatmen, and brown lace-wings‡).

Feeding information given as common names (e.g., moths, etc.), scientific classifications (e.g., family Lepidoptera, etc.) or both, depending on the source.

This table is intended only as a very general guideline. § Information not available from reference sources used. ◊Historical records of Greater long-nosed bats in Arizona refer to *L. curasoae*. However, records of *L. nivalis* from the Peloncillo Mountains near the New Mexico/Arizona border indicate this species may occur in Arizona. † Range and/or capture data includes Portal and the Chiricahua Wilderness in Arizona.

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Additional information from personal communication with John Whitaker and from *Mammalian Species* accounts for the following species: *Idionycteris phyllotis* (#208), *Lasiurus ega* (#515), *Myotis auriculus* (#191), *Myotis evotis* (#329), *Myotis grisescens* (#510), *Myotis sodalis* (#163) and *Eumops underwoodi* (#516).

Prey Selection in a Temperate Zone Insectivorous Bat Community

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I determined foods eaten by bats at Prairie Creek, Vigo County, Indiana, to test the null hypothesis that insectivorous bats eat primarily whatever is available. If bats eat what is available, then all bats taken at the same time and place should eat the same foods. I collected fecal samples from 486 bats of 8 species from 1993 through 1997 in a 650-ha deciduous forest in the Wabash River flood plain. *Eptesicus fuscus* and *Nycticeius humeralis* fed heavily on coleopterans, followed by hemipterans in *E. fuscus* and homopterans in *N. humeralis*. *Lasiurus borealis* fed most heavily on lepidopterans, followed by coleopterans and homopterans. *Pipistrellus subflavus* fed approximately equally on homopterans, coleopterans, and dipterans. The main foods were similar for *Myotis sodalis*, *M. lucifugus*, and *M. septentrionalis*: dipterans 1st, followed by lepidopterans, trichopterans, and then coleopterans in *M. lucifugus* and by coleopterans and then lepidopterans in the other 2 species. It is clear that bats at Prairie Creek selected from among the available foods. *Myotis septentrionalis*, a gleaner, did not eat foods appreciably different from other bats in the same genus.

Key words: bats, Chiroptera, food habits, Indiana

It has been suggested that insectivorous bats, especially *Myotis*, sometimes feed on whatever insects are available at a given time and place (Belwood and Fenton 1976; Fenton and Morris 1976). Availability of insects is very difficult to assess (Fenton 1987; Kunz 1988; Whitaker 1994). Because a large and diverse community of insectivorous bats occurs at my study area at Prairie Creek, Vigo County, Indiana (Whitaker 1996), this provided an excellent opportunity to test the hypothesis that insectivorous bats simply feed on the available insect taxa: if bats eat what is available, then all bats taken at the same time and place should essentially feed on the same foods.

In this study, I compare food habits among 8 species of bats in a single community, and between sexes and juveniles within species, to test the null hypothesis that insectivorous bats simply feed on whatever insects are available. In addition, foods of the gleaning bat Myotis septentrionalis (Brack and Whitaker 2001; Faure et al. 1993) were compared with foods eaten by other bats.

MATERIALS AND METHODS

Ten species of bats currently exist in Indiana, and 9 of these occur at Prairie Creek, which flows into the bottomlands of the Wabash River in southern Vigo County and bisects a 650-ha contiguous woodland before entering the Wabash River in Sullivan County to the south. Eight species are found at Prairie Creek throughout the warm seasons: the evening bat (*Nycticeius humeralis*), the big brown bat (*Eptesicus fuscus*), the northern myotis (*Myotis septentrionalis*), the red bat (*Lasiurus borealis*), the little brown myotis (*Myotis lucifugus*), the eastern pipistrelle (*Pipistrellus subflavus*), the Indiana myotis (*Myotis sodalis*), and the hoary bat (*Lasiurus cinereus*). The silver-haired bat (*Lasionycteris noctivagans*) is found during spring and autumn migration. The species are listed above in approximate order of decreasing abundance (Table 1). The study area and bat fauna were more completely described by Whitaker (1996).

I captured 881 bats of 8 of the species from 1994 through 1997 at Prairie Creek. All bats were released shortly after capture, but many were first placed in plastic bags and held ≤10 min to collect fecal samples.

I obtained fecal samples from 486 bats including all 8 species. In the laboratory, each fecal sample was examined using a 10–70x zoom dissecting microscope (Olympus America SZH, Melville, New York). The series of fecal pellets from each bat was treated as 1 sample. This was done to prevent bias from varying numbers of pellets per bat and because my experience shows that individual pellets within 1 fecal sample show much less variation than do samples from separate bats.

The fecal pellets from each bat were teased apart in a petri dish containing a small amount of alcohol. Food items were identified and the percentage volume of each item was visually estimated. Data were then summarized and total percentage volumes ([sum of

TABLE 1.—Major orders of insects and arachnids eaten by 7 species of bats at Prairie Creek study area, Vigo County, Indiana (given as percentage volume). Totals do not add to 100% because only major food items are included.

Species of bat	*n*	Coleoptera	Lepidoptera	Homoptera	Hemiptera	Diptera	Trichoptera	Neuroptera	Orthoptera	Hymenoptera	Araneae	Totals
Nycticeius humeralis	154	60.1A[a]	3.2D	20.4A	5.7	2.5C	2.2	1.2	0.7	3.9	0.0	99.9
Myotis septentrionalis	107	24.5B	20.7B	3.9B	3.1	37.5A,B	2.5	3.9	0.0	1.2	2.0	99.3
Eptesicus fuscus	85	84.2A	1.7D	2.1B	7.1	0.8C	0.2	2.0	0.1	2.0	0.0	100.2
Lasiurus borealis	45	9.9C	64.4A	10.7A	0.8	3.9C	0.3	2.8	5.0	2.2	0.0	100.0
Myotis lucifugus	51	15.1C	22.0B	3.1B	1.8	41.3A	15.2	0.3	0.0	0.8	0.0	99.6
Pipistrellus subflavus	27	22.6B	12.6C	35.7A	1.1	21.7B	3.0	0.0	0.0	3.3	0.0	100.0
Myotis sodalis	15	26.7B	21.5B	3.0B	0.0	45.8A	2.3	0.3	0.0	0.0	0.0	99.6

[a] Percentage volumes within columns (insect orders) that do not share a letter in common were significantly different ($P < 0.05$ using Student–Newman–Keuls multiple range tests).

individual volumes of food]/[total volume of all samples] × 100) were calculated to determine the foods of each species. Information on the most prevalent foods of each species was summarized to assess whether all species were eating the same foods. I used analysis of variance (ANOVA) on arcsine-transformed percentages to assess differences between major foods. Student–Newman–Keuls multiple range tests were used for mean separation of foods between species and between dates. Only significant differences ($P \leq 0.05$) are mentioned in the text. In some cases, I present results separately by sex, age group, or month. In cases with small sample sizes, I used the nonparametric Mann–Whitney test to assess significance of differences. A similarity index was calculated using the percentage volumes to show relative similarity of the diets, SI ¼ 2W(A þ B), where W ¼ the sum of the similarities between each of the pairs of foods, and A þ B ¼ 200 (100% volume in 1st species and 100% volume in 2nd).

Because *M. septentrionalis* often gleans, and the other species under consideration in this study are presumed to be aerial feeders, it would be logical to hypothesize that the food of *M. septentrionalis* might be quite different from that of the aerial feeders. To test this hypothesis, I compared the food of *M. septentrionalis* with that of the other species, particularly of *M. lucifugus* and *M. sodalis*, because they are the most similar in structure and have the most similar foods of the bats under consideration here.

RESULTS

Relative percentages of major foods of the 7 main bats at Prairie Creek showed many significant differences (Appendix I). Only 2 silver-haired bats were included in the sample, so the species could not be treated statistically. *E. fuscus* and *N. humeralis* fed most heavily on coleopterans followed by homopterans in *N. humeralis*. *L. borealis* fed most heavily on lepidopterans, followed by homopterans and coleopterans. *P. subflavus* fed on homopterans, coleopterans, and dipterans (35.7%, 22.6%, and 21.7%, respectively). With 1 exception, the main 3 foods by percentage volume were the same for *M. sodalis*, *M. lucifugus*, and *M. septentrionalis*: dipterans 1st, followed by lepidopterans, then coleopterans in *M. lucifugus* and by coleopterans then lepidopterans for the other 2 species. The exception was that the *M. lucifugus* fed heavily on trichopterans (15.2%), the only species to feed appreciably on that food, whereas coleopterans were only 15.1% of the diet.

Foods of bats of the genus Myotis.— The most heavily eaten foods of 107 individuals of *M. septentrionalis* (Table 1) from Prairie Creek were dipterans (37.5%), coleopterans (24.5%), and lepidopterans (20.7%). Among the beetles eaten by this species at Prairie Creek, scarabaeid beetles were most abundant. Spiders formed an appreciable portion of the diet overall (2.0%). The spiders are probably taken by gleaning. Juvenile *M. septentrionalis* had eaten 21.3% spiders, much of this item in July. On a seasonal basis, *M. septentrionalis* fed heavily on dipterans in April, May, July, and September. Coleopterans formed a relatively high percentage in May–August (17.7–74.7%), and a low percentage (8.8–11.5%) in April and September. Among coleopterans, scarabaeids were most heavily eaten in June (41.3%), and Diabrotica in August (14.0%). Lepidopterans formed a relatively high percentage in April (19.4%), then decreased through May and June but increased again through the rest of the year. Cicadellids were most heavily eaten in late summer, particularly in August. Brown lacewings (Hemerobiidae) formed a small but stable amount of the food throughout the season.

Mosquitos and scarabaeids formed 4.4% and 13.4% of the diet of female *M. septentrionalis*, and in both cases this was greater than the amount eaten by males (0.7% and 2.4% volume, respectively); total dipterans were higher in females than in males (41.4% and 24.0%, respectively), whereas lepidopterans and cicadellids were more heavily eaten by males than females (28.9%

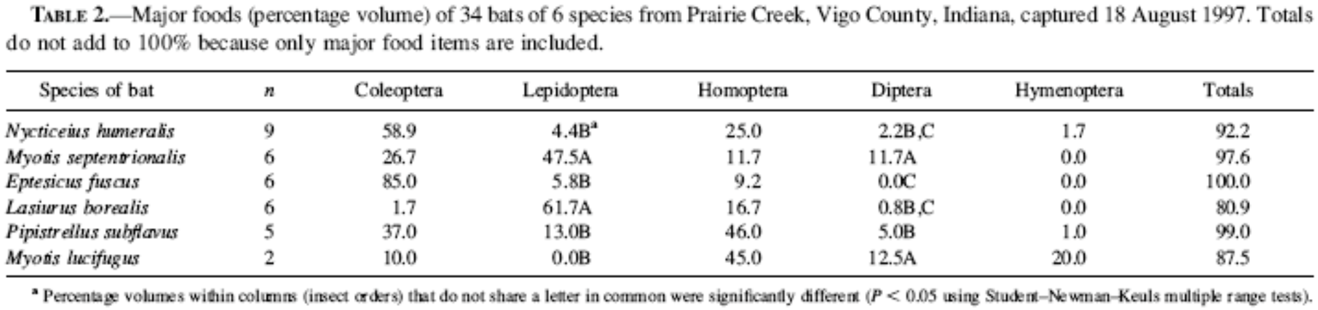


TABLE 2.—Major foods (percentage volume) of 34 bats of 6 species from Prairie Creek, Vigo County, Indiana, captured 18 August 1997. Totals do not add to 100% because only major food items are included.

Species of bat	*n*	Coleoptera	Lepidoptera	Homoptera	Diptera	Hymenoptera	Totals
Nycticeius humeralis	9	58.9	4.4B[a]	25.0	2.2B,C	1.7	92.2
Myotis septentrionalis	6	26.7	47.5A	11.7	11.7A	0.0	97.6
Eptesicus fuscus	6	85.0	5.8B	9.2	0.0C	0.0	100.0
Lasiurus borealis	6	1.7	61.7A	16.7	0.8B,C	0.0	80.9
Pipistrellus subflavus	5	37.0	13.0B	46.0	5.0B	1.0	99.0
Myotis lucifugus	2	10.0	0.0B	45.0	12.5A	20.0	87.5

[a] Percentage volumes within columns (insect orders) that do not share a letter in common were significantly different ($P < 0.05$ using Student–Newman–Keuls multiple range tests).

and 11.0%, as compared with 19.5% and 1.6%). The only differences that were significant were those of cicadellids. Only 4 juvenile *M. septentrionalis* are included, but they appeared to feed more (greater volume percentages) on coleopterans, cicadellids, and spiders and less on lepidopterans than did the adults.

The main foods of *M. lucifugus* were dipterans, lepidopterans, trichopterans, and coleopterans (Table 1). This was the only species that fed appreciably on trichopterans at Prairie Creek. None of the differences by season, sex, or age within this species were significant. The main foods of *M. sodalis* were dipterans, coleopterans, and lepidopterans (Table 1). All monthly samples were small, but collectively the 3 foods represented a major proportion of food of *M. sodalis* throughout the season. Dipterans were more heavily eaten by males, lepidopterans by females (Appendix I).

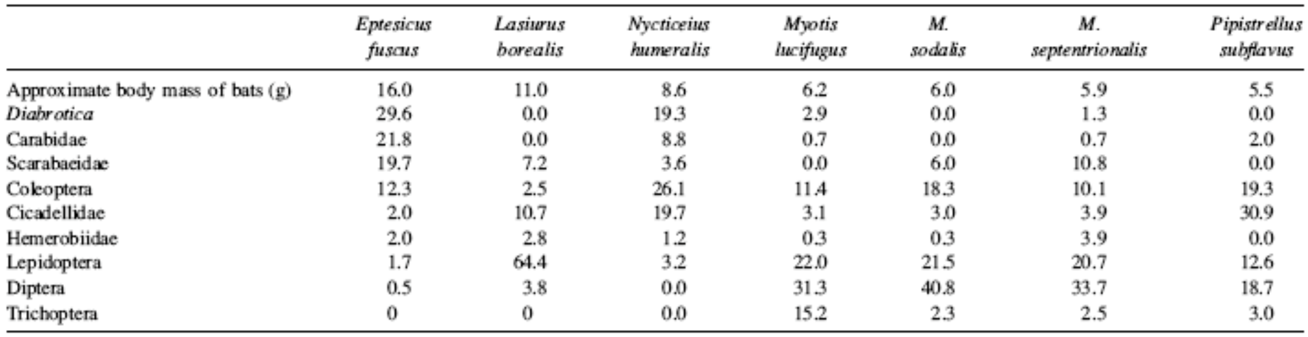
Foods of other species of bats.— The major foods of 154 individuals of *N. humeralis* (Table 1) were beetles (60.1%), homopterans (20.4%, mostly cicadellids), and hemipterans (5.7%). Coleopterans formed roughly this percentage of the food throughout the season, varying from 46.9% to 73.7% during the various months, whereas homopterans (cicadellids) were eaten by *N. humeralis* primarily in July, August, and September, presumably reflecting their availability in those months. Lepidopterans made up only 3.2% of the food overall. The most important coleopteran was the spotted cucumber beetle, Diabrotica undecimpunctata. Coleopterans were the most dominant food for *N. humeralis*, and miscellaneous or unidentified coleopterans were heavily eaten (over 10% of the volume) in every month, but were most eaten in June and July. Scarabaeids were heavily eaten in May but not later. Diabrotica undecimpunctata was heavily eaten in late summer. Trichoptera and Lepidoptera were major items in May only.

It is difficult to discern differences in foods between the sexes of *N. humeralis* because only 4 males were included. Foods were similar between adults and juveniles (Appendix I). However, there were no carabids in the scats of juveniles, whereas this item comprised 9.9% of the volume of food in adult females. Unidentified beetles tended to be higher in juveniles than in females, but this was not significant (38.4% compared with 23.7%, u ¼ 811, P ¼ 0.18). The carabids may have been fairly hard for the younger bats, and perhaps the difference in unidentified beetles could be due to inclusion of smaller beetles.

Eptesicus fuscus fed heavily on coleopterans. They were the main food of this species in every month but April, ranging from 83% to 98% beetles by volume from May to October. The sample for April from Prairie Creek consisted of only 2 bats, which ate 25% Lepidoptera, plus Hemiptera (15%) and Ichneumonidae (32.5%; Table 1; Appendix I). Beetles were eaten equally by both sexes, 84.4% in females, 83.8% in males, followed distantly by pentatomids (7.6%, 6.3%). Volumes of food eaten by males and females were quite similar in most cases, although hemerobiids were eaten in significantly greater amounts by females (u ¼ 704.5, P ¼ 0.004). Seasonally, scarabaeids were most heavily eaten in May, June, and July, with the values from May and June significantly higher than in all other months. Carabids were eaten in October, August, July, and May. Ichneumonids and lepidopterans formed a signifi- cantly greater volume of the diet in April (probably when prey was limited).

Lasiurus borealis favored moths (Table 1). Only a small number of red bats was taken in April–July or in October (1, 3, 1, 3, and 4 bats); lepidopterans formed 85%, 50%, 0%, 35%, and 85% of the volume in those months. In August and September, larger numbers of red bats were included (17 and 14) and moths formed 49% and 93% of the diet by volume. Lepidopterans thus formed a major part of the food of *L. borealis* throughout the year. Coleoptera had the 2nd greatest volume overall (10.7%), which varied during the months

TABLE 3.—Body size and foods (percentage volume) of bats at Prairie Creek, Vigo County, Indiana, arranged from largest to smallest species of bat.



	Eptesicus fuscus	*Lasiurus borealis*	*Nycticeius humeralis*	*Myotis lucifugus*	*M. sodalis*	*M. septentrionalis*	*Pipistrellus subflavus*
Approximate body mass of bats (g)	16.0	11.0	8.6	6.2	6.0	5.9	5.5
Diabrotica	29.6	0.0	19.3	2.9	0.0	1.3	0.0
Carabidae	21.8	0.0	8.8	0.7	0.0	0.7	2.0
Scarabaeidae	19.7	7.2	3.6	0.0	6.0	10.8	0.0
Coleoptera	12.3	2.5	26.1	11.4	18.3	10.1	19.3
Cicadellidae	2.0	10.7	19.7	3.1	3.0	3.9	30.9
Hemerobiidae	2.0	2.8	1.2	0.3	0.3	3.9	0.0
Lepidoptera	1.7	64.4	3.2	22.0	21.5	20.7	12.6
Diptera	0.5	3.8	0.0	31.3	40.8	33.7	18.7
Trichoptera	0	0	0.0	15.2	2.3	2.5	3.0

from 0% to 67%.

Homopterans (mostly cicadellids), coleopterans, dipterans, and lepidopterans were the most abundant foods in feces of 27 *P. subflavus* examined from Prairie Creek (Table 1). Cercopids were found in feces of males only, and dipterans were more abundant in females. Dipterans were highest in May, June, and September. Cicadellids were taken in ever increasing numbers from May through August. Coleopterans were present in the diet of *P. subflavus* and were relatively high in June–August; ants (Formicidae) occurred only in July (17.0%), trichopterans were highest in May (9.0%) and September (10.0%), and lygaeids were highest in June (15.0%). The only significant differences in diet by month for P. subflavus involved dipterans, cercopids, and lygaeids.

Fecal pellets from only 2 individuals of *L. noctivagans* were available. These were taken on the same date (3 October 1994), and each contained 5 foods with percentage volumes as follows: Lepidoptera (43.5%), brown lacewing, Hemerobiidae (30%), ant, Formicidae (7.5%), Diptera (2.3%), and midge, Chironomidae (1.5%).

Foods of bats eaten on a single night.— Foods of 34 bats of 6 species taken on 1 date at 1 site (16 August 1998) at Prairie Creek were compared as a further test of whether foods were taken based on availability. The foods eaten by these bats (Table 2) showed similar variation to the larger sample. In both samples, beetles were the main foods of both *N. humeralis* and *E. fuscus* and higher in *E. fuscus*. Moths were low in both. Cicadellids were important in both of these species but were much more important in *N. humeralis*.

Moths were the main food of *L. borealis*, followed by cicadellids. P. subflavus fed on cicadellids, beetles and moths; *M. septentrionalis* fed on moths, beetles, flies, and cicadellids; and *M. lucifugus* fed on cicadellids, ichneumons, and flies. Thus, on a single night with bats all captured at the same place, the various species fed on different prey but the diet was similar to that expected based on observations over longer periods (Table 1).

Food as related to size of bat.— The food habits of 7 species of bats from Prairie Creek were examined by decreasing size of bat (Table 3). There was no apparent relationship between size of bat and food. The largest bat was a beetle feeder (about 80% beetles), the 2nd largest was a moth feeder (64.4% moths), the 3rd largest was again a beetle (60%) and leafhopper (20%) feeder. The three species of *Myotis* were the most similar, even though one, *M. septentrionalis*, has the ability to glean. The species of *Myotis* fed heavily on dipterans, lepidopterans and coleopterans, although *M. lucifugus* took quite a few trichopterans. The smallest bat, the pipistrelle, fed on cicadellids, beetles, dipterans, and lepidopterans. No correlations existed between size of bat and proportion in the diet for Coleoptera (r ¼ 0.643, P ¼ 0.589), Lepidoptera (r ¼ 0.107, P ¼ 0.819), Cicadellidae (r ¼ 0.429, P ¼ 0.337), and Diptera (r ¼ 0.643, P ¼ 0.119).

Similarity of diets among species.— Similarity of foods eaten by the various species is indicated by similarity indices (SI). The 3 species of *Myotis* have the highest similarity in food habits (Fig. 1). *P. subflavus* fits loosely into this grouping, whereas it is much less consistent with the *E. fuscus–N. humeralis* group at 0.429. *P. subflavus* shows a SI index with *N. humeralis* of 553. This is because both fed highly on Coleoptera and Hemiptera. *L. borealis* also fits loosely into this group, with a SI of 0.402. Likewise, *L. borealis* is distant but closer to the *Myotis* stem than to the *E. fuscus–N. humeralis* stem.

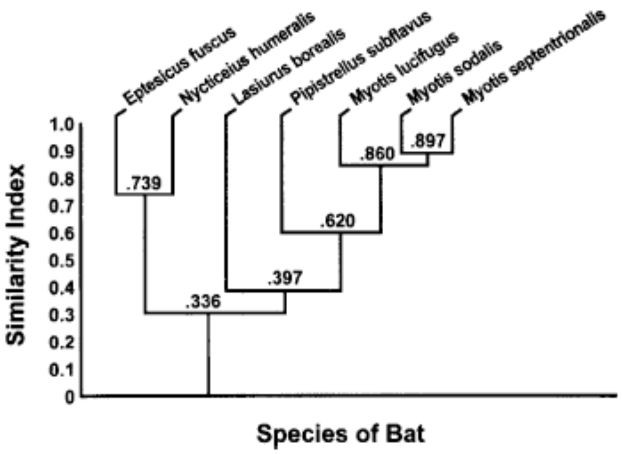


Figure 1. Dendrogram showing dietary relatioships of bats at Prairie creek, Vigo County, Indiana. The highest numbers indicate the greatest similarity in food habits.

DISCUSSION

The bats under study were selecting different foods from among the available items. Why? This is a complicated question, but has been partially discussed by Brigham (1990), Fenton (1987), Kunz (1988), and Whitaker (1994). By necessity, foods eaten by bats are most similar to available foods when foods are limited because the bats have little choice at that time. This is most likely to occur early and late in the season (Whitaker 1995) or perhaps in the high latitudes (see Barclay 1985). When conditions are good, such as in midseason, bats usually select from a variety of various beetles, moths, flies, homopterans, hemipterans, some hyme- nopterans, and often others.

Certain foods, such as caddisflies, termites, and flying ants, are irregularly available but are apparently highly desired (see Brigham 1990). Reasons for selectivity probably ultimately relate to an initial evolutionary division of food supplies by bats through competitive exclusion, as suggested by O'Shea and Vaughan (1980) and as discussed by Wiens (1977). It is presumably advantageous for different species of bats to feed on different foods to minimize competition. Once they begin to feed on differing foods, they can undergo evolutionary adaptation to better feed on their differing prey. Bat species differ in size, speed, behavior, echolocation, and strength of jaws, and insects vary greatly in size, speed, and behavior. All of these factors, and probably more, allow bats to fly in different habitats and in different ways and to feed on differing foods.

Because bats have the ability to fly fairly long distances, a note is necessary on the availability of food and flight. All the species had access to the entire Prairie Creek area and all of its food resources. However, because of their varying habits and behaviors, flight speed, preferred foraging habitats, and echolocation characteristics, the various species of bats forage in different areas, presumably to take advantage of selected foods where they occur. However, it is not advantageous for bats to become overspecialized to feed on only 1 or a few kinds of insects. Rather, even though they have some feeding adaptations, they have retained the ability to feed on a large number of items, which serves to allow them to take more of whatever is available when food is limited.

Eptesicus fuscus and *N. humeralis* have heavy jaws (Freeman 1981), allowing them to feed on larger beetles and hemipterans. *L. borealis* has long narrow wings (Aldridge and Rautenbach 1987; Fenton 1983), allowing them to fly fast to capture moths, many of which have various protective mechanisms. *Myotis* and *P. subflavus* have broad wings and slow flight (Aldridge 1986; Fenton 1983), allowing them to fly more slowly in crowded habitats. Bats also differ greatly in size. In Indiana, for example, bats range from *P. subflavus*, with an 18-cm wingspread and a small body and mouth, to *L. cinereus*, with a wingspread up to about 38 cm and with a large mouth. This allows for major differences in the size of foods that can be eaten. Insects eaten by bats must be small enough to be overcome in flight but large enough to be efficient to take. Adaptation by size classes of insects is not entirely apparent from my data. For example, the coleopterans eaten by *E. fuscus* (which has a body mass of 16.0 g) average much larger than those eaten by *M. lucifugus* (mass of 6.2 g). Many of these differences are masked by grouping insect prey remains under ordinal categories such as Coleoptera, Lepidoptera, or Diptera. Differences in sizes of food items among species of bats would probably be much more pronounced if we could identify all foods of bats to family or species and to quantify variation in size of prey. See Whitaker and Clem (1992), Whitaker (1994), and Brigham and Saunders (1990) for more information on *N. humeralis* and *E. fuscus*.

Trichopterans deserve special comment. They, along with flying ants and termites, are apparently highly desirable to many species of bats, as they are eaten by many species of bats when available, although they are intermittent in occurrence. That *M. lucifugus*, but no other species at Prairie Creek, fed heavily on these was unexpected. It would appear that trichopterans were not

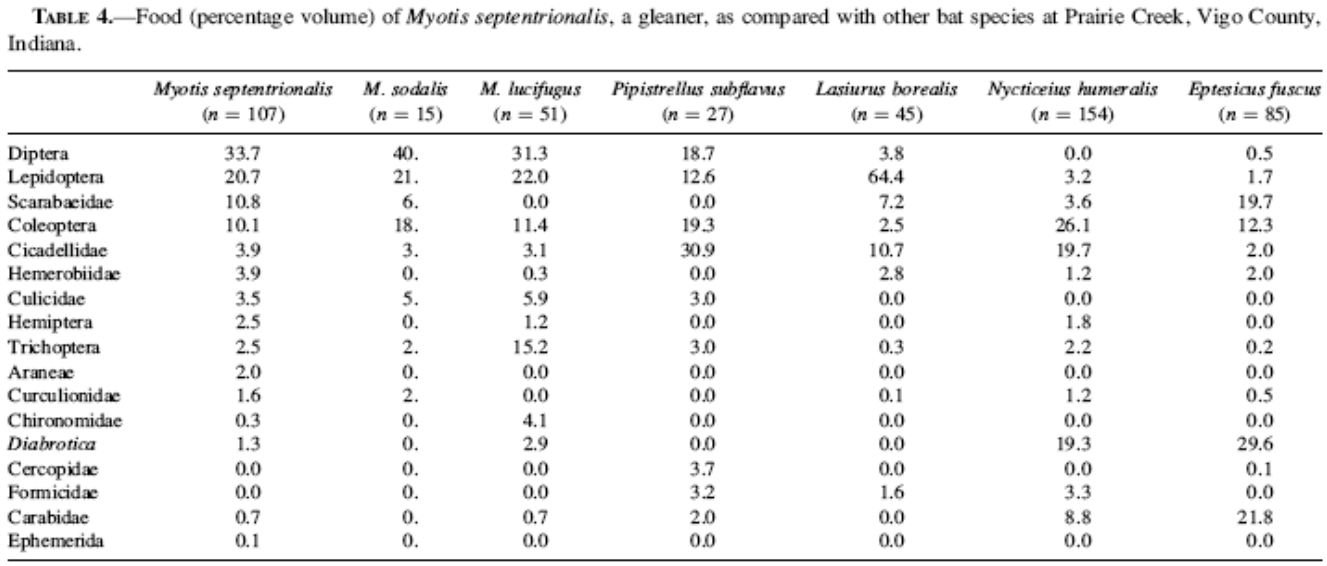


TABLE 4.—Food (percentage volume) of *Myotis septentrionalis*, a gleaner, as compared with other bat species at Prairie Creek, Vigo County, Indiana.

	Myotis septentrionalis ($n = 107$)	*M. sodalis* ($n = 15$)	*M. lucifugus* ($n = 51$)	*Pipistrellus subflavus* ($n = 27$)	*Lasiurus borealis* ($n = 45$)	*Nycticeius humeralis* ($n = 154$)	*Eptesicus fuscus* ($n = 85$)
Diptera	33.7	40.	31.3	18.7	3.8	0.0	0.5
Lepidoptera	20.7	21.	22.0	12.6	64.4	3.2	1.7
Scarabaeidae	10.8	6.	0.0	0.0	7.2	3.6	19.7
Coleoptera	10.1	18.	11.4	19.3	2.5	26.1	12.3
Cicadellidae	3.9	3.	3.1	30.9	10.7	19.7	2.0
Hemerobiidae	3.9	0.	0.3	0.0	2.8	1.2	2.0
Culicidae	3.5	5.	5.9	3.0	0.0	0.0	0.0
Hemiptera	2.5	0.	1.2	0.0	0.0	1.8	0.0
Trichoptera	2.5	2.	15.2	3.0	0.3	2.2	0.2
Araneae	2.0	0.	0.0	0.0	0.0	0.0	0.0
Curculionidae	1.6	2.	0.0	0.0	0.1	1.2	0.5
Chironomidae	0.3	0.	4.1	0.0	0.0	0.0	0.0
Diabrotica	1.3	0.	2.9	0.0	0.0	19.3	29.6
Cercopidae	0.0	0.	0.0	3.7	0.0	0.0	0.1
Formicidae	0.0	0.	0.0	3.2	1.6	3.3	0.0
Carabidae	0.7	0.	0.7	2.0	0.0	8.8	21.8
Ephemerida	0.1	0.	0.0	0.0	0.0	0.0	0.0

widespread at Prairie Creek, but that they were abundant where *M. lucifugus* was feeding for a short period in midsummer. Apparently other species were not aware of the trichopterans.

The various species of bats at Prairie Creek differed in the major foods eaten. A number of mosquitos (Culicidae) were eaten by bats examined during this study, although most bats, contrary to popular opinion, do not eat many mosquitos (Whitaker and Long 1998). The study area is in a swamp where mosquitos were numerous. Whitaker and Long (1998) have proposed that most of the mosquitos eaten by bats may be from male swarms. This may be the situation at Prairie Creek, or it may be that so many mosquitos were present that it was inevitable that some were taken by the bats.

Studies of wing morphology by Aldridge (1986), Aldridge and Rautenbach (1987), and Norberg and Rayner (1987) and of echolocation by Neuweiler (1984) and Neuweiler and Fenton (1988) have led to hypotheses about foraging habitats and strategies of various species of bats. Bats with broad wings can fly slowly and hover, and bats with high frequency and short duration calls (whispering bats) can pick up detail at short range. These calls have the added advantage of not being audible at a very great range, thus helping keep prey from being warned. These flight and echolocation characteristics help bats to find and pick items from surfaces, i.e., to glean. Analysis of food habits can provide clues that a species might be a gleaner, through the presence of non-flying items, such as spiders, crickets, or caterpillars.

Myotis septentrionalis has the wing structure and echolocation calls characteristic of gleaners, and Miller and Treat (1993) recorded this species picking insects off a backlit screen. Faure et al. (1993) also demonstrated this species to be a gleaner. This species often feeds on spiders. In a sample of 172 fecal pellets from Arkansas examined by Whitaker, spiders occurred in 8 (4.7%) fecal pellets and made up an estimated 1.3% of the volume (J. D. Wilhide, in litt.). Brack and Whitaker (2001) found spiders in 16 of 63 (25.4%) fecal pellets *M. septentrionalis* taken by harp trap at Copperhead Cave, a mine in Vermillion County, Indiana, forming 9.1% of the total volume of food in that sample.

Comparison of the food of *M. septentrionalis* was not radically different from that of *M. sodalis* or *M. lucifugus* (Table 47). The similarity of these data might suggest that these 3 species are feeding in much the same manner, whether it be gleaning or hawking or both. Spiders were the only clearly non-flying items taken regularly during this study and provide the strongest evidence for gleaning, but they were taken only by *M. septentrionalis*. Because the remainder of the food was so similar, I suspect that *M. septentrionalis* and the other 2 species were getting most of their food by hawking, but that *M. septentrionalis* is supplementing this by gleaning (mostly spiders). I consider this hypothesis as tenable, but I think that there would probably be more differences in foods if this were the case.

Possibly all 3 species of *Myotis* were spending some time gleaning. If so, it would appear that all 3 should take numerous spiders. That this hypothesis could be tenable is supported by data on *M. lucifugus* from Alaska. *M. lucifugus* is not considered to be a gleaner and usually does not eat many spiders. However, Whitaker and Lawhead (1992) examined 100 fecal pellets from *M. lucifugus* from Alaska. These bats were using 3 foods, lepidopterans (71.1% volume), spiders (16.8%), and dipterans (3.7%). The spiders were found in 36 of the pellets. Because of the 24-h daylight, bats in Alaska must feed in daylight in June. I suggest that the large percentage of spiders eaten by this species in Alaska indicates that these bats were spending much of their foraging time in the forest gleaning rather than hawking insects in daylight in the open air, where exposure to diurnal predatory birds could be substantial. If the Alaskan bats were getting spiders by gleaning and thus avoiding predators, it might follow that much of their other food (i.e., many or most of the lepidopterans and dipterans) were also captured by gleaning. If that were true, I suggest that many of the lepidopterans and dipterans eaten by *M. septentrionalis* at Prairie Creek could have been gotten by gleaning, and further, if M. lucifugus gleans in Alaska, then it and *M. sodalis* might also glean at Prairie Creek.

The occurrence of spiders as food items indicates that *M. septentrionalis* is gleaning to some degree, but there was no solid evidence that the other 2 species of *myotis* were gleaning at all. This suggests that *M. septentrionalis* gleaned more than the other 2 species, but that none of the 3 species was spending appreciable time gleaning. This appears to me to be the most tenable hypothesis for the bats at Prairie Creek.

Perhaps many species of bats, such as *M. lucifugus*, can glean at times, and some, such as *M. septentrionalis*, glean more often and become adapted for it. Faure et al. (1993) found that the calls of the gleaning insectivorous bat *M. septentrionalis* are less detectable to noctuid moths than are those of aerial-feeding *M. lucifugus*. It is possible that *M. lucifugus* (and *M. sodalis*) glean more than previously suspected even though they are not as specifically adapted to glean as *M. septentrionalis*. If so, it would seem likely that these species may use different styles of echolocation when gleaning than when aerial hawking. See Anthony and Kunz (1977), Brack and Laval (1985), and Brack and Whitaker (2001) for additional information on food of these bats.

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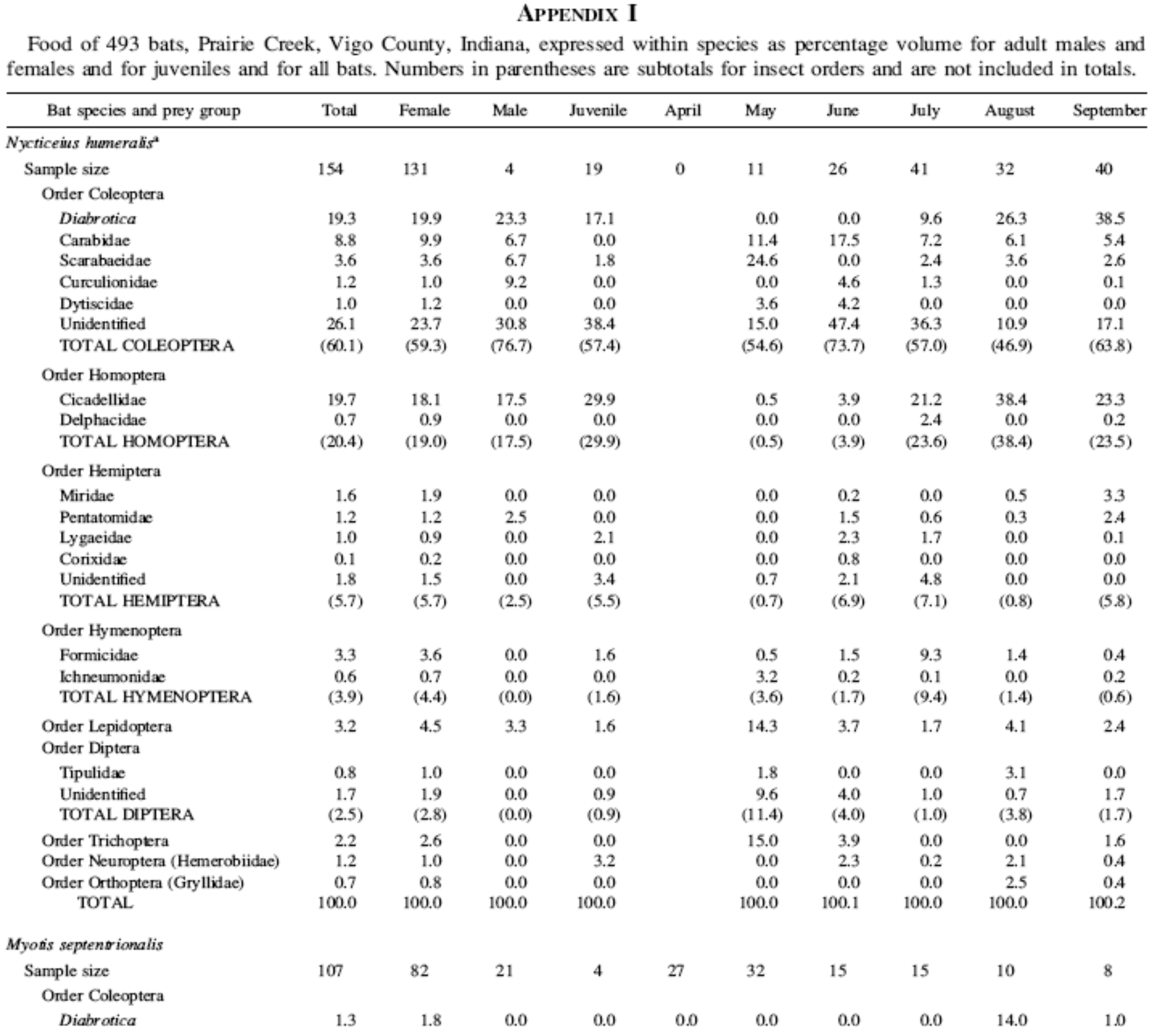

APPENDIX I

Food of 493 bats, Prairie Creek, Vigo County, Indiana, expressed within species as percentage volume for adult males and females and for juveniles and for all bats. Numbers in parentheses are subtotals for insect orders and are not included in totals.

Bat species and prey group	Total	Female	Male	Juvenile	April	May	June	July	August	September
Nycticeius humeralis[a]										
Sample size	154	131	4	19	0	11	26	41	32	40
Order Coleoptera										
Diabrotica	19.3	19.9	23.3	17.1		0.0	0.0	9.6	26.3	38.5
Carabidae	8.8	9.9	6.7	0.0		11.4	17.5	7.2	6.1	5.4
Scarabaeidae	3.6	3.6	6.7	1.8		24.6	0.0	2.4	3.6	2.6
Curculionidae	1.2	1.0	9.2	0.0		0.0	4.6	1.3	0.0	0.1
Dytiscidae	1.0	1.2	0.0	0.0		3.6	4.2	0.0	0.0	0.0
Unidentified	26.1	23.7	30.8	38.4		15.0	47.4	36.3	10.9	17.1
TOTAL COLEOPTERA	(60.1)	(59.3)	(76.7)	(57.4)		(54.6)	(73.7)	(57.0)	(46.9)	(63.8)
Order Homoptera										
Cicadellidae	19.7	18.1	17.5	29.9		0.5	3.9	21.2	38.4	23.3
Delphacidae	0.7	0.9	0.0	0.0		0.0	0.0	2.4	0.0	0.2
TOTAL HOMOPTERA	(20.4)	(19.0)	(17.5)	(29.9)		(0.5)	(3.9)	(23.6)	(38.4)	(23.5)
Order Hemiptera										
Miridae	1.6	1.9	0.0	0.0		0.0	0.2	0.0	0.5	3.3
Pentatomidae	1.2	1.2	2.5	0.0		0.0	1.5	0.6	0.3	2.4
Lygaeidae	1.0	0.9	0.0	2.1		0.0	2.3	1.7	0.0	0.1
Corixidae	0.1	0.2	0.0	0.0		0.0	0.8	0.0	0.0	0.0
Unidentified	1.8	1.5	0.0	3.4		0.7	2.1	4.8	0.0	0.0
TOTAL HEMIPTERA	(5.7)	(5.7)	(2.5)	(5.5)		(0.7)	(6.9)	(7.1)	(0.8)	(5.8)
Order Hymenoptera										
Formicidae	3.3	3.6	0.0	1.6		0.5	1.5	9.3	1.4	0.4
Ichneumonidae	0.6	0.7	0.0	0.0		3.2	0.2	0.1	0.0	0.2
TOTAL HYMENOPTERA	(3.9)	(4.4)	(0.0)	(1.6)		(3.6)	(1.7)	(9.4)	(1.4)	(0.6)
Order Lepidoptera	3.2	4.5	3.3	1.6		14.3	3.7	1.7	4.1	2.4
Order Diptera										
Tipulidae	0.8	1.0	0.0	0.0		1.8	0.0	0.0	3.1	0.0
Unidentified	1.7	1.9	0.0	0.9		9.6	4.0	1.0	0.7	1.7
TOTAL DIPTERA	(2.5)	(2.8)	(0.0)	(0.9)		(11.4)	(4.0)	(1.0)	(3.8)	(1.7)
Order Trichoptera	2.2	2.6	0.0	0.0		15.0	3.9	0.0	0.0	1.6
Order Neuroptera (Hemerobiidae)	1.2	1.0	0.0	3.2		0.0	2.3	0.2	2.1	0.4
Order Orthoptera (Gryllidae)	0.7	0.8	0.0	0.0		0.0	0.0	0.0	2.5	0.4
TOTAL	100.0	100.0	100.0	100.0		100.0	100.1	100.0	100.0	100.2
Myotis septentrionalis										
Sample size	107	82	21	4	27	32	15	15	10	8
Order Coleoptera										
Diabrotica	1.3	1.8	0.0	0.0	0.0	0.0	0.0	0.0	14.0	1.0

APPENDIX I.—Continued.

Bat species and prey group	Total	Female	Male	Juvenile	April	May	June	July	August	September
Unidentified	10.1	8.4	13.0	28.8	5.0	4.8	22.7	20.9	14.5	8.0
TOTAL COLEOPTERA	(24.5)	(25.4)	(19.7)	(31.3)	(9.8)	(17.7)	(74.7)	(21.5)	(33.5)	(11.5)
Order Homoptera										
Cicadellidae	3.9	1.6	11.0	13.8	1.1	0.6	3.0	5.3	13.0	7.5
Delphacidae	0.1	0.0	0.2	0.0	0.0	0.0	0.3	0.0	0.0	0.0
TOTAL HOMOPTERA	(3.9)	(1.6)	(11.2)	(13.8)	(1.1)	(0.6)	(3.3)	(5.3)	(13.0)	(7.5)
Order Hemiptera										
Lygaeidae	0.6	0.8	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0
Unidentified	2.5	3.1	0.0	2.5	2.8	2.0	0.0	2.0	4.0	6.9
TOTAL HEMIPTERA	(3.1)	(3.9)	(0.0)	(2.5)	(2.8)	(4.1)	(0.0)	(2.0)	(4.0)	(6.9)
Order Hymenoptera (Ichneumonidae)	1.2	0.8	3.1	0.0	0.0	2.0	0.0	4.3	0.0	0.0
Order Lepidoptera	20.7	19.5	28.9	2.5	19.4	13.8	5.3	34.1	33.0	41.0
Order Diptera										
Culicidae	3.5	4.4	0.7	0.0	7.6	3.3	0.0	4.3	0.0	0.0
Chironomidae	0.3	0.5	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0
Unidentified	33.7	36.6	23.3	28.8	55.4	48.3	1.2	13.0	7.0	31.9
TOTAL DIPTERA	(37.5)	(41.4)	(24.0)	(28.8)	(63.0)	(52.5)	(1.2)	(17.3)	(7.0)	(31.9)
Order Trichoptera	2.5	2.4	3.1	0.0	0.0	5.2	5.8	0.0	0.0	1.3
Order Neuroptera (Hemerobiidae)	3.9	2.6	9.5	0.0	2.6	3.8	6.0	5.3	5.5	0.0
Araneae	2.0	1.6	0.0	21.3	0.7	0.2	0.0	10.0	4.0	0.0
Unidentified insect	0.7	0.9	0.0	0.0	0.6	0.0	3.7	0.0	0.0	0.0
Order Ephemeroptera	0.1	0.0	0.5	0.0	0.0	0.3	0.0	0.0	0.0	0.0
TOTAL	100.0	100.1	100.0	100.0	100.0	100.1	100.0	100.0	100.0	100.1
Eptesicus fuscus[b]										
Sample size	85	51	34	0	2	8	3	16	30	19
Order Coleoptera										
Diabrotica	29.6	24.6	37.1		0.0	0.0	0.0	6.3	28.9	70.3
Carabidae	21.8	22.1	21.3		0.0	25.0	0.0	28.8	29.7	2.1
Scarabaeidae	19.7	19.1	20.5		0.0	73.3	81.7	30.6	11.1	0.4
Curculionidae	0.5	0.8	0.2		0.0	0.0	0.0	0.0	0.2	2.1
Dytiscidae	0.3	0.5	0.0		0.0	0.0	0.0	1.6	0.0	0.0
Unidentified	12.3	17.2	4.9		27.5	0.0	13.3	23.8	10.8	8.1
TOTAL COLEOPTERA	(84.2)	(84.4)	(83.9)		(27.5)	(98.3)	(95.0)	(90.9)	(80.7)	(83.0)
Order Homoptera										
Cicadellidae	2.0	2.1	1.9		0.0	0.0	0.0	1.6	2.4	1.5
Cercopidae	0.1	0.2	0.0		0.0	0.0	0.0	0.0	0.3	0.0
TOTAL HOMOPTERA	(2.1)	(2.3)	(1.9)		(0.0)	(0.0)	(0.0)	(1.6)	(2.7)	(1.5)
Order Hemiptera										
Pentatomidae	6.5	7.3	5.4		15.0	1.5	0.0	2.8	11.1	7.3
Lygaeidae	0.2	0.0	0.6		0.0	0.0	0.0	0.0	0.0	1.1
Coreidae	0.3	0.3	0.3		0.0	0.0	0.0	0.6	0.5	0.0
TOTAL HEMIPTERA	(7.1)	(7.6)	(6.3)		(15.0)	(1.5)	(0.0)	(3.4)	(11.6)	(8.4)
Order Hymenoptera (Ichneumonidae)	2.0	2.2	1.7		32.5	0.0	0.0	0.0	1.5	2.3
Order Lepidoptera	1.7	2.1	1.0		25.0	0.0	5.0	0.0	1.1	2.1
Order Diptera										
Tipulidae	0.2	0.4	0.0		0.0	0.0	0.0	0.0	0.3	0.5
Culicidae	0.0	0.0	0.0		0.0	0.3	0.0	0.0	0.0	0.0
Chironomidae	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0	0.1
Unidentified	0.5	0.4	0.6		0.0	0.0	0.0	0.0	0.7	0.6
TOTAL DIPTERA	(0.8)	(0.8)	(0.6)		(0.0)	(0.3)	(0.0)	(0.0)	(1.0)	(1.2)
Order Trichoptera	0.20	0.3	0		0.0	0.0	0.0	0.0	0.5	0.0
Order Neuroptera (Hemerobiidae)	2.0	0.2	4.6		0.0	0.0	0.0	4.1	1.0	1.1
Order Orthoptera (Gryllidae)	0.1	0.2	0.0		0.0	0.0	0.0	0.0	0.0	0.5
TOTAL	100.0	100.0	100.0		100.0	100.3	100.0	100.0	100.0	100.2
Lasiurus borealis[c]										
Sample size	45	33	12	0	1	3	1	3	17	14

APPENDIX I.—Continued.

Bat species and prey group	Total	Female	Male	Juvenile	April	May	June	July	August	September
Order Coleoptera										
Diabrotica	0.0	0.1	0.0		0.0	0.0	0.0	0.0	0.1	0.0
Scarabaeidae	7.2	9.9	0.0		0.0	61.7	0.0	46.7	0.0	0.0
Curculionidae	0.1	0.2	0.0		0.0	1.7	0.0	0.0	0.0	0.0
Unidentified	2.5	3.4	0.0		15.0	3.3	5.0	18.3	1.7	0.0
TOTAL COLEOPTERA	(9.9)	(13.5)	(0.0)		(15.0)	(66.7)	(5.0)	(65.0)	(1.8)	(0.0)
Order Homoptera (Cicadellidae)	10.7	12.5	5.8		0.0	0.0	0.0	0.0	26.9	1.8
Order Hemiptera (Pentatomidae)	0.8	1.1	0.0		0.0	0.0	0.0	0.0	2.2	0.0
Order Hymenoptera										
Formicidae	1.6	2.1	0.0		0.0	0.0	45.0	0.0	1.5	0.0
Ichneumonidae	0.6	0.5	1.2		0.0	0.0	0.0	0.0	0.0	1.8
TOTAL HYMENOPTERA	(2.2)	(2.6)	(1.2)		(0.0)	(0.0)	(45.0)	(0.0)	(1.5)	(1.8)
Order Lepidoptera	64.4	58.5	80.5		85.0	0.0	50.0	35.0	49.4	92.9
Order Diptera										
Otitidae	0.1	0.2	0.0		0.0	0.0	0.0	0.0	0.0	0.4
Unidentified	3.8	5.2	0.0		0.0	33.3	0.0	0.0	1.5	3.2
TOTAL DIPTERA	(3.9)	(5.3)	(0.0)		(0.0)	(33.3)	(0.0)	(0.0)	(1.5)	(3.6)
Order Trichoptera	0.3	0.5	0.0		0.0	0.0	0.0	0.0	0.9	0.0
Order Neuroptera (Hemerobiidae)	2.8	1.4	6.7		0.0	0.0	0.0	0.0	2.7	0.0
Order Orthoptera (Gryllidae)	5.0	4.7	5.8		0.0	0.0	0.0	0.0	13.2	0.0
TOTAL	100.0	100.0	100.0		100.0	100.0	100.0	100.0	100.1	100.1
M. lucifugus[a]	51	33	18	0	12	9	5	13	5	5
Sample size										
Order Coleoptera										
Diabrotica	2.9	1.1	6.4		0.0	0.0	0.0	2.7	4.0	19.0
Carabidae	0.7	0.0	1.9		2.9	0.0	0.0	0.0	0.0	0.0
Chrysomeliidae	0.1	0.0	0.3		0.4	0.0	0.0	0.0	0.0	0.0
Unidentified	11.4	14.9	5.0		0.0	17.8	46.0	9.2	10.0	4.0
TOTAL COLEOPTERA	(15.1)	(15.9)	(13.6)		(3.3)	(17.8)	(46.0)	(11.9)	(14.0)	(23.0)
Order Homoptera (Cicadellidae)	3.1	2.1	5.0		0.0	1.1	2.0	3.9	18.0	0.0
Order Hemiptera										
Lygaeidae	0.6	0.9	0.0		0.0	1.7	3.0	0.0	0.0	0.0
Unidentified	1.2	1.8	0.0		2.1	0.0	0.0	1.9	0.0	2.0
TOTAL HEMIPTERA	(1.8)	(2.7)	(0.0)		(2.1)	(1.0)	(3.0)	(1.9)	(0.0)	(2.0)
Order Hymenoptera (Ichneumonidae)	0.8	0.0	2.2		0.0	0.0	0.0	0.0	8.0	0.0
Order Lepidoptera	22.0	19.9	25.8		33.7	18.9	15.0	18.5	15.0	31.0
Order Diptera										
Culicidae	5.9	5.7	6.4		11.3	16.7	3.0	0.0	0.4	0.0
Chironomidae	4.1	6.1	0.6		2.9	19.9	0.0	0.0	0.0	0.0
Unidentified	31.3	34.7	25.0		46.3	23.3	1.0	23.5	20.0	44.0
TOTAL DIPTERA	(41.3)	(46.4)	(32.0)		(60.4)	(59.4)	(4.0)	(23.5)	(20.4)	(44.0)
Order Trichoptera	15.2	12.8	19.4		0.0	0.0	30.0	40.4	19.6	0.0
Order Neuroptera (Hemerobiidae)	0.3	0.2	0.6		0.4	1.1	0.0	0.0	0.0	0.0
Unidentified insect	0.5	0.0	1.4		0.0	0.0	0.0	0.0	5.0	0.0
TOTAL	100.0	100.0	100.0		100.0	100.0	100.0	100.0	100.0	100.0
Pipistrellus subflavus										
Sample size	27	18	9	0	0	5	2	5	13	2
Order Coleoptera										
Carabidae	2.0	0.6	5.0			0.0	0.0	9.0	0.8	0.0
Chysomelidae	1.3	0.0	3.9			0.0	0.0	7.0	0.0	0.0
Unidentified	19.3	24.2	9.4			0.0	30.0	5.0	33.5	0.0
TOTAL COLEOPTERA	(22.6)	(24.7)	(18.3)			(0.0)	(30.0)	(21.0)	(34.2)	(0.0)
Order Homoptera										
Cicadellidae	30.9	29.4	33.9			11.0	15.0	26.0	47.6	0.0
Cercopidae	3.7	0.0	11.1			0.0	0.0	0.0	0.0	50.0
Delphacidae	1.1	0.0	3.3			0.0	0.0	4.0	0.8	0.0
TOTAL HOMOPTERA	(35.7)	(29.4)	(48.3)			(11.0)	(15.0)	(30.0)	(48.4)	(50.0)

Appendix I.—Continued.

Bat species and prey group	Total	Female	Male	Juvenile	April	May	June	July	August	September
Order Hemiptera (Lygaeidae)	1.1	1.7	0.0			0.0	15.0	0.0	0.0	0.0
Order Hymenoptera										
Formicidae	3.2	4.2	1.1			0.0	0.0	17.0	0.0	0.0
Ichneumonidae	0.2	0.0	0.6			0.0	0.0	0.0	0.4	0.0
TOTAL HYMENOPTERA	(3.3)	(4.2)	(1.7)			(0.0)	(0.0)	(17.0)	(0.4)	(0.0)
Order Lepidoptera	12.6	11.4	15.0			13.0	0.0	25.0	11.2	2.5
Order Diptera										
Culicidae	3.0	3.3	2.2			12.0	0.0	4.0	0.0	0.0
Unidentified	18.7	21.9	12.2			55.0	40.0	0.0	5.8	37.5
TOTAL DIPTERA	(21.7)	(25.3)	(14.4)			(67.0)	(40.0)	(4.0)	(5.8)	(37.5)
Order Trichoptera	3.0	3.3	2.2			9.0	0.0	3.0	0.0	10.0
TOTAL	100.0	100.0	100.0			100.0	100.0	100.0	100.0	100.0
M. sodalis										
Sample size	15	10	5	0	3	5	4	1	0	2
Order Coleoptera										
Scarabaeidae	6.0	9.0	0.0		0.0	0.0	22.5	0.0	0.0	0.0
Curculionidae	2.3	3.5	0.0		0.0	0.0	0.0	35.0	0.0	0.0
Unidentified	18.3	14.0	27.0		0.0	8.0	48.8	0.0	0.0	20.0
TOTAL COLEOPTERA	(26.7)	(26.5)	(27.0)		(0.0)	(8.0)	(71.3)	(35.0)	(0.0)	(20.0)
Order Homoptera (Cicadellidae)	3.0	4.5	0.0		0.0	0.0	0.0	30.0	0.0	7.5
Order Lepidoptera	21.5	30.3	4.0		38.3	0.0	10.0	35.0	0.0	66.5
Order Diptera										
Culicidae	5.0	7.5	0.0		3.3	1.0	15.0	0.0	0.0	0.0
Unidentified	40.8	27.2	68.0		56.7	85.0	1.3	0.0	0.0	6.0
TOTAL DIPTERA	(45.8)	(34.7)	(68.0)		(60.0)	(86.0)	(16.3)	(0.0)	(0.0)	(6.0)
Order Trichoptera	2.3	3.5	0.0		0.0	6.0	1.3	0.0	0.0	0.0
Order Neuroptera (Hemerobiidae)	0.3	0.5	0.0		1.7	0.0	0.0	0.0	0.0	0.0
Unidentified insect	0.3	0.0	1.0		0.0	0.0	1.3	0.0	0.0	0.0
TOTAL	100.0	100.0	100.0		100.0	100.0	100.1	100.0	0.0	100.0

[a] Four *Nycticeius humeralis* sampled in October had 54.5% *Diabrotica* (Coleoptera); 21.3% Miridae, 0.8% Pentatomidae, 3.8% Lygaeidae (25.8% total Hemiptera); 0.5% Formicidae, 10.0% Ichneumonidae (10.5% total Hymenoptera); 0.5% unidentified Diptera; 8.8% Neuroptera (Hemerobiidae).

[b] Seven *Eptesicus fuscus* sampled in October had 35.0% *Diabrotica*, 37.1% Carabidae, 11.4% unidentified Coleoptera (83.6% total Coleoptera); 5.7% Homoptera (Cicadellidae); 22.1% Hymenoptera (Ichneumonidae); 1.4% unidentified Diptera; 7.1% Neuroptera (Hemerobiidae).

[c] Four *Lasiurus borealis* sampled in October had 80.0% Lepidoptera and 20.0% Neuroptera (Hemerobiidae). Two *L. borealis* sampled in November had 2.0% Hymenoptera (Ichneumonidae) and 98.0% Lepidoptera.

[d] Two *Myotis lucifugus* sampled in October had 100% unidentified Diptera.

Bats and Integrated Pest Management

Seventy percent of all bats eat insects, including many crop and forest pests.

A cooperative publication of the USDA Natural Resources Conservation Service, the Wildlife Habitat Management Institute, and Bat Conservation International, Inc.

Amazing Bat Facts

Over 1,000 kinds of bats account for about a quarter of all mammal species, and most are highly beneficial.

Bats are the only mammals capable of self-propelled flight, and they live on every continent except Antarctica.

Contrary to popular misconceptions, bats are not blind, do not become entangled in human hair and seldom transmit disease to other animals or humans.

Not only do bats see as well as other mammals, they also use echolocation to detect objects as fine as a human hair in total darkness,

Though bats are long-lived (some living up to 34 years), they reproduce slowly, Most species bear and nurse just one pup per year.

The pallid bat (*Antrozous pallidus*) of western North America is immune to the stings of scorpions and even the seven-inch (125-cm.) centipedes upon which it feeds.

Townsend's big-eared bats (*Corynorhinus townsendii*) can maneuver like helicopters to pluck insects from foliage or to drink from tiny pools. In contrast, Mexican free-tailed bats (*Tadarida brasiliensis*) are built like jets, require large open spaces to maneuver and fly up to 10,000 feet (3,000m) high.

Like most animals, bats suffer from habitat loss and environmental pollution, but the primary cause of their decline is wanton destruction by humans.

Loss of bats can increase the demand of chemical pesticides, jeopardize whole ecosystems, and harm human economies.

Agricultural Allies

Bats are primary predators of beetles, moths, leaf-hoppers, and other insects that cost farmers and foresters billions of dollars every year. They also devour mosquitoes in our backyards.

Without predators, insects would soon overwhelm the earth. Like birds, bats consume enormous quantities. Mexican free-tailed bats (*Tadarida brasiliensis*) from just three caves near San Antonio, Texas, eat approximately a million pounds nightly, including many crop pests.

Illustrative of the impact that even small colonies of bats can have, just 150 big brown bats (*Eptesicus fuscus*) can eat sufficient cucumber beetles each summer to protect farmers from 33 million of these beetles' root worm larvae, pests that cost American farmers and estimated billion dollars annually.

One Georgia pecan grower was losing 30% of his pecan crop to hickory shuckworms and other major southeastern pests. For the past two years, after installing bat houses, he has seen no further crop damage. One bat house now hosts a colony of more than 2,000 bats.

One little brown myotis (*Myotis lucifugus*) can catch 1,200 mosquito-sized insects in just one hour, sometimes catching two in a single second. A nursing mother eats more than her own body weight nightly, meaning that colonies can consume vast numbers nightly.

Many garden pests can hear bats from over 100 feet (30m) away and will avoid areas where bats are present. Researchers have shown that, by playing even fake bat sounds over test plots of corn, they can scare corn earworm moths away, reducing damage from their larva by 50%.

A red bat (*Lasiurus borealis*) that eats even 100 moths may prevent egg-laying that could otherwise produce 25,000 new caterpillars that could attack farmer's crops.

Silver-haired bats (*Lasionycteris noctivagans*), western long eared myotis (*Myotis evotis*) and many other bat species help keep countless forest insects in check.

Pallid bats (*Antrozous pallidus*) benefit ranchers by consuming large quantities of grasshoppers and crickets.

The hoary bat (*Lasiurus cinereus*), the only land mammal native to Hawaii, often feeds on sugarcane leafhoppers, a serious pest to Hawaii's premier agricultural crop, and on the island's highly destructive wood termites.

Incorporating Bats into Integrated Pest Management

The most important threat to bats is loss of natural roosts. You can help, and reduce insect pests, by providing alternative homes for bats that feed on your property by:

- **building** a bat house, and placing it at least 10-12 feet (3-4m) off the ground on a pole or the side of a building,
- **working** with highway departments to create roosts in nearby bridges,
- **and decreasing** disturbance to nearby bat roosts in caves and mines by educating the local community about the importance of bats, providing signs at the entrances of caves or mines where bats live or erecting bat friendly gates at entrances to minimize human disturbance.

The Bat House Builder's Handbook and the *Building Homes for Bats* video provide easy to follow instructions for attracting bats.

The *Bats and Mines* resource publication provides detailed plans for protecting bats in caves and mines.

The *Bats in American Bridges* handbook provides instructions on how to benefit from attracting thousands of bats to bridges.

The *Forest Managemnt & Bats* publication provides basic forest management practices that improve forest health and productivity which also maintain and enhance habitat for bats.

The *Water for Wildlife* handbook for landowners and range managers describes proven methods for increasing wildlife safety ad accessibility at artificial watering features without diminishing their usefulness for livestock.

All are available from Bat Conservation International.

Enhancing Natural Habitat

Bats need more than just a nice place to roost during the day. They must feed and drink every night. Having a variety of good habitat types in close proximity will make your property more attractive to bats. Promote good habitat by:

- Providing clean, open water in ponds or lakes.
- Maintaining hedge-rows and wind breaks.
- Preserving areas along forest edges as well as old trees.

Common Insect-eating Bats

Eastern red bat, *Lasiurus borealis*
little brown myotis, *Myotis lucifugus*
Mexican free-tailed bat, *Tadarida brasiliensis*
pallid bat, *Antrozous pallidus*
big brown bat, *Eptesicus fuscus*
silver-haired bat, *Lasionycteris noctivagans*

Living Safely With Bats

Like most other mammals, bats can contract rabies. However, the risk of exposure from bats is extremely remote for anyone who simply keeps them outside and leaves them alone. To protect your family, vaccinate dogs and cats and caution children never to handle any unfamiliar animal.

Contact Information

USDA Natural Resources Conservation Service (NRCS)
Contact your local NRCS Field Office
(A directory of all states and their offices can be found at www.nrcs.usda.gov)

Wildlife Habitat Management Institute
100 Webster Circle, Suite 3
Madison, MS 39110
(607) 607-3131
www.ms.nrcs.uda.gov/whmi/

For more information about attracting and living safely with bats, or to obtain resource publications, contact:
Bat Conservation International
P.O. Box 162603
Austin, Texas 78716
(512) 327-9721
www.batcon.org

Economic Importance of Bats in Agriculture

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Insectivorous bat populations, adversely impacted by white-nose syndrome and wind turbines, may be worth billions of dollars to North American agriculture.

White-nose syndrome (WNS) and the increased development of wind-power facilities are threatening populations of insectivorous bats in North America. Bats are voracious predators of nocturnal insects, including many crop and forest pests. We present here analyses suggesting that loss of bats in North America could lead to agricultural losses estimated at more than $3.7 billion/year. Urgent efforts are needed to educate the public and policy-makers about the ecological and economic importance of insectivorous bats and to provide practical conservation solutions.

Infectious Disease and Wind Turbines

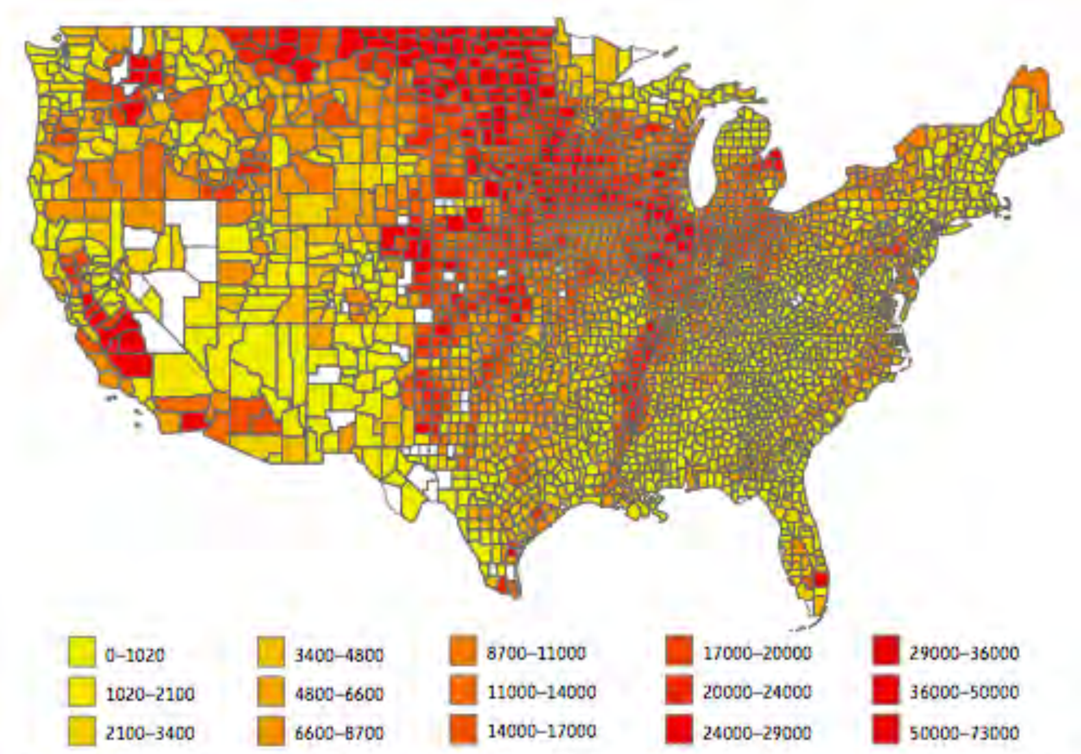
Insectivorous bats suppress populations of nocturnal insects (1, 2), but bats in North America are under severe pressure from two major new threats. WNS is an emerging infectious disease affecting populations of hibernating cave-dwelling bats throughout eastern North America (3). WNS is likely caused by a newly discovered fungus (*Geomyces destructans*). This fungus infects the skin of bats while they hibernate and is thought to trigger fatal alterations in behavior and/or physiology (e.g., premature depletion of energy reserves) (3, 4). Since February 2006, when WNS was first observed on bats in upstate New York, *G. destructans* has spread west of the Appalachian Mountains and into Canada. To date, over one million bats have probably died, and winter colony declines in the most affected region exceed 70% (5). Populations of at least one species (little brown bat, *Myotis lucifugus*) have declined so precipitously that regional extirpation and extinction are expected (5).

At the same time, bats of several migratory tree-dwelling species are being killed in unprecedented numbers at wind turbines across the continent (6, 7). Why these species are particularly susceptible to wind turbines remains a mystery, and several types of attraction have been hypothesized (6). There are no continental-scale monitoring programs for assessing wildlife fatalities at wind turbines, so the number of bats killed across the entire United States is difficult to assess. However, by 2020 an estimated 33,000 to 111,000 bats will be killed annually by wind turbines in the Mid-Atlantic Highlands alone (7). Obviously, mortality from these two factors is substantial and will likely have long-term cumulative impacts on both aquatic and terrestrial eco- systems (5, 7). Because of these combined threats, sudden and simultaneous population declines are being witnessed in assemblages of temperate-zone insectivorous bats on a scale rivaled by few recorded events affecting mammals.

Economic Impact

Although much of the public and some policy-makers may view the precipitous decline of bats in North America as only of academic interest, the economic consequences of losing so many bats could be substantial. For example, a single colony of 150 big brown bats (*Eptesicus fuscus*) in Indiana has been estimated to eat nearly 1.3 million pest insects each year, possibly contributing to the disruption of population cycles of agricultural pests (8). Other estimates suggest that a single little brown bat can consume 4 to 8 g of insects each night during the active season (9, 10), and when extrapolated to the one million bats estimated to have died from WNS, between 660 and 1320 metric tons of insects are no longer being consumed each year in WNS-affected areas (11).

Estimating the economic importance of bats in agricultural systems is challenging, but published estimates of the value of pest suppression services provided by bats ranges from about $12 to $173/acre (with a most likely scenario of $74/acre) in a cotton-dominated agricultural landscape in south-central Texas (12). Here, we extrapolate these estimates to the entire United States as a first assessment of how much the disappearance of bats could cost the agricultural industry [see supporting online material (SOM)].



The worth of insectivorous bats. Estimated annual value of insectivorous bats in the agricultural industry at the county level. Values (×$1000 per county) assume bats have an avoided-cost value of ~$74/acre of cropland (*12*). (See SOM for details.)

Assuming values obtained from the cotton-dominated agro-ecosystem in Texas, and the number of acres of harvested cropland across the continental United States in 2007 (13), we estimate the value of bats to the agricultural industry is roughly $22.9 billion/ year. If we assume values at the extremes of the probable range (12), the value of bats may be as low as $3.7 billion/year and as high as $53 billion/year. These estimates include the reduced costs of pesticide applications that are not needed to suppress the insects consumed by bats (12). However, they do not include the "downstream" impacts of pesticides on ecosystems, which can be substantial (14), or other secondary effects of predation, such as reducing the potential for evolved resistance of insects to pesticides and genetically modified crops (15). Moreover, bats can exert top- down suppression of forest insects (1, 2), but our estimated values do not include the benefit of bats that suppress insects in forest eco- systems because economic data on pest-control services provided by bats in forests are lacking. Even if our estimates are halved or quartered, they clearly show how bats have enormous potential to influence the economics of agriculture and forestry.

Although adverse impacts of WNS on bat populations have occurred relatively rapidly, impacts of wind energy development appear to pose a more chronic, long-term concern. WNS has caused rapid and massive declines of hibernating bats in the northeastern United States, where this disease has persisted for at least 4 years (5). Thus, the coming growing season may be the first in which the adverse effects of this disease will become notice- able. Because of regional differences in crop production, the agricultural value of bats in the U.S. Northeast may be comparatively small relative to much of the United States (see the figure) (SOM). However, evidence of the fungus associated with WNS was recently detected in the Midwest and Great Plains, where the estimates of the value of bats to agriculture are substantial (see the figure). Additionally, because this region has the highest onshore wind capacity in North America, increased development of wind energy facilities and associated bat fatalities in this region can be expected (16). Thus, if mortality of bats associated with WNS and wind turbines continues unabated, we can expect noticeable economic losses to North American agriculture in the next 4 to 5 years.

Policy

A recently stated goal of the United Nations

Environment Programme is to demonstrate the value of biodiversity to policy-makers and the public (17). In keeping with this goal, we hope that the scale of our estimates and the importance of addressing this issue will resonate both with the general public and policy-makers. Bats provide substantial eco- system services worldwide, and their benefits to human economies are not limited to North America. For example, pioneering research in tropical ecosystems shows the importance of plant-visiting bats in the pollination of valuable fruit crops (18, 19). Although the economic impacts of mass mortality of bats associated with WNS appear to be confined, at present, to North America, wind turbines are also causing bat fatalities in Europe (20), and the potential for WNS to spread to other parts of the world is unknown.

We suggest that a wait-and-see approach to the issue of widespread declines of bat populations is not an option because the life histories of these flying, nocturnal mammals— characterized by long generation times and low reproductive rates—mean that population recovery is unlikely for decades or even centuries, if at all. Currently, there are no adequately validated or generally applicable methods for substantially reducing the impacts of WNS or wind turbines on bat populations. To date, management actions to restrict the spread of WNS have been directed primarily toward limiting anthropogenic spread (e.g., cave and mine closures and fungal decontamination protocols) (21). Other proactive solutions for understanding and ameliorating the effects of WNS include developing improved diagnostics to detect early-stage infections and fun- gal distribution in the environment; defining disease mechanisms; investigating the potential for biological or chemical control of the fungus; and increasing disease resistance through habitat modification, such as creation of artificial or modified hibernacula that are less conducive to disease development and transmission (11, 22). Other approaches, such as culling of infected bats have been widely discussed and dismissed as viable options for control (23). New research also shows that altering wind turbine operations during high-risk periods for bats significantly reduces fatalities (24, 25). Specific action on these issues will benefit from scientific research carefully aimed at providing practical conservation solutions for bats in the face of new threats and at assessing their economic and ecological importance. We as scientists should also make concerted efforts to develop and use more effective methods for educating the public and policy-makers about the ecosystem services provided by bats.

Bats are among the most overlooked, yet economically important, non-domesticated animals in North America, and their conservation is important for the integrity of ecosystems and in the best interest of both national and international economies. In our opinion, solutions that will reduce the population impacts of WNS and reduce the mortality from wind-energy facilities are possible in the next few years, but identifying, substantiating, and applying solutions will only be fueled in a substantive manner by increased and widespread awareness of the benefits of insectivorous bats among the public, policy- makers, and scientists.

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Supporting Online Material
www.sciencemag.org/cgi/content/full/332/6025/41/DC1

10.1126/science.120136

Bats Limit Arthropods and Herbivory in a Tropical Forest

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Bats are diverse and abundant insectivores that consume many herbivorous insects (1, 2). Insect herbivory, in turn, constrains plant reproduction and influences plant diversity and distribution (3). However, the impact of bat insectivory on plants has never been studied. Previous studies measuring top-down reduction of insect herbivory focused on birds (4–6) but actually measured the combined impact of birds and bats because predator exclosures were left in place day and night. Partitioning the effects of each predator group is essential for both basic ecological questions, such as the top-down maintenance of tropical diversity (3), and applied studies, such as the biological control of agricultural pests (2, 6). We experimentally separated the ecological effects of insectivorous birds from those of insectivorous bats in a tropical lowland forest in Panama.

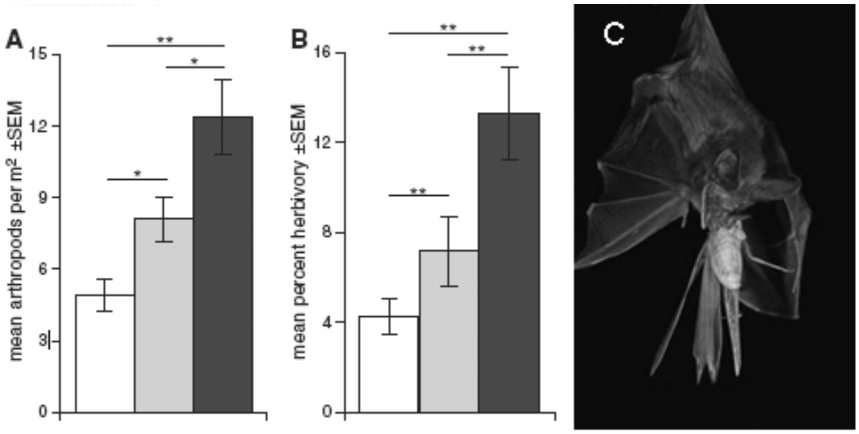

Fig. 1. (A) Mean number of arthropods per m2 per census. (B) Mean herbivory as percent of total leaf area. White bars represent controls (birds and bats present); yellow bars, diurnal exclosures (birds absent and bats present); and blue bars, nocturnal exclosures (bats absent and birds present); $^*P < 0.05$ and $^{**}P < 0.005$ according to Tukey's HSD. (C) A bat (Micronycteris microtis) consuming a katydid, Barro Colorado Island, Panama. [Photo: C. Ziegler]

We covered plants with mesh exclosures that permitted access to arthropods but prevented birds or bats from gleaning them off of the plants. However, we left our exclosures in place only during the day or night, allowing us to compare arthropod abundance and herbivory on plants inaccessible to bats (nocturnal exclosures, $N = 42$), plants inaccessible to birds (diurnal exclosures, $N = 35$), and uncovered controls ($N = 43$) in a randomized block design using five common understory plant species. We visually censused arthropods throughout the 10-week study to test the direct effect of treatment (i.e., absence of bats or birds) on insect and other arthropod abundance and measured leaf damage incurred during the study to test the indirect effect of treatment on herbivory (7).

Nocturnal (bat) and diurnal (bird) exclosures each directly increased arthropod abundance on plants, and nocturnal exclosures had a significantly stronger effect than diurnal exclosures (table S1 and Fig. 1A) [repeatedmeasures generalized linear model (GLM) treatment $F2,75 = 17.11$, $P < 0.001$; all Tukey's honestly significantly different (HSD) posthoc pairwise comparisons between treatments, $P < 0.05$]. Control plants averaged 4.9 ± 0.7 (SEM) arthropods per m2 of leaf area per census; birdexclosed plants, 8.1 ± 1.0; and bat-exclosed plants, 12.4 ± 1.6. Nocturnal and diurnal exclosures also each indirectly increased herbivory, and nocturnal exclosures again had a significantly stronger effect than diurnal exclosures (Fig. 1B; univariate GLMtreatment $F2,75 = 41.89$, $P < 0.001$, all Tukey's HSD posthoc pairwise comparisons between treatments $P < 0.005$). Control plants averaged 4.3 ± 0.8% leaf area lost to herbivory; bird-exclosed plants; 7.2 ± 1.6%; and bat-exclosed plants, 13.3 ± 2.1% (7).

Treatment effects on both arthropod abundance and herbivory were consistent across plant species, and potential confounding variables such as light intensity, number of new leaves emerged during the study, and total leaf area neither differed between treatments nor interacted with treatment in either GLM (7).

Our data suggest that bat predation both directly reduces arthropod abundance on plants and indirectly reduces herbivory. We also show that the ecological effects of insectivorous gleaning bats can be considerably stronger than those of birds. Our estimates of the direct and indirect impacts of both groups are likely conservative because (i) predation away from exclosures also reduces herbivory (2), (ii) very large arthropods may have been excluded along with bats and birds, (iii) predatory arthropods in the exclosures may have mitigated the effect of bird or bat exclusion (table S1), and (iv) topdown reduction of herbivory may be greater in the more-productive forest canopy (5). Gleaning insectivorous bats are common in tropical and temperate lowland forests; thus, it is likely that bat predation of herbivorous insects reduces herbivory in the temperate zone as well (7). Given their ecological importance, bats should be included in future conservation plans aimed at preserving the integrity of tropical forests and also considered in agricultural management strategies based on natural pest control (2, 6).

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Supporting Online Material
www.sciencemag.org/cgi/content/full/320/5872/71/DC1
Materials and Methods
Table S1
References

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Bats Limit Insects in a Neotropical Agroforestry System

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Top-down limitation of herbivores is an important ecosystem service that facilitates agricultural production (1). Several experiments in natural andmanaged ecosystems demonstrate the importance of avian predators in arthropod control (2). Although insectivorous bats are expected to have major impacts on arthropods (3), few studies have quantified the effects of bats on standing crops of arthropods. Because all previous exclosure-based studies of avian insectivory have left exclosures up during the night, it is possible that a proportion of predation attributed to birdsmay represent predation by foliage-gleaning bats. Here, we report an exclosure experiment conducted in a Mexican coffee agroforest, in which we directly measured the impact of predation by foliage-gleaning birds and bats on arthropods found on coffee plants.

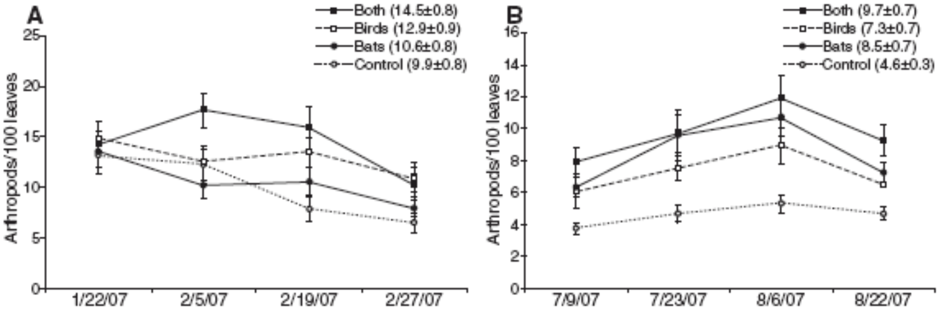

Fig. 1. Mean number of arthropods ± SEM per 100 coffee leaves in four exclosure treatments in (A) dry season and (B) wet season. “Both” indicates birds and bats excluded (!); “Birds,” only birds excluded ("); “Bats,” only bats excluded (#); and “Control,” no predators excluded ($). Numbers after treatment name in

We used exclosures made of agricultural netting erected around individual coffee plants in Finca Irlanda, an organic shade coffee plantation harboring abundant populations of ≥120 bird species and ≥45 bat species. We established 22 blocks of four treatments: birds-only excluded (exclosure netting in place only during the day), bats-only excluded (netting in place only during the night), both excluded (netting in place day and night), and control (no netting). We visually censused noncolonial arthropods (primarily insects, but also spiders, harvestmen, and mites) on all plants at the beginning of the experiments, every 2 weeks thereafter, and at the end of the experiment. We conducted the experiment for a 7-week period beginning January 2007 (dry season) and for an 8-week period beginning June 2007 (wet season).

Exclusion of birds and bats resulted in significant increases in total arthropods on experimental plants, although a significant amount of variation was also explained by foliage biomass and initial arthropod density (table S1). On average, total arthropod densities on plants from which both predators were excluded were 46% higher than those observed on control plants. There was a clear seasonal effect with regard to bats: Although bats did not have significant effects on arthropod densities in the dry season, their impacts were highly significant in the wet season, with an 84% increase in arthropod density in bat-only exclosures, exceeding the effects of birds (Fig. 1). In neither season was there a significant interaction between bats and birds, indicating an additive effect. Regardless of season, arthropod densities increased the most on plants from which both birds and bats were excluded (Fig. 1). These seasonal and additive patterns held for various arthropod taxa (table S2), although only birds significantly reduced spiders. Although predator exclusions resulted in increased arthropod density, no significant differences were seen between treatments in the prevalence or the intensity of leaf damage.

At our site, bats were as important as birds in regulating insect populations across the course of the year. We suspect that increased impacts of birds in the dry season may result from an influx of insectivorous overwintering migrants from North America (4). We have no data on the absolute density of bats versus birds; however, at our site the capture rates (and presumably abundance) and reproductive activity of bats increased during the wet season. Bats’ relatively higher surface area may result in greater heat loss and concomitantly higher energy requirements (5), and reproduction increases females’ energetic needs; thus, increased bat abundance and reproduction in the wet season may result in an increased impact of bat predation on understory arthropods. Our results are consistent with arguments that functional diversity is central to the maintenance of ecosystem services (6). In this case, the presence of these two vertebrate taxa maintains a functional difference that enhances the efficacy of arthropod reduction. Previous exclosure studies have not differentiated between diurnal and nocturnal predators, attributing observed changes to birds. We suggest that these studies of the impacts of "bird" predation may have underestimated the importance of bats in limiting insects.Bat populations are declining worldwide (7), butmonitoring programs and conservation plans for bats lag far behind those for birds. Declining bat populations may compromise critical ecosystem services, making an improved understanding of their conservation status vital.

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Tables S1 and S2

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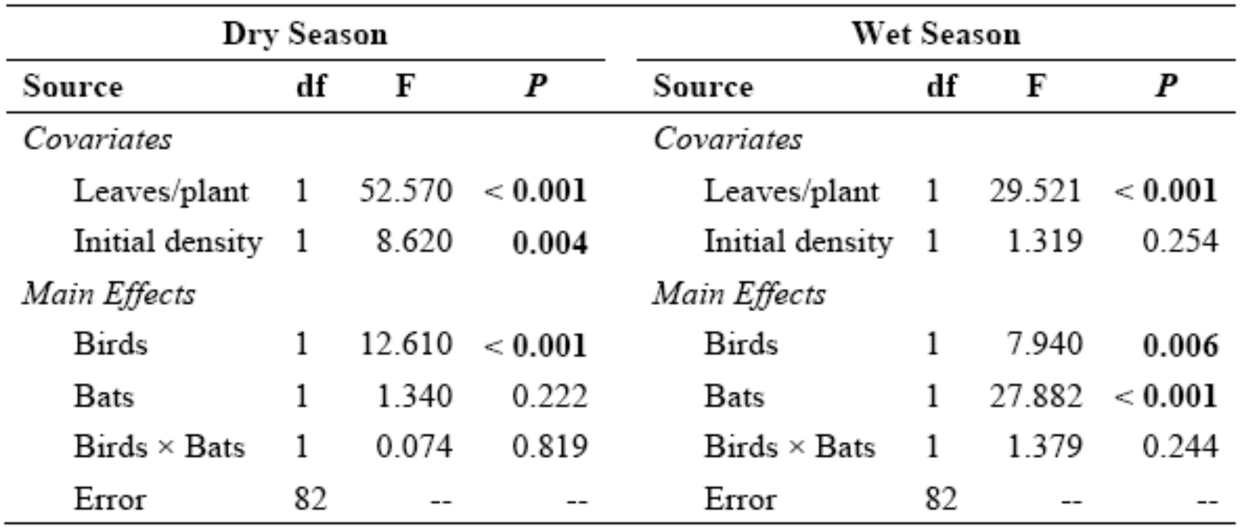
Table S1. Results of repeated-measures factorial ANCOVA for the effects of bird predation, bat predation, season, and their interactions on the density of all non-colonial arthropods on coffee plants, using number of leaves per plant and initial arthropod densities as covariates. *N*=88 for each season. *

* All data ln(x+1) transformed prior to analysis. Repeated-measures ANCOVA on total numbers of arthropods conducted using a 2°—2 factorial design with birds excluded (2 levels, birds present and birds excluded) and bats excluded (2 levels, bats present and bats excluded) as main effects; separate analyses were conducted for the wet and dry seasons. This design allows for testing of linear (additive or substitutive) versus nonlinear (synergistic or antagonistic) interactions between predator types.



Dry Season				Wet Season			
Source	df	F	*P*	Source	df	F	*P*
Covariates				*Covariates*			
Leaves/plant	1	52.570	< **0.001**	Leaves/plant	1	29.521	< **0.001**
Initial density	1	8.620	**0.004**	Initial density	1	1.319	0.254
Main Effects				*Main Effects*			
Birds	1	12.610	< **0.001**	Birds	1	7.940	**0.006**
Bats	1	1.340	0.222	Bats	1	27.882	< **0.001**
Birds × Bats	1	0.074	0.819	Birds × Bats	1	1.379	0.244
Error	82	--	--	Error	82	--	--

Table S2. Dry and wet season densities of commonly-observed arthropod taxa (mean of census values±SEM) by size class and order for experimental plants ("Both," birds and bats excluded; "Birds," birds excluded; "Bats," bats excluded; "Control," no predators excluded) and significance of repeated-measures ANCOVA (*N,* degrees of freedom, main effects, and covariates as in Table S1).

	Arthropods/100 leaves (Dry Season)					**Arthropods/100 leaves (Wet Season)**				
Arthropods	**Both**	**Birds**	**Bats**	**Control**	***P****	**Both**	**Birds**	**Bats**	**Control**	***P****
Total	14.53±0.83	12.94±0.92	10.57±0.78	9.94±0.82	**0.001**[a] 0.250[c]	9.73±0.73	7.28±0.68	8.50±0.66	4.61±0.30	**0.006**[a] **<0.001**[c]
By size										
Large	3.14±0.40	2.58±0.33	1.52±0.13	1.31±0.16	**0.024**[a] 0.346[c]	3.13±0.26	2.02±0.23	2.54±0.21	1.35±0.09	**0.010**[a] **<0.001**[c]
Small	11.39±0.66	10.35±0.75	9.05±0.71	8.63±0.78	**<0.001**[a] 0.302[c]	6.60±0.53	5.26±0.49	5.95±0.59	3.26±0.25	**0.001**[a] **<0.001**[c]
By order										
Aranae	2.76±0.20	2.09±0.22	2.08±0.36	1.89±0.26	**0.004**[a] 0.103[c]	1.70±0.33	1.42±0.24	1.59±0.53	0.74±0.07	**0.015**[a] 0.073[c]
Blattodea	0.56±0.12	0.55±0.13	0.27±0.07	0.29±0.08	**0.018**[a] 0.504[c]	0.96±0.16	0.68±0.16	0.71±0.12	0.38±0.08	**0.039**[a] **0.002**[c]
Coleoptera	2.78±0.43	2.22±0.34	1.05±0.15	1.92±0.39	**0.002**[a] 0.341[c]	2.44±0.21	1.83±0.25	2.10±0.21	1.02±0.08	**0.002**[a] **<0.001**[c]
Homoptera	5.19±0.50	4.38±0.38	3.65±0.31	2.79±0.21	**<0.001**[a] **0.028**[c]	2.47±0.18	1.86±0.18	2.30±0.20	1.22±0.11	**0.011**[a] **<0.001**[c]
Lepidoptera	0.19±0.03	0.18±0.06	0.15±0.03	0.13±0.04	0.087[a] 0.079[c]	0.14±0.03	0.16±0.04	0.14±0.02	0.10±0.03	0.476[a] 0.421[c]
Orthoptera	0.42±0.08	0.23±0.05	0.24±0.06	0.10±0.04	**0.005**[a] 0.108[c]	0.86±0.18	0.44±0.12	0.60±0.10	0.30±0.06	0.373[a] **<0.002**[c]

* Value for top line indicates P-value based on F statistic for bird predation, bottom line for bat predation; values significant at the 0.05 level are in bold.

Placement of Nets for Bats: Effects on Perceived Fauna

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ABSTRACT - We used mist nets to survey bats at 41 sites throughout the Shawnee National Forest in southern Illinois during the summers of 1999 and 2000. Unlike most previous studies, we placed nets in the interior of forest stands as well as the more typical placement along edge habitats associated with water. We captured 417 individual bats representing 10 species. Of these, 168 individuals (40.3%) and 8 species were collected in interior forest. Northern long-eared bats (*Myotis septentrionalis*) were caught significantly more often in interior forest, whereas red bats (*Lasiurus borealis*), eastern pipistrelles (*Pipistrellus subflavus*), and big brown bats (*Eptesicus fuscus*) were netted more often in edge habitats. In contiguous forest, especially within the geographic range of *M. septentrionalis*, a more accurate measure of bat diversity and relative abundance is obtained by placing nets in interior forest as well as edge habitats.

INTRODUCTION

Determination of bat community composition, species richness, diversity, and abundance is often important in formulating comprehensive forest management plans. The most direct method for surveying bats is to use capture methods such as mistnetting. Capture methods are also the only currently accepted methods for surveying endangered species. Capture data can be used to assess diversity and relative abundance of different bat species in a given region (Gardner et al. 1996, Jung et al. 1999, Kunz 1973, Lacki and Hutchinson 1999). Most mistnetting surveys focus on areas where capture success is traditionally highest, typically stream or flight corridors (Kunz and Kurta 1988). Placement of mistnets in interior forests is used less often because of perceived lower bat activity and therefore reduced capture success, and possible problems of accessibility.

We used mistnets to determine summer distribution and relative abundance of bats in southern Illinois and their association with different habitat variables. We placed nets along roads or other habitat edges, in association with intermittent or permanent streams ("traditional" placement), and in forest interiors ("nontraditional" placement). Here we report on the importance of net placement on diversity and relative abundance of bat species that were captured.

METHODS

We sampled 41 sites in southern Illinois. Sites were primarily within Shawnee National Forest and were dominated by an overstory of oak (*Quercus* spp.) and hickory (*Carya* spp.). Sites were selected based on distance to a water source, size of surrounding contiguous forest, and accessibility.

We amassed a total of 339 net nights during 80 nights from 18 May through 18 August 1999, and 12 May through 20 July 2000. Netting procedures followed the Indiana Bat Protocol (USFWS 1999). Generally, four net sets were used at a site. Two sets were placed over the nearest water source, nearly all of which were intermittent or perennial streams or small rivers near roads or other edge habitats ("traditional" placement; Kunz and Kurta 1988). Two additional sets were placed in interior forest ("nontraditional" placement). All interior nets were placed 50 to 500 m from edge habitat. Netting sites were selected to represent a variety of understory cover and canopy closure. Nets were opened at dusk (approximately 2000 h) and monitored for 6 hours until 0200 h. Nets were checked for captured bats every 20 minutes.

We recorded the species, sex, age (juvenile/adult), reproductive status, mass, and forearm length of each captured bat. We used chisquare tests to analyze: 1) the selection of presumptive foraging habitat by comparing use by each species of bat (as determined by the number of captures of that species), versus the number of net sets in each habitat type (traditional vs. nontraditional); and 2) sex ratio of the total number of bats captured. A Shannon-Wiener Diversity Index of bat captures was calculated for edge, interior, and total captures.

RESULTS

We captured 417 bats representing 10 species (Table 1) for an overall netting success of 1.23 captures per net night. A mean of 2.90 ± 0.72 species was captured at each site. There was no significant difference between number of males (n = 211) and females (n = 206) captured ($\chi2 = 0.06$, df = 1, $P > 0.5$). Seventy-seven percent (n = 322) of all individuals captured were northern long-eared bats (*Myotis septentrionalis*, 41.7%), red bats (*Lasiurus borealis*, 18.0%), or eastern pipistrelles (*Pipistrellus subflavus*, 17.5%). These three species exhibited significant differences in habitat use. Northern long-eared bats were captured in forest interior significantly more often than expected ($\chi2 = 26.6$, df = 1, $P < 0.0001$). Conversely, red bats were captured in edges more than expected ($\chi2 = 37.5$, df = 1, $P < 0.0001$), as were eastern pipestrelles ($\chi2 = 38.5$, df = 1, $P < 0.0001$). Although sample sizes were smaller, we also captured big brown bats (*Eptesicus fuscus*) in edges significantly more than in the interior ($\chi2 = 11.64$, df = 1, $P < 0.001$). With the exception of southeastern bats (*Myotis austroriparius*) and silver-haired bats (*Lasionycteris noctivagans*), all species captured in edge habitat were also caught in interior forest (Table 1). Species diversity of captured bats was close to 1.7 times higher in edge habitat than in interior habitat.

DISCUSSION

Of the 12 species of bats whose range includes Illinois (Hoffmeister 1989), we captured all but gray bats (*Myotis grisescens*) and Rafinesque’s big-eared bats (*Corynorhinus rafinesquii*). Our results differed from previous surveys for bats in Illinois and adjacent states (Clark and Clark 1987, Gardner et al. 1996, Hofmann et al. 1999, Kunz 1973, LaVal et al. 1977, Layne 1958), which report eastern pipistrelles, red bats, and big brown bats as the most common species. Northern long-eared bats were routinely captured, but were never particularly abundant. In contrast, they were the most abundant species taken in our study, comprising 41.7% of all individuals captured. Our results are more similar to those of Lacki and Hutchinson (1999) in northeastern Kentucky than to previous studies in Illinois.

Differences in our capture results compared to other studies are likely due to our sampling methodology. Previous investigators (Clark and Clark 1987, Gardner et al. 1996, Hofmann et al. 1999, Kunz 1973) used “traditional” methods of placing nets over perennial streams, roads, and trails used as flyways. This may limit sampling to bats that use open corridors; those species not using these habitats may be underrepresented. We suggest that populations of northern long-eared bats may have been underestimated in previous research because of biased sampling effort. To accurately sample an area for bats, “traditional” net sets, as well as “non-traditional” interior forest sets, should be used. By sampling a variety of habitat types in an area, a more accurate estimate of the bat fauna and the habitats used can be determined. Lacki and Hutchinson (1999) set nets in interior forest as well as edge; 70% of northern long-eared bats they captured were in interior net sets. Our study showed similar results. Of 174 northern long-eared bats captured, 121 (69.5%) were captured in interior forest. Furthermore, of the total 417 bats we captured, 168 (40.3%) were caught in the interior forest. Species diversity was lower in interior forest because of the large number of northern long-eared bats captured when compared to the other seven species (Table 1). Given the extensive geographic range of northern long-eared bats, future studies of bat community structure in eastern North America should include nets set in interior forest habitat.

It is important to note that as many Indiana bats (*Myotis sodalis*), a federally endangered species, were caught with interior sets as were taken at edge sites. Without interior net sets we would have missed Indiana bats at 50% of netting locations.

We captured relatively few hoary bats (*Lasiurus cinereus*) and silver- haired bats (*Lasionycteris noctivagans*) (Table 1). We do not suggest, however, that these species are necessarily rare in Illinois. Mistnetting samples an extremely small area relative to that used by free-flying bats, and foraging bats appear to detect and avoid nets. Some species may not be represented because their normal flight activities are outside the sampling range of the equipment (O’Farrell and Gannon 1999). Acoustic sampling of bat communities can detect the presence of those species that routinely fly at great heights or are otherwise beyond the sampling capabilities of mistnets and harp traps (O’Farrell and Gannon 1999). However, because echolocation characteristics are very similar among some species, identification of bats to species level may not always be possible with acoustic sampling (Hart et al. 1993, Jung et al. 1999, Kalcounis et al. 1999). Mistnetting, including sets in “nontraditional” interior habitat, along with acoustic sampling should provide the most complete inventory of bat diversity.

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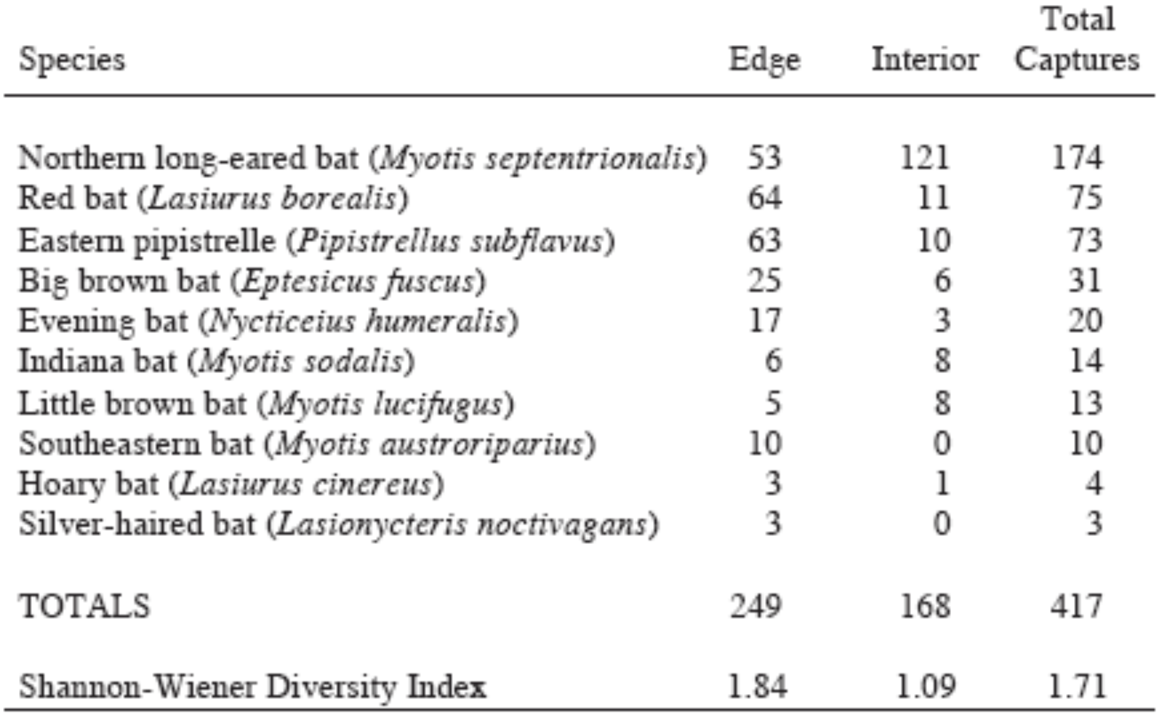

Species	Edge	Interior	Total Captures
Northern long-eared bat (*Myotis septentrionalis*)	53	121	174
Red bat (*Lasiurus borealis*)	64	11	75
Eastern pipistrelle (*Pipistrellus subflavus*)	63	10	73
Big brown bat (*Eptesicus fuscus*)	25	6	31
Evening bat (*Nycticeius humeralis*)	17	3	20
Indiana bat (*Myotis sodalis*)	6	8	14
Little brown bat (*Myotis lucifugus*)	5	8	13
Southeastern bat (*Myotis austroriparius*)	10	0	10
Hoary bat (*Lasiurus cinereus*)	3	1	4
Silver-haired bat (*Lasionycteris noctivagans*)	3	0	3
TOTALS	249	168	417
Shannon-Wiener Diversity Index	1.84	1.09	1.71

Table 1. Number of each species captured at 41 sites in the Shawnee NF, IL, for 339 mit net nights in either edge habitat or interior forest during the summer of 1999 and 2000.

Mist Net Effort Required to Inventory a Forest Bat Species Assemblage

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ABSTRACT

Little quantitative information exists about the survey effort necessary to inventory temperate bat species assemblages. We used a bootstrap re-sampling algorithm to estimate the number of mist net surveys required to capture individuals from 9 species at both study area and site levels using data collected in a forested watershed in northwestern California, USA, during 1996–2000. The mean number of simulated surveys required to capture individual species varied with species' rarity and ranged from 1.5 to 44.9. We retrospectively evaluated strategies to reduce required survey effort by sub-sampling data from 1996 to 1998 and tested the strategies in the field during 1999 and 2000. Using data from 1996 to 1998, the mean number of simulated surveys required to capture 8 out of 9 species was 26.3, but a 95% probability of capture required .61 surveys. Inventory efficiency, defined as the cumulative proportion of species detected per survey effort, improved for both the study area and individual sites by conducting surveys later in summer. We realized further improvements in study area inventory efficiency by focusing on productive sites. We found that 3 surveys conducted between 1 July and 10 September at each of 4 productive sites in this 10- km2 study area resulted in the capture of 8 species annually. Quantitative estimation of the survey effort required to assess bat species occurrence improves the ability to plan and execute reliable, efficient inventories. Results from our study should be useful for planning inventories in nearby geographical areas and similar habitat types; further, the analytical methods we used to assess effort are broadly applicable to other survey methods and taxa.

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KEY WORDS: bats, inventory, species accumulation, species richness, survey effort, survey protocol.

Bats are important components of biodiversity that are often underrepresented in conservation and management plans because of a lack of information on population status and habitat requirements (Pierson 1998, Richards and Hall 1998). Nevertheless, increased interest in bats (Fenton 1997) coupled with their status as species of concern in many areas (Bogan et al. 1996) has increased the number of inventories aimed at documenting species occurrence (Weller and Zielinski 2006). To date, this work has often been conducted with little guidance (but see Resources Inventory Committee 1998, Vonhof 2002) or evaluation of the survey effort required to conduct an accurate inventory. In planning an inventory, an important question is the number of surveys required to detect species with a given level of confidence (Zielinski and Stauffer 1996, Ke´ry 2002, Sherwin et al. 2003).

Studies of other taxa have evaluated the spatial and temporal replication and survey duration necessary to estimate abundance and establish trends over time (Link et al. 1994, Lewis and Gould 2000, Thompson et al. 2002, Watson 2004) or to estimate number of species detected with increasing effort (Bury and Corn 1987, Block et al. 1994). Evaluations of survey effort necessary to describe bat species assemblages are limited to Australia and the Neotropics (Mills et al. 1996, Moreno and Halffter 2000, Aguirre 2002, Bernard and Fenton 2002). A similar assessment of survey effort has not been made for temperate bat assemblages of North America or Europe despite a large number of surveys conducted in these areas. Estimates of survey effort required to document tropical bat species assemblages provide little guidance for inventories in temperate areas because of differences in species, habitats, and objectives. Tropical areas generally support a larger number of lesser-known bat species, and a frequent objective is to compare the numbers of species present among areas of conservation concern. Hence, the relevant metric for many tropical inventories is the number of species detected for a given level of effort and is frequently addressed using species

Table 1. Number and timing of mist net surveys conducted to capture bats in Pilot Creek watershed, northern California, USA, 1996–2000.

Survey effort	1996	1997	1998	1999	2000
Date of first survey	30 Jun	16 Jun	8 Jun	2 Jul	12 Jul
Date of last survey	18 Sep	8 Sep	6 Sep	30 Aug	7 Sep
No. of surveys on or before 30 Jun	1	6	11	0	0
No. of surveys on or before 31 Jul	13	20	24	5	4
No. of surveys after 31 Jul	10	21	23	7	8
No. of different sites surveyed	9	17	17	4	4
No. of surveys at focal sites	10	19	19	12	12
Total no. of surveys	23	41	47	12	12

accumulation curves (Moreno and Halffter 2000, Estrada and Coates-Estrada 2001, Aguirre 2002, Bernard and Fenton 2002).

In temperate areas where the bat fauna generally comprises fewer, better-known species, questions regarding survey effort are typically goal oriented and may focus on efficiency of survey effort. Relevant questions include 1) given a goal of detecting species X, how many surveys are required? or 2) given a goal of detecting Y% of the species in an area, how many surveys should be conducted? Such questions have not been addressed for a temperate bat assemblage and, though conventional species accumulation curves can provide post hoc assessments of survey completeness, they do not do so in a predictive manner.

Activity patterns of temperate bats vary greatly both spatially and temporally (Hayes 1997, 2000). Consequently, multiple surveys are needed to detect individual species and an even greater number to detect all species that use an area. Given limited resources, it is imperative that inventories are both accurate (species are detected and correctly identified) and efficient (measured by species detected/survey). Whereas accuracy can be improved simply by increasing the number of surveys (White 2004), the greater challenge is to do so efficiently. We examined sampling accuracy and efficiency using results from mist net surveys conducted in a forested watershed in northern California, USA. Our goals were to quantify the survey effort necessary to inventory the summer bat species assemblage and evaluate practical measures to improve efficiency of inventories in this area.

STUDY AREA

Our study area was within the Pilot Creek watershed in the Six Rivers National Forest in northwestern California (408370N, 1238360W). The watershed was approximately 55 km from the Pacific Ocean at an elevation range of 950– 1,320 m. This area was characterized by steep, rugged terrain, commonly gaining 200 m in elevation for each kilometer of distance. This 100-km2 watershed had hundreds of small tributaries, but only Pilot Creek and the lower reaches of its larger tributaries maintained surface flows throughout summer. Sixty percent of the watershed was late-successional forest, including the headwaters area where our study took place. Vegetation was dominated by Douglas-fir (*Pseudotsuga menziesii*), but white fir (*Abies concolor*) and oaks (*Quercus chrysolepis*, *Q. kelloggii*, and *Q. garryana*) were also common. There were no known caves, mines, bridges, or buildings in our study area.

The nearest weather station was approximately 20 km away at the Mad River Ranger Station (elevation 846 m). Mean annual precipitation during the study was approximately 195 cm, of which 2.0 cm accumulated from June through August. Mean minimum temperatures for June, July, and August were 7.28 C, 9.48 C, and 8.98 C, respectively; mean maximum temperatures were 25.98 C, 30.28 C, and 30.48 C, respectively.

METHODS

We attempted to capture bats in mist nets at water sources and along suspected flight corridors during their summer activity period. We defined a survey as a single night of mist netting at a site. We selected suitable mist net sites that spanned a variety of habitats used by bats, with the goal of maximizing number of species captured in the study area. We conducted surveys to meet the needs of our and 2 other studies (Seidman and Zabel 2001, Weller and Zabel 2001). During 1996–1998 (period 1), we surveyed 9–17 sites per year during June–September (Table 1). In total, we surveyed 28 different sites including 12 sites along Pilot Creek, 2 along perennial tributaries to Pilot Creek, 10 on intermittent streams, 2 on roads, one at a pond, and one at a meadow edge. All survey sites fell within a 9.8-km2 polygon in the upper half of the watershed. During period 1, we conducted surveys at sites where we suspected capture efforts to be successful and subsequently revisited sites

Table 2. Field results, by species, from 135 mist net surveys for bats in Pilot Creek watershed, northern California, USA, 1996–2000.

Species	Species code	No. surveys captured	% surveys captured	Yr captured	No. of surveys until first capture
Myotis californicus	MYCA	92	68.1	All	8
Lasionycteris noctivagans	LANO	59	43.7	All	5
M. evotis	MYEV	39	28.9	All	1
M. volans	MYVO	36	26.7	All	1
M. thysanodes	MYTH	29	21.5	All	10
Eptesicus fuscus	EPFU	19	14.1	All	16
M. yumanensis	MYYU	13	9.6	1997–2000	48
Corynorhinus townsendii	COTO	6	4.4	1996–1998	5
Lasiurus cinereus	LACI	3	2.2	1999–2000	121
M. lucifugus[a]	MYLU	2	1.5	1998	109
Lasiurus blossevilli[a]	LABL	1	0.7	1998	109

[a] We did not consider this species in analysis of core species as described in text.

where we captured multiple species or individuals. Such an approach is commonly used to document species presence in an area and we refer to it as conventional methods. By the end of 1997, we had identified 4 sites that were particularly effective. Subsequently, we conducted a disproportionate number of surveys at these sites, which we refer to as focal sites. Three of the focal sites were along Pilot Creek, spaced 570 m and 3.7 km apart; the fourth focal site was at an intermittent stream.

We chose the number, length, and configuration of nets to suit the physical characteristics of each site. Mist nets were 2.6 m high and ranged in length from 6 to 12 m. We used an average of 3.6 nets per survey (SD 1/4 0.8, range 1/4 2–6). Surveys began at sunset and continued for a minimum 3 hours or until an hour passed after the last bat was captured, whichever was longer. We conducted surveys regardless of temperature but not during periods of precipitation. Mean temperature at survey end was 13.08 C (SD 1/4 3.58 C, range 1/4 6.0–24.58 C).

We used survey results from period 1 to explore some of the spatial and temporal effects on survey effort required to capture individual and multiple species of bats. Using all surveys from period 1, we estimated number of annual surveys required to 1) first capture each species and 2) cumulatively detect multiple species. We then evaluated strategies for reducing annual survey effort by comparing these results to several subsets of these data: 1) surveys conducted after 30 June (post-Jun), 2) surveys conducted after 31 July (post-Jul), and 3) surveys at focal sites during these date ranges. We selected 30 June to approximate the end date of low nighttime temperatures that can depress bat activity (Maier 1992, Hayes 1997, Erickson and West 2002); 31 July approximated the date when we first captured juveniles. The presence of volant juveniles can increase the number of individuals of a species active in an area (Maier 1992, Schulz 1999) and consequently improve chances of capturing those species. We applied strategies that appeared effective based on results from period 1 in the field during 1999 and 2000 (period 2) to evaluate their applicability.

Additionally, we used results of focal site surveys to evaluate the effort required to assess species richness at individual sites. We sampled from the complete set of surveys conducted at each focal site from 1996 to 2000 to estimate the number of surveys necessary to accumulate species at the site level. We also compared the number of species captured at individual sites using the full data set to post-June and post-July surveys.

We generated bootstrap estimates (sensu Efron and Tibshirani 1993) of the number of surveys required to meet each objective by randomly drawing from data pools created by sub-setting the original data set based on when surveys were conducted and whether all sites or only focal sites were included. The bootstrap routine drew surveys, with replacement, from each pool of surveys and recorded the number of simulated surveys until a particular species was first captured or a specified number of species was captured. When number of species captured was the objective, we made random draws until all species in the pool of surveys were present in the simulated sample. Because a single draw included the complete species assemblage captured at a single site and date combination, interspecific correlations in occurrence were maintained in the bootstrap samples. We generated summary statistics from the distribution of 10,000 samples from each data pool. We conducted sampling and summary statistics using SAS Release 8.1 (SAS Institute, Cary, NC).

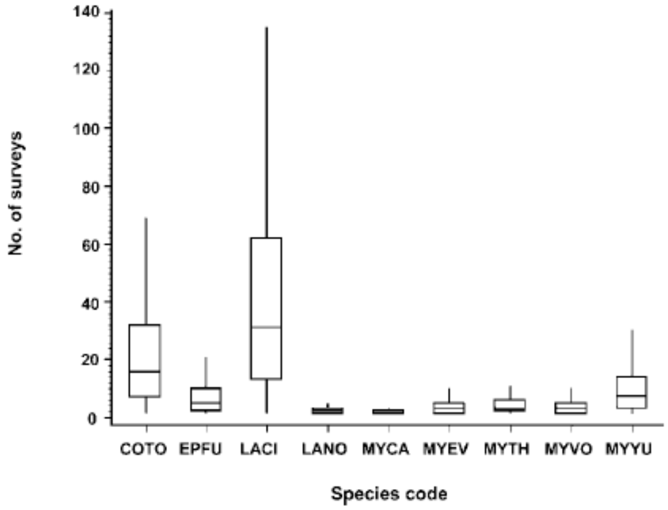

Figure 1. Simulated number of mist net surveys to capture individual bat species in Pilot Creek watershed, northern California, USA, 1996–2000.

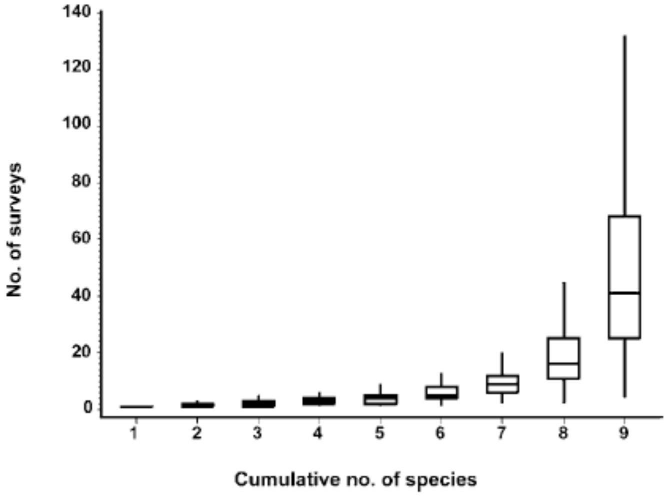

Figure 2. Simulated number of mist net surveys required to accumulate 1–9 species of bats in Pilot Creek watershed, northern California, USA, 1996–2000.

RESULTS

We captured 11 species of bats in 135 surveys over 5 years (Tables 1, 2). We captured 2 species (*Myotis lucifugus* and *Lasiurus blossevilli*) only in 1998; we omitted these species from the 9 core species (sensu Magurran and Henderson 2003) analyzed here. When we included all surveys from 1996 to 2000 in the pool, the mean number of simulated surveys required to first detect a species ranged from 1.5 surveys for *M. californicus* to 44.9 surveys for *L. cinereus*. The 95th percentile, which corresponds to the estimated number of simulated surveys required to ensure a 95% probability of capture, varied from 3 to 136 surveys for those 2 species (Fig. 1). The mean number of simulated surveys required to cumulatively capture all 9 core species was 53 surveys; achieving a 95% probability of capturing the core species would have required 138 surveys (Fig. 2). By comparison, despite up to 47 surveys per year, we captured _8 core species in the field annually (Tables 1, 2).

Using the data pool from period 1, when we used conventional methods, a mean of 26.3 simulated surveys were required to cumulatively capture 8 of the core species and 61 surveys were required to achieve a 95%probability of capturing those species. The number of surveys required to first capture each individual species was reduced by including only post-June surveys and further reduced by including only post-July surveys in nearly every case (Table 3). Similarly, including only post-June or post-July surveys decreased by 18% the mean number of simulated surveys needed to capture 8 species. The simulated effort necessary to cumulatively capture 7 of the core species decreased 16% using post-June data and 29% using post-July data (Table 3). Pooling only focal site surveys over all dates reduced the mean number of simulated surveys required to first detect all but 1 individual species (*M. yumanensis*) during period 1 (Table 3). The increase in simulated effort required to cumulatively capture 8 core species by surveying focal sites in period 1 was due to the large number of surveys until the first capture of *M. yumanensis*. By contrast, the simulated effort to capture 6 and 7 species using focal sites in period 1 decreased by 17%and 19%, respectively, when compared to surveys at all sites (Table 3).

Using the data pool from post June surveys at focal sites during period 1 reduced the simulated number of surveys required to capture each species when compared to focal site surveys from all dates and for all species except *M. yumanensis* when compared to post June surveys at all sites (Table 3). However, the simulated number of surveys required to capture 3 individual species (*C. townsendii*, *L. noctivagans*, and *M. yumanensis*) and to cumulatively capture 7 and 8 core species was greater using post-July than post-June surveys at focal sites (Table 3).

We applied these findings in the field during period 2,

Table 3. Simulated mean number of mist net surveys required to capture bats in Pilot Creek watershed, northern California, USA, 1996–2000.

	Period 1 (1996–1998)						Period 2 (1999–2000)	
	All sites			Focal sites			Focal sites	
Survey goal	All dates[a]	PostJun	PostJul	All dates	PostJun	PostJul	PostJun	PostJul
Cumulative no. of species								
8	26.3	21.6	21.6	27.2	20.3	26.5	12.0	11.2
7	11.6	9.8	8.2	9.5	7.2	7.7	6.8	6.4
6	6.5	5.7	4.4	5.4	4.2	3.8	4.6	4.4
First capture of species								
Corynorhinus townsendii	18.8	15.4	18.1	7.9	6.0	8.1		
Eptesicus fuscus	7.4	6.2	4.1	6.8	5.2	3.4	5.9	3.8
Lasiurus cinereus							8.2	7.5
Lasionycteris noctivagans	2.2	2.4	2.0	1.8	1.8	1.9	2.7	3.0
Myotis californicus	1.5	1.4	1.2	1.4	1.2	1.2	1.3	1.2
M. evotis	3.5	3.4	2.7	2.5	2.3	2.0	3.4	5.0
M. thysanodes	4.9	4.0	3.6	4.9	3.6	3.5	4.0	3.0
M. volans	4.1	3.9	2.8	2.8	2.4	1.9	2.7	3.0
M. yumanensis	14.2	11.7	9.1	23.9	17.7	24.2	4.8	4.9

[a] Referred to as conventional methods in text.

when we surveyed each focal site 3 times per year post-June (Table 1). Despite conducting only 12 annual surveys, we captured 8 core species in the field during both years (Table 2). Among the 7 core species that we captured in both period 1 and period 2, the simulated effort necessary to capture all but one species (*L. noctivagans*) was less in period 2 (Table 3). The mean number of simulated surveys in period 2 required to cumulatively capture 8 core species was 46% as much as the effort required for all sites and dates in period 1. The 95th percentile for the simulated number of surveys required to cumulatively capture 8 species was reached in 26 surveys in period 2 compared to 61 surveys in period 1 (43% of the effort). The strategy used during period 2 was also more efficient at detecting commonly captured species; the mean number of simulated surveys to accumulate 6 species was 71% of that required in period 1 (Table 3) and the simulated effort required to achieve 95% probability of capturing 6 species was 9 surveys in period 2 compared to 14 surveys in period 1 (64% of the effort). Sampling from the pool of post July surveys from period 2 reduced the simulated number of surveys required to accumulate 6–8 species but had mixed effects on individual species when compared to the full set of surveys from period 2 (Table 3).

We conducted 17 field surveys at each of 3 focal sites and 21 surveys at the other focal site between 1996 and 2000. We captured 8 core species at each of the 3 sites along Pilot Creek and 5 core species at the upland site. The simulated mean number of surveys required to capture 8 core species at the 3 sites along Pilot Creek was 18.5 and ranged from 14.1 to 27.2 surveys among the 3 sites. Capture of 7 species required a mean of 9.2 (range1/47.3–12.3) simulated surveys. Capture of 8 core species at the 3 focal sites along Pilot Creek required a mean of 15.9 (range1/412.7–22.7) post-June simulated surveys and 14.2 (range 1/4 13.1–15.9) post-July surveys. Capture of 5 species at the upland site required a mean of 25.7 simulated surveys.

DISCUSSION

Survey effort necessary to capture bats varied by species, sites surveyed, and time periods over which we conducted surveys. Although we captured the most common species with relatively modest survey effort, pursuit of uncommon species precipitated a sharp rise in required effort. Studies in reconnaissance. Of course, identification of focal sites required a preliminary phase of sampling to identify the most successful sites. When pilot studies are not practical, surveying additional sites, rather than repeated surveys at existing sites, is a more effective inventory strategy for uncommon species (Colwell and Coddington 1994, MacKenzie and Royle 2005).

Despite averaging 4–10 individuals and 2–3 species per survey, each of the 4 focal sites had _1 survey in which we only captured one bat. Even during the most productive periods (i.e., after 31 Jul) .14 mist net surveys were required to capture all species that occurred at an individual site within this study area. This is similar to the number of mist net surveys required to capture up to 18 species within small habitat patches in tropical Mexico (Moreno and Halffter 2000). By contrast, it has been reported that species richness at a site can be adequately described with 2–3 surveys using bat detectors in Europe (Ahle´n and Baagøe 1999) or harp traps in Australia (Mills et al. 1996). Note also that the level of effort necessary to capture species occurring at an individual site approached that required to capture species in the entire study area. Similar results were found in inventories of bats in Mexico (Moreno and Halffter 2000) and Martes in California (Zielinski and Stauffer 1996), where the effort necessary for a reliable inventory of an individual stratum approached or exceeded the effort necessary to inventory a larger area comprising multiple strata. This may be because study area inventories incorporate both spatial and temporal replication through the use of multiple survey sites, whereas a site inventory can only include temporal replication.

As with other analytical methods (e.g., species accumulation curves), assessment of inventory completeness and strategies for improving efficiency in our study required an initial survey effort to generate a pool of sample data with which to work. Conventionally, inventory effectiveness has been inferred from species accumulation curves by inspection for inflection points that indicate a decrease in returns on one's survey investment (Bury and Corn 1987, Estrada and Coates-Estrada 2001). In systems with greater species richness, models were fit to species accumulation curves to estimate the number of species expected in an area and inventory completeness was assessed based on detection of a given proportion (e.g., 90%) of the expected species (Sobero´n and Llorente 1993, Flather 1996, Moreno and Halffter 2000). In our study, rather than determine the number of species detected for a given level of effort, we asked how much effort was required to confidently detect a given species or number of species. Hence, the relationship between species detected and survey effort in our study (Fig. 2) is the inverse of conventional species accumulation curves.

Additionally, our approach provides a probability-based approach to inventory planning and evaluation. Thresholds for proportion of the species assemblage to target can be set a priori in order to identify the number of surveys that might be necessary to meet objectives. For instance, the number of surveys necessary to achieve a 95%probability of capturing a specified number of species could be prescribed as minimum required survey effort. Estimates of required survey effort can simplify planning and allow informed tradeoffs between inventory accuracy and resources available to conduct work. For instance, simulations indicated that capture of 8 of the 9 core species in our study required less than half of the effort necessary to capture all 9 species. If detection of 7 of the core species was considered sufficient, this could be accomplished with a 50–70% further reduction in effort (Table 3).

Our analytical approach also quantifies survey effort necessary to capture individual species when, as in most temperate areas, it is more important to establish which species, rather than how many species, are present (Watson 2004). Establishing the probability of capture or detection with a given level of effort provides a defensible means of quantifying whether sufficient effort has been applied to detect a species, given that it is present (Zielinski and the Neotropics, where number of species and diversity of habitats were greater, have required 18–70 mist net surveys to capture 90% of the estimated species richness (Moreno and Halffter 2000, Aguirre 2002, Bernard and Fenton 2002). Hence, we were surprised that, using conventional methods, .26 surveys were required to capture 8 of the 9 core species in our relatively small, vegetatively homogenous, study area. This level of spatiotemporal replication was necessary to compensate for our incomplete understanding of the relationship between bat activity and a number of biotic and abiotic factors including weather conditions, insect availability, and reproductive condition of bats (Maier 1992, Hayes 1997, Erickson and West 2002). Additionally, all bats in our study are in the family Vespertilionidae, which are reportedly difficult to capture using mist nets (Kalko 1998, Moreno and Halffter 2000); this may help explain why the levels of effort we observed were comparable to those in Neotropical study areas.

Because the level of effort required to capture uncommon species of bats may exceed the means of some biologists (Weller and Zielinski 2006), it is important to elucidate strategies for improving survey efficiency. In our study area, conducting surveys later in the summer and focusing efforts on the most productive sites reduced the number of surveys required to meet inventory objectives. Although post June surveys consistently reduced effort required to achieve inventory objectives, post July surveys produced mixed results, perhaps as a result of too few total survey nights remaining to capture some species. We generated a relatively complete inventory of the species in our study area using a density of approximately 4 focal sites/10 km2. Compared to surveying sites of unknown quality, limiting surveys to focal sites improved the rate of species accumulation, saved time, and simplified logistics by eliminating additional site Stauffer 1996, Ke´ry 2002, Sherwin et al. 2003). Future projects in nearby areas and similar habitats could use our estimates of sample effort for planning purposes when designing inventories for individual species. However, caution must be exercised when applying our estimates elsewhere because they result from work in a single study area. Similar analytic methods should be applied to data from multiple study areas before meaningful conclusions about capture probabilities, and their variability, for individual species can be made.

Our estimates of required survey effort were based solely on results of mist net surveys. Several studies have concluded that a combination of mist net and acoustic-monitoring surveys provide more complete bat inventories than employing one or the other technique alone (Kuenzi and Morrison 1998, Murray et al. 1999, O'Farrell and Gannon 1999, Duffy et al. 2000). Use of acoustic methods in our study likely would have decreased the number of surveys required to document the presence of some species at both the site and study area level. However, because some species are difficult to detect or identify from their echolocation calls (Murray et al. 1999, O'Farrell and Gannon 1999), capture surveys will continue to be a vital component of bat inventories; and quantifying the effort necessary to do so reliably is important. Further, the analytical approach demonstrated here for assessing required mist net survey effort could be profitably applied to quantify survey effort for other (e.g., acoustic) inventory techniques.

MANAGEMENT IMPLICATIONS

We demonstrated that multiple mist net surveys are necessary to capture most species of bats in a forested area. The strategies we identified for improving inventory efficiency, such as conducting surveys later in the summer and focusing survey effort on productive sites, are likely to be effective in similar habitats and nearby geographic areas, but should be validated first. The goal-oriented analysis of survey effort we introduced is broadly applicable to evaluate completeness and improve efficiency of inventories conducted in other areas, using other survey methods, and for other taxa.

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An Improved Trap for Bats

by Merlin D. Tuttle

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Numerous methods of collecting bats have been developed, the most important of which are summarized by Constantine (1958: 17) and by Greenhall and Paradiso (1968: 8-19). Most of these are useful only under relatively restricted conditions. Even the widely-used “mist net” requires constant attention, soon becomes damaged, and entangles bats to such an extent that rapid handling of large numbers is impossible. Constantine (1958) first described an “automatic bat-collecting device” capable of taking large samples. Unlike “mist nets” Constantine’s trap did not require excessive labor for the removal of captured bats. His original trap, which caught more than 45,000 free-tailed bats, was too bulky for general use, but modifications (Constantine, 1958; 1962; 1969) produced smaller, folding traps, which were easily transported by two men. Each of Constantine’s traps consisted of a single rectangular frame, supporting fine vertical wires spaced at one-inch intervals and kept taut. These traps proved satisfactory for vampires and for fast flying free-tailed bats, but were not generally useful in capturing other species.

In order to trap efficiently the highly maneuverable vespertilionid and emballonurid bats, I have developed a trap, which employs a double frame and other modifications. This trap is easily portable by one man and can be assembled or broken down in 45 minutes. It can be used under a wide range of conditions and has proven successful in capturing many temperate and tropical species.

The trap consists of two rectangular frames held two inches apart by four 3/4-inch (.64 centimeters, cm) threaded steel rods (Fig. 1a). The sides of the frames consist of aluminum tubes (inside diameter, 29 millimeters, mm; outside diameter, 32 mm) 72 inches (182.9 cm) long. A hole is drilled 1-1/4 inches (3.2 cm) from each end of each tube for bolting the frame together (Fig. 1b), and two more located 3-1/4 and 4-1/4 inches (8.3 and 10.8 cm) up from the base on each side are for attachment of the bag support plates (Fig. le). The extra set of holes allows for vertical adjustment of the bag. Additional holes are drilled 22–3/4 and 27-3/4 inches (57.8 and 70.5 cm) from the base to allow for attachment of legs (Fig. 1d).

The upper and lower ends of each frame are identical, consisting of two 62-inch (157.5 cm) lengths of aluminum tubing (inside diameter, 2.5 cm; outside diameter, 2.8 cm). The ends of each tube are cut at 45 degrees, and a 6-inch (15.2 cm) length of the same size of tubing is welded at that angle (Fig. 1b). The end pieces are drilled to match the holes previously drilled in the sides into which they telescope and are bolted. Holes are drilled 5-1/4 and 21-1/2 inches (13.3 and 54.6 cm) from each end (Fig. 1b) for support of the aluminum angle to which the wires are attached.

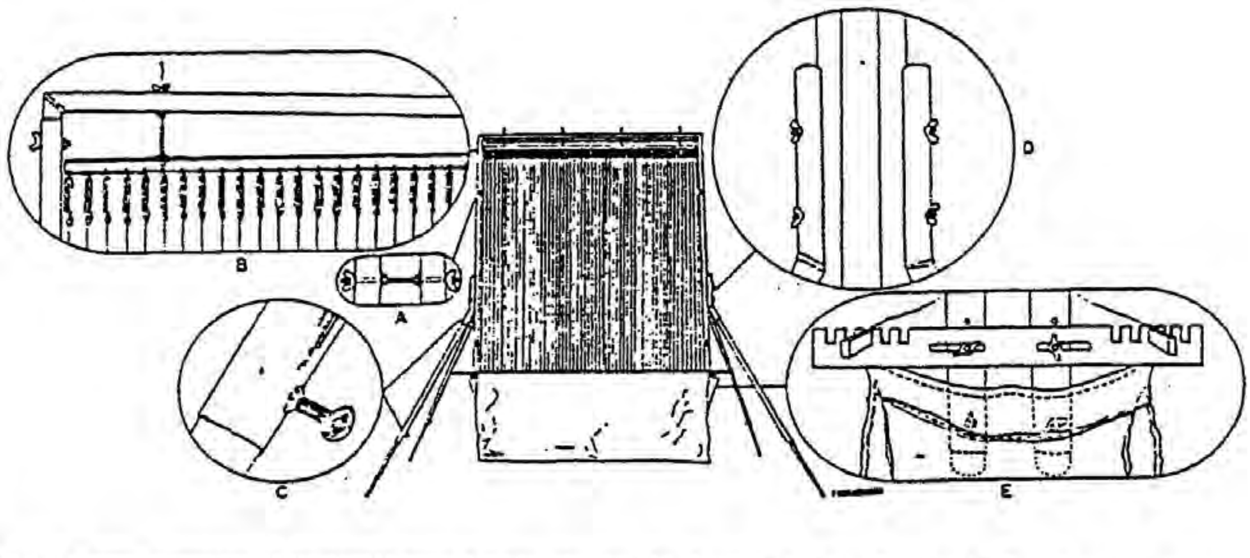

Fig. 1. Schematic drawing of the double-frame bat trap, showing details of construction. Drawing by Tom Swearingen.

For attachment of wire strands a section of angled aluminum 59 inches (149.9 cm) long is drilled to match the holes already present in the frame (Fig. 1b). One section is bolted to the base whereas the other is attached to the top by means of four 5-inch (12.7 cm) threaded steel rods (Fig. 1b), which allow for adjustment of wire tension. Prior to installation on the frame the angled sections are drilled at 1-inch (2.5 cm) intervals to allow for attachment of wires (Fig. 1b).

Receptacles for the legs are formed by welding 10-1/2 and 4-1/4-inch (26.7 and 10.8 cm) pieces of aluminum tubing (inside diameter, 2.9 cm; outside diameter 3.2 cm) together at an angle of 80 degrees (Fig. 1d). Each 10½-inch (26.7 cm) section is drilled 3-1/4 and 8-1/4 inches (8.3 and 21.0 cm) from its upper end, allowing for attachment to the frame (Fig. 1d). A hole is drilled on the inner side of the 4-1/2-inch (11.4 cm) section 1-1/4 inches (3.2 cm) from the lower end, and a 1/4-inch (.64 cm) nut is welded over the hole (Fig. 1c). Each leg consists of two 36-inch (91.4 cm) sections of telescoping aluminum tubing (inside diameter, 2.5 cm; outside diameter, 2.8 cm fitting over inside diameter, 2.0 cm; outside diameter, 2.2 cm). The outer section is drilled 2-1/4 inches (5.7 cm) from one end, and a 1/4-inch (.64 cm) nut is welded over the hole (Fig. 1c). The legs are attached to the leg receptacles and adjusted for length by use of thumb bolts (Fig. 1c).

The canvas bag is 25 inches (63.5 cm) deep by 60 inches (152.4 cm) long and 14 inches (35.6 cm) wide at the top. The original material is 60 inches (152.4 cm) long and 54 inches (137.2 cm) wide, allowing 2 inches (5.1 cm) extra per side which is folded outward and sewed down along the entire length. This leaves space for the supporting rods (Fig. 1e) from which the bag is suspended. Both ends are completely lined with plastic on the inside, and a strip of plastic 5 inches (12.7 cm) wide and 15 inches (38.1 cm) long is sewed vertically to the bag adjacent to the ends beginning at the top of the bag. It is important that all seams be turned to the outside so that bats cannot climb out. An additional plastic flap 18 inches (45.7 cm) wide and 60 inches (152.4 cm) long is sewed along the edge, to the outside of the bag, 2 inches (5.1 cm) below the top on both sides of the bag. Then each flap is sewed again along the length of the inside of the bag 6 inches from the top, allowing a 10-inch (25.4 cm) flap to hang free on each side. Bats are unable to climb the plastic and take shelter beneath the flaps. Metal grommets should be attached along the bottom of the bag, in the middle, and at both ends to act as drains in case of rain.

A bag support plate (Fig. le) is bolted to each end of the trap 4-1/2 inches (11.4 cm) above the base. Each plate consists of a single piece of aluminum 14 inches (35.6 cm) long, 1/8-inch (.32 cm) thick, and 116 inches (3.8 cm) wide. Five vertical slots are cut 5/8-inch (1.59 cm) deep by 1/4-inch (.64 cm) wide, at 1/2-inch (1.27 cm) intervals, beginning 1/2-inch (1.27 cm) from the end of each plate (Fig. le). Horizontal slots 2 inches (5.1 cm) long by 1/4-inch (.64 cm) wide begin 4 inches (101 cm) from each end (Fig. le). The latter allow for adjustment of distance between the frames. The bag is hung from the support plates by means of two 72-inch (182.9 cm) aluminum rods, 1/2-inch (1.27 cm) wide by 1/4-inch (.64 cm) thick. The following nuts, bolts, and washers are required in order to assemble the trap (all are 1/4-inch (.64 cm) in diameter): 36 wing nuts, 44 regular nuts, 28 washers; (to support attachments to angled aluminum), 14 3-inch (7.62 cm) bolts, 10 1-1/2 inch (3.8 cm) bolts, four 2-inch (5.1 cm) bolts, and eight thumb nuts. At least 12 of the nuts must be aluminum in order to permit heliarc welding for attachment to legs.

In order to string the trap with wire, the wing nuts on the four 5-inch (12.7 cm) threaded rods at the top of the trap (Fig. 1b) are loosened until each rod projects 3 inches below the frame. Springs are attached at 1-inch intervals along the top (Fig. lb), and the trap is strung with .008-inch (.20 mm) diameter stainless spring steel wire. Each strand is tied individually starting at one side and working to the other. Strands should be pulled until barely tight in order to insure uniformity of tension. When the trap is strung the wing nuts at the top can be tightened slightly in order to adjust for any bow in the middle of the frame.

Capture success for bats encountering such a trap is largely dependent upon two adjustments. Of greatest importance is the tension of the vertical wires. Generally, the wires should be tightened until no slack remains, but little or no more. Special conditions, however, necessitate occasional adjustment, depending on the speed and angle of approach of the bats. The tautness of the wires should be directly proportional to the speed of the bat. When bats escape by bouncing off, the wires should be loosened, and when they pass completely through both frames, tightened. The spacing of wires between the two frames is normally 3 inches. When the distance between the frames is either increased or decreased the number of bats capable of passing through both seems to increase. It is possible, however, that slight adjustment in width between the frames would increase the trap's effectiveness for a particular species or body size of bat.

Like "mist nets," traps are set wherever bats are likely to pass; traps are effective in cave entrances, over trails and streams, under small bridges, under trees in open fields, and at water holes and feeding sites. Because one trap covers an area of only 6 by 5 feet, naturally "closed-in" sites along a suspected flyway are usually selected, or else brush or netting is used to reduce the area through which bats may fly.

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A Comparison of Mist Nets and Two Designs of Harp Traps for Capturing Bats

by Charles M. Francis

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Two widely used methods for capturing bats away from their roosts are mist nets and harp traps (Kunz and Kurta, 1988; Tuttle, 1974). In Australia, Tidemann and Woodside (1978) found that harp traps were about 10 times more effective than mist nets at catching small to medium-sized vespertilionids and rhinolophids. In Costa Rica, LaVal and Fitch (1977) found that traps were about 1.7 times as effective as nets. However, there is some evidence of variation among species in their susceptibility to traps. LaVal and Fitch (1977) reported that large phyllostomids frequently were caught in mist nets and rarely were trapped, whereas the reverse was true for several small vespertilionids. Such interspecific variation in susceptibility can affect the choice of capture methods for a particular study, and must be considered in community studies if the number of captures is used as an index of relative abundance of species (Fleming, 1986).

In this paper, I compare the effectiveness and selectivity of mist nets and harp traps in the understory of Malaysian rain forest. I also compare the relative success of two different designs of harp traps. The original harp traps had a single bank (row) of wires and were effective for capturing fast-flying bats such as molossids, but not for more maneuverable species (Constantine, 1958). Subsequently, traps with two banks of lines were used widely (Tidemann and Woodside, 1978; Tuttle, 1974), but even these may capture less than half the bats encountering them (Kunz and Anthony, 1977). I developed new designs of harp traps with additional banks of lines, and present here data on the trapping efficiency of four-bank traps compared with two-bank traps.

The study was conducted between 1981 and 1987 in two areas of lowland rain forest in Malaysia: Pasoh Forest Reserve in Peninsular Malaysia (2E58'N, 102E17'E), and Sepilok Forest Reserve in Sabah, northern Borneo (5E52'N, 117E56'E). The forest in both areas was unlogged and dominated by trees of the family Dipterocarpaceae. The canopy was 30-60 m tall, and blocked much of the light except where treefalls had created gaps. All trapping and netting was done in the understory < 2 m above the ground along a network of trails.

Harp traps were built from modifications of the design of Tidemann and Woodside (1978). The original design included collapsible horizontal and vertical poles for the

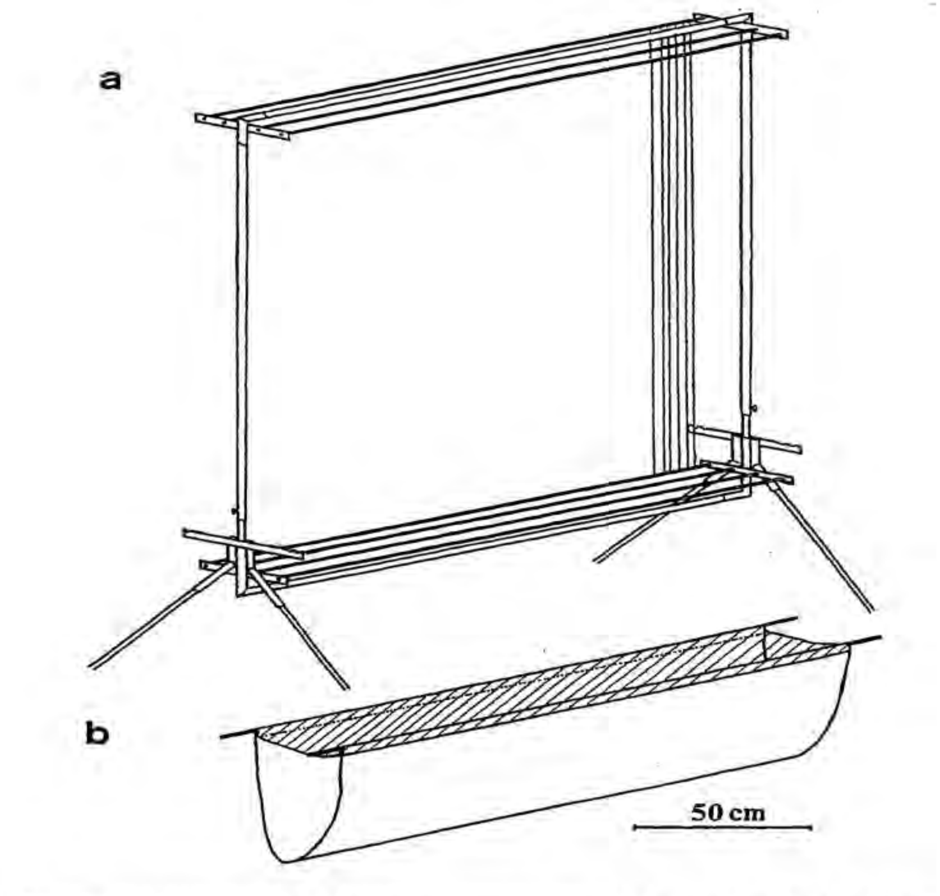

Fig. 1. Diagram of a four-bank harp trap showing: a, the assembled trap; and b, the capture bag. Most of the fishing lines are omitted for clarity. The hatched area on the bag indicates plastic flaps used to keep bats from escaping. In operation, the capture bag is suspended from the notched bars at the bottom of the trap.

frame, but I used single poles to increase rigidity and to simplify construction. The first trap was built with wooden poles and metal joints, but was unsatisfactory because it lacked stability. The remaining traps were built with aluminum frames (Fig. 1). The corners were welded to the horizontal poles in some traps and were detachable in others. The traps were portable, as they could be dismantled into a bundle about 160 cm long and 15 cm in diameter, and weighing 6-8kg. Dismantling or assembly of the traps took 5-10 min. Some traps were modified to accommodate as many as four banks of lines by widening the crossbars and the bag (Fig. 1). All traps were strung with 0.20-mm diameter (2.7-kg test) nylon fishing line, tied just barely taut. When the traps were set, tension was applied by lengthening the vertical poles of the frame 10-15 cm (7-10% of total length). Lines were spaced 2.5 cm apart within each bank, and banks were 7.5 cm apart. Line spacing on adjacent banks was offset by 1.25 cm for two- and three-bank traps. On four-bank traps the middle two banks were aligned with each other, but offset from the outer banks.

Traps usually were placed across well-established trails or small stream beds, and were moved at 1-4-day intervals. They were set all night and inspected one or more times in the evening, then again shortly after dawn. Occasionally, I watched them for short periods at dusk. One to three traps were set each night, for a total of 126 trap-nights at Sepilok (two-bank and three-bank traps), and 53 trap-nights at Pasoh (40 nights with two-bank traps, 13 nights with four-bank traps). Captures in the three-bank trap were not distinguished consistently from those in the two-bank traps, so I could not evaluate relative efficiencies of different designs of traps at Sepilok.

More than 98% of mist netting was done with 12- by 2-m nets with 36-mm mesh, although occasionally one or two 6- by 2-m nets also were used. Nets were set at approximately 50-m intervals along a grid of trails, and were open continuously for 2-5 days. They were inspected once or twice in the early evening and again at dawn for bats, then at 2-h intervals through the day for birds. On a few nights I watched single nets continuously for about an hour at dusk. An average of 25 nets was set simultaneously, and operated for 27 nights at Pasoh (675 net-nights) and 39 nights at Sepilok (975 net-nights).

Trapping coincided with netting on most nights at Pasoh, but at Sepilok traps were set on many nights in addition to those when nets were set. Captured bats were weighed to 0.1 g with a Pesola spring balance to determine the average mass of each species. Species identifications follow Payne and Francis (1985), except for species found only in Peninsular Malaysia which follow Medway (1978). Analyses initially were performed separately for the two sites, but because the results were essentially the same in both areas, only combined data are presented here.

During the study, I caught 798 bats in traps (4.46/trap-night) and only 222 in nets (0.135/net-night). The greater efficiency of traps is particularly notable considering they had only about 12% of the surface area of nets (3 m2 for traps compared with 24 m2 for most of the nets). Expressed by area, nightly captures in traps averaged 1.49 bats/m2 compared with only 0.0057 bats/m2 in nets. However, if bats tended to follow trails, such a comparison may not be justified because the area of each net over a trail was similar to that of each trap.

Nets and traps were examined only a few times each night, so some bats may have escaped between inspections. Most mornings I found holes in nets made by bats that were caught but escaped. I also saw a few bats escape from the top of the trap bags, so the capture rate for both nets and traps would have been greater had they been watched continuously.

Megachiropterans were captured at similar rates in traps and nets, but microchiropterans were captured nearly 60 times more frequently in traps (Table 1). The low rate of capture of Microchiroptera in nets was probably related to their abilities to escape from nets and to detect nets with echolocation, thus avoid them. Most Microchiroptera caught in nets had chewed part of the net around them, and some were seen to escape before I could secure them. In contrast, Megachiroptera caused relatively little damage to nets, thus, were unlikely to have escaped often. When observing nets and traps at dusk, I noted that most Microchiroptera encountering nets avoided hitting them, whereas those encountering traps generally were captured or flew through the lines. I did not observe Megachiroptera encounter nets or traps, but they would be unlikely to detect and avoid either because none of the species captured in this study is known to echolocate.

For both suborders of bats, species of large body size generally were more susceptible to capture in nets (Table 1). In mist nets, both the medium-sized *Cynopterus brachyotis* (mean body mass = 26g) and the smaller *Balionycteris maculata* (13g) were caught commonly (47 and 43 captures, respectively). One to three individuals each of six other species, ranging in size from 14 to 75g, also were netted. In harp traps, nine of 10 fruit bats captured were *B. maculata*; only one *C. brachyotis* was caught. Many microchiropteran species were captured in traps and nets, but most individuals of smaller species were taken in traps.

The trend for larger species to be captured relatively more frequently in mist nets also held for each of the three families of Microchiroptera with more than two species in the sample (Table 1). Additionally, there were differences among families of Microchiroptera in trapping rate independent of body size. The small and medium-sized Rhinolophidae were netted more frequently than similarly sized Hipposideridae (Table 1). Four of five *Emballonura alecto* (6.4g) and *E. monticola* (5.4g) were captured in nets despite their small size. All five *Megaderma spasma* (25.6g) and all six *Nycteris javanica* (15.6g) were netted despite the frequent capture of larger species of Hipposideros in traps.

Some of the interspecific differences in capture frequency of Microchiroptera could be related to variation in the structure of their echolocation calls. Call structure for most Malaysian bats has not been described, but data are available on the constant-frequency components of calls of four species of Rhinolophus and six of Hipposideros from peninsular Malaysia (Feng and Tyrell, in press; Heller, 1985). I compared these frequencies with the number of captures of each of these 10 species. In general, species with high-frequency calls were small and rarely were caught in nets. However, small species (< 10g) with lower-frequency calls (*H. ridleyi*, 61 kHz; *R. sedulus*, 64 kHz; *R. refulgens*, 98 kHz) were netted relatively more often than similarly sized species with high-frequency calls (*H. sabanus*, 200 kHz; *H. cervinus*, 126-142 kHz; *H. bicolor*, 141 kHz). The ratio of captures in traps to captures in nets was 23:7 for low-frequencies and 296:9 for high frequencies (Fisher's exact test, $P < 0.001$). The larger species (> 12g) had lower-frequency calls (< 76 kHz), and were netted even more often than smaller species with calls of similar frequency. The ratio of captures in traps to captures in nets was 73:68 for large bats and 14:4 for the two small species with the lowest frequencies (Fisher's exact test, $P = 0.04$). This suggests that both call frequency and body size influence capture rate in nets. The relatively high rate of capture of *Rhinolophus* in nets, compared to *Hipposideros*, may be

Table 1. Comparison of the number of captures of bats in mist nets and harp traps, by suborder, and within each suborder and major family of Microchiroptera, by species grouped into size classes. Combined data from Pasoh and Sepilok in Malaysia.

Category		Mass [a] (g)	Mist nets n	Mist nets Rate (bat/100 net-nights)	Harp traps n	Harp traps Rate (bat/100 net-nights)	P [b]
Suborders:	Megachiroptera		98	5.9	10	5.6	<0.001
	Microchiroptera		124	7.5	788	440.2	
Species w/in suborder:	Megachiroptera	10-20	48	2.9	9	5.0	<0.01
		20-80	50	3.0	1	0.6	
	Microchiroptera	3-5	1	0.1	127	70.9	<0.001
		5-10	38	2.3	526	293.9	
		10-20	68	4.1	124	69.3	
		20-60	17	1.0	11	6.1	
Species within family:	Hipposideridae	5-10	11	0.7	341	190.5	<0.001
		10-20	5	0.3	50	27.9	
		20-50	12	0.7	11	6.1	
	Rhinolophidae	5-10	8	0.5	22	12.3	0.04
		10-20	56	3.4	63	35.2	
	Vespertilionidae	3-5	1	0.1	128	71.5	<0.001
		5-10	15	0.9	161	89.9	
		10-20	1	0.1	11	6.1	

[a] Bats were assigned to size categories based on the mean body mass of the species

[b] log-likelihood ratio test (G-test) whether captures were independent of trap type. For Hipposideridae and Vespertilionidae, the two largest size categories were combined because of small sample sizes

related to the generally lower-frequency calls of the former.

Data from Pasoh Forest Reserve were used to compare four-bank traps with two-bank traps. Overall, two-bank traps caught 170 bats in 40 trap-nights (4.3 bats/trap-night), whereas four-bank traps caught 110 bats in 13 trap-nights (8.5 bats/ trap-night). However, these totals include records of two-bank traps from several different trapping sessions, whereas the four-bank traps were used only in late August 1987. During the latter session, a two-bank trap, set in approximately the same locations as the four-bank traps although on different nights, caught only 12 bats in eight trap-nights (1.5 bats/trap-night). Thus, it appears that four-bank traps were 2-6 times more efficient than two-bank traps. However, further data are required to confirm the difference statistically because of high variation in nightly trapping success.

There were significant differences in the effectiveness of the two types of traps for different species of bats. Capture rates for 5-10 g bats were similar in both two-bank and four-bank traps (2.5 and 3.0 bats/ trap-night, respectively; 101 and 39 individuals). However, smaller bats were caught slightly more frequently in two-bank traps (0.5 and 0.2 bats/trap-night; 21 and three individuals), whereas larger bats were caught much less frequently (1.1 and 5.0 bats/trap-night; 45 and 65 individuals). Overall, the relative differences were highly significant ($G = 34.0$, $P < 0.0001$).

Personal observations on a few nights indicated that fewer bats flew straight through four-bank traps than two-bank traps. Because of darkness, I could not determine the position of the wings when bats hit the traps, but those bats flying through the lines invariably hit them with sufficient force to make a clearly audible “twang.” This suggests that many bats, especially larger species, have sufficient momentum to force their way between two banks of line, but insufficient to fly through four. However, despite the improved efficiency, some bats still can fly through the four-bank traps.

The observed differences between traps and nets in capturing Malaysian bats support previous studies showing harp traps to be more effective than mist nets (Laval and Fitch, 1977; Tidemann and Woodside, 1978). This study also confirms the existence of interspecific variation in relative susceptibility to traps or nets (Laval and Fitch, 1977). For studying community structure, an ideal trapping method produces captures of bats in proportion to the abundance of each species in the community. Other sampling methods can be used, however, provided that the extent of their biases can be estimated. It was not possible from this study to determine the exact biases because the actual number of each species in the forest was not known.

The greater ability of some bats to escape from mist nets is a factor that influences number of captures. All Megachiroptera are frugivorous or nectarivorous; their teeth have rounded or pointed crowns that did not appear to be effective at cutting nets. Frugivorous phyllostomids also have reduced dentition and frequently are captured in nets (Laval and Fitch, 1977), suggesting that they similarly may be inefficient at chewing nets. In contrast, all Microchiroptera caught in this study were insectivorous; their teeth have sharp cutting edges with which they readily chewed holes in nets to enable escape.

Body size also is related to trapping success. The greater momentum of large bats apparently increased their ability to fly straight through harp traps, at least those with two banks. This suggests that large bats were under-sampled by two-bank traps. In addition, large bats generally have higher wing loadings and cannot turn as sharply (Aldridge, 1987). This could have resulted in over-sampling of large bats by mist nets if the bats were less able to avoid nets.

Interspecific variation in echolocation calls also appears to influence capture rates in nets. Megachiroptera, of which none of the species in this study are known to echolocate, were caught frequently in mist nets. They rely entirely on vision for navigation, and it is unlikely, in the darkness of the forest understory, that they could detect either mist nets or traps before hitting them. In contrast, all species of Microchiroptera probably are capable of detecting mist nets by echolocation, although with different degrees of resolution. Species with high-frequency calls seemed to be least susceptible to mist nets, possibly because these frequencies better resolve small targets such as knots in mist nets (Feng and Tyrell, in press). Alternatively, bats with high-frequency calls may be adapted for short-distance maneuvering, because their calls attenuate more rapidly and probably have a shorter range (Novice, 1977). Variation in echolocation calls also may have influenced captures in traps. Most bat species examined in the laboratory can echolocate vertical wires < 0.2 mm in diameter even at much greater spacing than the lines on traps (Novick, 1977). Kunz and Anthony (1977) noted that # 30% of Myotis lucifugus detected and avoided traps placed near their roost. However, those bats may have used vision, because the observations were conducted at dusk in relatively open areas. Further data are required to determine whether bats that hit traps fail to detect them, or detect them and attempt to fly through them.

Other factors that can affect capture rates of bats include microhabitat and height at which the trapping device is set, opportunities for bats to avoid the device, proximity to food or water supplies, ambient weather and light conditions, age and experience of the bats, and behavior (e.g., commuting or foraging) of the bats (Constantine, 1958; Kunz and Anthony, 1977; Kunz and Kurta, 1988). Insofar as the effects of these factors vary among species, the proportion of species in the sample will be biased.

It is unlikely that any capture method will produce a completely unbiased sample. Factors other than biases also may influence the choice of capture methods for a particular study. Of methods tested in this study, four-bank traps were the most effective, at least for Microchiroptera, and were probably least biased. However, they are slightly more expensive, more time-consuming to build and set, and weigh slightly more than two-bank traps. Further experiments with different spacing, sizes, or tensions of lines may show that other designs of traps are even more effective. Also, for some groups of bats such as Megachiroptera, mist nets apparently were as effective as traps. Given their low cost and portability, mist nets still may be preferable for some studies, even of Microchiroptera, especially if they are watched closely to minimize escapes (Kunz and Kurta, 1988). However, the potential biases must be considered during analysis. Simple capture rates with any method should be used as an index of relative abundance with caution.

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Comparison of Sampling Methods for Inventory of Bat Communities

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From 1999 to 2005, we sampled the bat fauna of Catalonia (northeastern Spain, Mediterranean region) using 3 methods (bat detectors, mist nets, and roost surveys) and determined the total number of bat species present (S 1/4 22). Twelve bat species and 5 acoustic groups (_5 different species) were identified using bat detectors, 17 species were found during roost inspections, and 13 species were trapped using mist nets. However, mist nets yielded the highest species richness per number of individuals sampled, as demonstrated by rarefaction. Some species were always either over- or under-sampled according to the sampling method used. We also evaluated 3 guilds of bats defined by summer roost preferences, documenting a significant correlation between guild and detection method; cavity-roosting bats were underrepresented when only bat detectors and mist-net surveys were used, whereas rock crevices or man-made structure and tree guilds were underrepresented when only roosts were surveyed. Different techniques should be used to assess the richness of bat communities and we recommend combining all the methods described above in future bat surveys.

Key words: bat communities, bat detectors, Mediterranean region, mist nets, roosts, sampling methods, species richness, surveys

The order Chiroptera is the 2nd most diverse order of mammals (Wilson and Reeder 2005) and exhibits great numerical, taxonomical, functional, and ecological diversity (Simmons and Conway 2003; Stevens and Willig 2002). However, assessing the distribution of bat species and the composition of bat communities is a challenge (Jaberg and Guisan 2001) because their nocturnal behavior, large home ranges, and the problems associated with species identification in flight (Walsh and Harris 1996) make accurate surveys difficult.

Studies of bat distribution and habitat preferences use different sampling techniques to describe the great complexity of bat communities. From the analysis of specimens housed in museum collections (Lopez-Gonzalez 2004) to the use of advanced technology (i.e., bat detectors—Vaughan et al. 1997), numerous different methods of sampling bats are currently in use, although today most researchers employ a combination of techniques (Duffy et al. 2000; Jaberg and Guisan 2001).

Bat detectors enable bats to be studied in greater detail and are now employed by most researchers in censuses of bat faunas (Barataud 1998; Ciechanowski 2002; Pauza and Pauziene 1998) and in the analysis of habitat use (Avila-Flores and Fenton 2005; Vaughan et al. 1997; Wickramasinghe et al. 2004). Despite their shortcomings (Hayes 2000), bat detectors frequently are used in annual monitoring programs (Walsh et al. 2001). However, scientists have become concerned with the validity of data derived from this method. Over the last decade a growing number of studies have examined the advantages and disadvantages of techniques using bat detectors (Ahle´n and Baagoe 1999; Barclay 1999; Hayes 2000) and various authors have analyzed sampling methods for bats in a search for better bat survey strategies (Duffy et al. 2000; Murray et al. 1999; O'Farrell and Gannon 1999). Despite the fact that acoustic sampling methods seem to yield greater species richness than captures (Murray et al. 1999; O'Farrell and Gannon 1999), almost all authors agree that echolocation monitoring should be but one component of bat surveys and that a combination of techniques is required for more comprehensive inventories (Barclay 1999; O'Farrell and Gannon 1999).

Mist nets have several drawbacks: they are time-consuming to set up, need to be placed in flyways or water sources with good canopy coverage over the net, cause stress in animals, and, moreover, obtain biased samples of bat species assemblages (Murray et al. 1999). Harp traps are less stressful; however, the species sampled varies with body size, flight patterns, and type of echolocation (Duffy et al. 2000). On the other hand, bat detectors cause no stress to bats, although the data theyproduce also are biased, because high-flying bats and those that emit low-intensity calls are underrepresented (Barclay 1999; Duffy et al. 2000).

Other techniques should be considered in bat survey studies. Finding roosts in man-made structures or in caves and mines represents a useful survey method; several bat species can be inventoried in roosts or when they leave roosts at sunset (Mitchell-Jones and McLeish 1999; Tuttle et al. 2000). Another technique that should be considered is bat-box surveys. These artificial roost sites should not be viewed merely as alternative roosts sites (Brittingham and Williams 2000; Flaquer et al. 2006; Lourenço and Palmeirim 2004) and are useful for providing data on bat communities, especially in areas with a lack of old trees bearing natural roosting sites (Flaquer et al. 2007). Bat boxes may be particularly effective for surveying bats in woodland habitats; for example, at least 73% of British bats are known to have roosted in boxes (Mitchell-Jones and McLeish 1999; Stebbings and Walsh 1991).

Because of their peculiar climatic and ecological features, Mediterranean countries differ remarkably from the areas of Europe where most data on habitat use by bats have been gathered. Yet, little is known about habitat preference in bats in the Mediterranean Region (Russo and Jones 2003). From 1999 to 2005, we studied the bat fauna in and around 10 natural areas distributed along the Catalan Mediterranean coastline in northeastern Spain. Captures of bats with mist nets and roost surveillance were combined with the use of ultrasonic detectors. We discuss the advantages and disadvantages of each method and compare the efficiency of each technique for assessing species richness of bats. Additionally, we provide recommendations for future monitoring and survey strategies in this region.

MATERIALS AND METHODS

Study area.—The Catalan coast is located in the northeastern Iberian Peninsula (408429N, 08509E) and comprises 580 km of coastline and littoral and pre-littoral mountain ranges covering 31,000 km2 and ranging from sea level to 1,700 m in elevation. The predominant climate is Mediterranean (annual mean temperatures around 158C and annual precipitation between 500 and 700 mm/year). Climate varies with topography, although summers generally are dry and hot (precipitation , 200 mm/year and mean temperatures around 208C), whereas spring and autumn are wet. Vegetative communities are dominated by *Quercetum ilicis galloprovinciale* and *Quercus mediterraneo montanum*, although scattered beech (*Fagus sylvatica*) forest could be found in the coldest areas.

Identification of bats.—Bats were identified in the field based on morphological and dental criteria in live bats (Arthur and Lemaire 1999; De Paz and Benzal 1990; Helversen 1989; Menu and Popelard 1987; Palmeirim 1990; Schober and Grimmberger 1996). Additionally, we used ultrasonic bat detectors (models D230 and D240x; Pettersson Elektronics AB, Uppsala, Sweden) with frequency division, heterodyne, and time expansion (_10) systems, as well as a portable digital tape (SONY TCD-D8; Sony Corporation, Tokyo, Japan) and a laptop computer to record echolocation and social calls (Ahle´n 1990; Barataud 1996; Russ 1999). Sounds were analyzed by Bat Sound (Pettersson Elektronics AB). We used a sample frequency of 44,100 samples/s, 16 bits/sample, and automatic fast Fourier transform (a mathematical formula for calculating frequency data from time data) with a Hanning window (Russ 1999). Recordings were screened for the presence of the characteristic social calls emitted during the mating period (Russ 1999; Russo and Jones 1999) and calls were identified by means of a library of known echolocation call sequences for each species. Identification of the soprano pipistrelle (*Pipistrellus pygmaeus*) and Schreibers's bat (*Miniopterus schreibersii*) were based on presence of social calls, observations of wing-shape in good conditions, or both (Ahle´n 1990). For the purposes of acoustic identification, we treated the following pairs of species as single ‘‘taxa’’: lesser/greater mouse-eared bats (*Myotis blythii/M. myotis*), Natterer's/Geoffroy's bats (*Myotis nattereri/M. emarginatus*), Daubenton's/long-fingered bats (*Myotis daubentonii/M. capaccinii*), noctule/greater noctule (*Nyctalus noctula/N. lasiopterus*), and brown/gray long-eared bats (*Plecotus auritus/P. austriacus*—Ahle´n 1990; Ahle´n and Baagoe 1999; Barataud 1996).

Bat survey techniques.—Between 1999 and 2005, we randomly used 3 different approaches for sampling bat species richness of bats (bat detectors, mist nets, and inspection of roosts), from April to November, in 10 natural areas located along the Catalan coast.

In all, we surveyed 418 independent bat detector stations at heights from sea level to 1,629 m above sea level (_X 1/4 359 m 6 417 SD). We used D240x and D230 bat detectors and activity was quantified by counting the number of passes per 10 min at each point (Wickramasinghe et al. 2003). The D230 detector was tuned to use frequency division, which provides for both broadband (records all frequencies) and continuous

TABLE 1.—Frequencies of occurrence of the 22 bat species and number of species detected by 3 bat-sampling methods in a coastal Mediterranean area.

Species	Mist nets	Roost surveillance	Bat detectors
Rhinolophus ferrumequinum		7.76	0.1
R. hipposideros		3.46	0.05
R. euryale		7.29	0.12
Myotis myotis		2.46	0.61[a]
M. blythii	2.36	0.02	
M. nattereri		0.45	
M. emarginatus	0.79	11.43	
M. daubentonii	3.94	0.38	2.95[b]
M. capaccinii		0.01	
Pipistrellus pipistrellus	20.47	0.24	29.22
P. pygmaeus	14.17	13.56	40.79
P. nathusii		0.01	
P. kuhlii	3.15	0.19	4.68
Hypsugo savii	20.47		4.8
Nyctalus leisleri	7.09		1.15
N. noctula/N. lasiopterus			0.15
Eptesicus serotinus	6.3	0.69	4.36
Barbastella barbastellus	3.15		1.39
Plecotus austriacus	13.39	0.66	1.92[c]
P. auritus	3.15		
Miniopterus schreibersii	1.57	51.37	0.01
Tadarida teniotis			7.72
Number of species	13	17	17

[a] Species pairs with *M. blythii*.
[b] Species pairs with *M. capaccinii*.
[c] Species pairs with *P. auritus*.

(records all bat passes) recording. We recorded the output from frequency division on channel 1 of the portable digital recorder and we used the time-expanded output from detector D240x to record bat calls from each pass on channel 2 of the portable recorder (Vaughan et al. 1997). According to Ahle´n and Baagoe (1999), time-expansion sounds retain call structure and have high sound quality and so can be analyzed to identify species. Additionally, we used the heterodyne system from the detector D240x scanned up and down to cover all frequencies (Ahle´n and Baagoe 1999).

We used standard techniques to mist net bats (O'Farrell and Gannon 1999). Net heights varied from 2.5 to 3 m and lengths varied from 3 to 18 m and were placed along or around waterways, ponds, and flyways. The amount of time employed and the number of nets used depended on the physical characteristics of each location (O'Farrell and Gannon 1999). In all, we established 68 independent stations with mist nets representing 3,561 m2 of mist-net collecting surface operating for a total of 175.4 h. These stations were situated at elevations between 41 and 1,481 m above sea level (_X 1/4 643 6 373 m). We operated mist nets for 173.8 6 82.7 min (range 60–590 min) and had a mean length of 17.1 6 8.1 m (range 3–35 m).

We used standard techniques to find roosts (mines, caves, and man-made structures—Mitchell-Jones and McLeish 1999; Tuttle et al. 2000), and we applied guidelines established by Mitchell-Jones and McLeish (1999) to identify and count bats in roosts. The 271 roosts found and visited were situated at elevations from sea level to 1,300 m above sea level (_X 1/4 346 6 312 m) and were visited 2.0 6 3.1 times (range 1–28; total visits 541). Roosts sampled more than once were visited in different seasons or years (O'Farrell and Gannon 1999).

Statistical analysis.—We used 3 statistical approaches to identify and quantify possible sampling biases between the 3 different methodologies employed in the study. First, we used a log-linear analysis to search for differences between the 3 sampling methods in the species composition and abundance of bat communities (Torre et al. 2004). This technique allowed us to determine what species were under- or oversampled by each sampling method. The standardized residuals after the log-linear analysis were used to represent the degree of deviance from the null model (no under- or oversampling of a species by a sampling method), and the statistical significance was verified by examining the components of maximum likelihood comparing these values with the critical level of significance (*v*2 1/4 3.84, d.f. 1/4 1, P , 0.05). Second, we used the nonparametric Kruskal–Wallis test (Zar 1996) for comparing methods, because species richness and abundance did not have a normal distribution within the sampling methods and had a heterogeneity of variances. Because no post hoc tests are available for nonparametric tests, we conducted pairwise comparisons and used Bonferroni corrections to correct for significance level (Rice 1989); thus, our acceptable critical region was P 1/4 0.05/ 3 1/4 0.0166.

Finally, given that the total number of individuals observed varied among methods, we used rarefaction to provide a meaningful interpretation of the different species richness found in each of the 3 sampling methods. Rarefaction takes into account species richness and abundance and allows comparisons between assemblages of equivalent numbers of individuals. We used Ecosim 7.0 software (N. J. Gotelli and G. L. Entsminger 2001, Ecosim: null models software for ecology, http://www.garyentsminger.com/ecosim/index.htm) to generate individual-based rarefaction curves of species richness and associated variance for each of the 3 sampling methods (Lambert et al. 2005; Torre et al. 2004). The computer sampling algorithm of the program randomly draws a sample of specified size from the total sample and computes a mean and a variance for species richness after 1,000 iterations. The individual-based data sets were obtained after pooling replicated samples into single ones for each sampling method (Gotelli and Colwell 2001).

The statistical comparison of species richness by rarefaction curves and of the number of individuals depends on the correct assessment of the number of individuals captured, counted, detected, or a combination of these. Roost surveys and mist netting both allow determination of the number of individuals counted or trapped for every species sampled, despite that the number of individuals sampled represent a fraction of the population. Bat detectors, on the other hand, count bat passes but cannot identify individuals. The number of passes detected likely is correlated to the number of individuals (Wickramasinghe et al. 2003), although there is no way of enumerating exactly the number of individuals present on the basis of passes counted because bat detector samples may count the same individual more than once. This will have a negative effect on estimates of species richness carried out by rarefaction (i.e., species richness will be underestimated).

All methods and procedures used in the present study followed the guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists (Animal Care and Use Committee 1998).

RESULTS

In all, the 3 sampling methods detected 22 species of bats in the study area and revealed qualitative and quantitative differences between bat communities according to the sampling method. Twelve bat species and 5 acoustic groups (_5 different species) were identified using bat detectors, 17 species were found during roost inspections, and 13 species were trapped using mist nets (Table 1). Some species were identified by only 1 method (roost surveys: Nathusius's pipistrelle [*Pipistrellus nathusii], M. nattereri*, and *M. capaccinii*; mist nets: *Plecotus auritus*; bat detectors: European free-tailed bat [*Tadarida teniotis*]), although some of these species form part of acoustic pairs.

A log-linear analysis was performed with frequencies of occurrence for all the identified species (22) and for each sampling method, yielding highly significant differences (interaction of species _ method: G 1/4 12,842, d.f. 1/4 42, P , 0.0001). All the species sampled except *M. capaccinii* and *P. nathusii* showed significant differences between the 3 sampling methods in their frequencies of occurrence. Members of the family Rhinolophidae and *M. myotis, M. nattereri*, *M. emarginatus*, and *M. schreibersii* were oversampled by roost inspections, but under-sampled by bat detectors (Fig. 1A). On the other hand, *P. auritus, P. austriacus, M. daubentonii*, common pipistrelle (*P. pipistrellus*), Kuhl's pipistrelle (*P. kuhlii*), Savi's pipistrelle (*Hypsugo savii*), serotine (*Eptesicus serotinus*), western barbastelle (*Barbastella barbastellus*), and Leisler's noctule (*Nyctalus leisleri*) were oversampled by the use of bat detectors and mist nets, but under-sampled by roost inspections (Fig. 1B). P. pygmaeus was oversampled by bat detectors and under-sampled by roost inspections and nets, *T. teniotis* was oversampled by bat detectors and under-sampled by roost inspections, and *M. blythii* was oversampled by net sampling. Some species, such as *P. pygmaeus* and *P. pipistrellus*, were detected mainly by bat detectors (40.8% and 13.6%, respectively), whereas others were most often detected by roost inspections, such as *M. schreibersii* and *R. ferrumequinum* (51.4% and 7.8%, respectively), or by mist netting, such as *H. savii* and *P. austriacus* (20.5% and 13.4%, respectively; Table 1).

A 2nd log-linear analysis was performed by grouping bat species into 3 guilds on the basis of their summer roost preferences: cavities (*Rhinolophus* sp., *M. myotis, M. blythii, M. nattereri, M. capaccinii, M. emarginatus, P. austriacus, P. auritus*, and *M. schreibersii*), trees (*Nyctalus*, *P. nathusii*, and *B. barbastellus*), and rock or man-made structure crevices (*P. pipistrellus*, *P. pygmaeus*, *M. daubentonii*, *P. kuhlii*, *H. savii*, *E. serotinus*, and *T. teniotis*). Once again, differences in frequencies of occurrence between sampling methods for the 3 guilds were highly significant (interaction of guild _ method: G 1/4 9,679, d.f. 1/4 4, P , 0.0001) and were found for the 3 paired comparisons. As can be seen in Fig. 2, roost inspections oversampled cavity-dwelling species, but under-sampled both the crevice- and tree-roosting guilds. Bat detectors oversampled the crevice-roosting guild and, to a lesser extent, the tree roosting guild, whereas they under-sampled the cavity-roosting guild. Finally, mist nets oversampled the crevice- and tree roosting guilds, but under-sampled the cavity-roosting guild.

We observed a high degree of agreement in species occurrence frequencies for bat detectors and mist netting and, in most cases, both methods over- or under-sampled estimates for the same species.

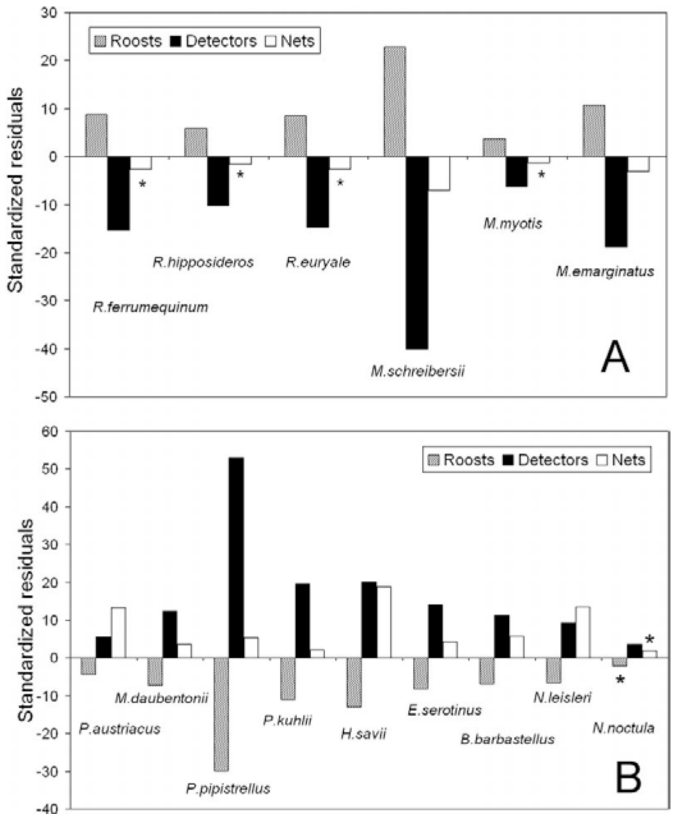
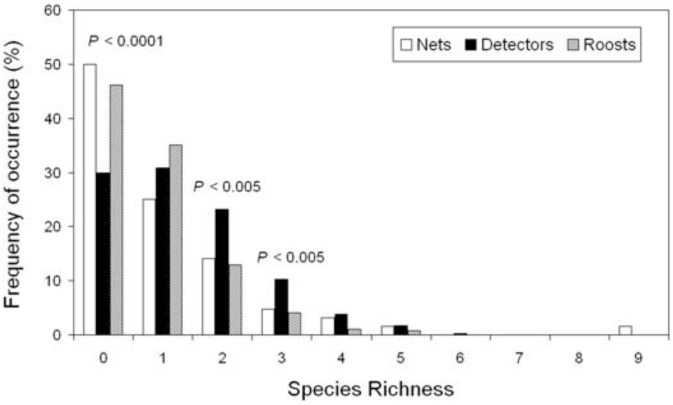


FIG. 1.—Standardized residuals after a log-linear analysis showing A) bat species oversampled by roost surveys and undersampled by bat detectors and mistnetting, and B) species undersampled by roost surveys and oversampled by bat detectors and mistnetting (interaction of species _ method: G 1/4 12,842, d.f. 1/4 42, P , 0.0001). All species showed significant differences in frequencies of occurrence between methods. Positive residuals: oversampling of a species; negative residuals: undersampling of a species. Residuals marked with asterisk were not significantly different from zero. Some species are acoustic pairs in the case of bat detectors (see Table 1).

A log-linear analysis performed using the frequencies of occurrence from stations with 0–9 species detected by all sampling methods yielded highly significant differences (interaction of species richness _ method: G 1/4 47.45, d.f. 1/4 18, P , 0.0001). Mist nets and roost surveys showed a higher proportion of sampling stations with negative records (50% and 46% with no species recorded, respectively), whereas bat detectors showed a higher proportion of sampling stations with 2 and 3 species (23% and 10% of the total stations, respectively; Fig. 3). Frequencies of occurrence of 1, 4, 5, 6, and 9 species per station did not differ between sampling methods (Fig. 3).



The number of individuals sampled differed greatly between methods, with a total of 13,477 individuals counted in roost inspections, 6,031 bat passes (contacts) counted with bat detectors, and only 128 bats captured in mist nets. The mean number of species detected per station by bat detectors was 1.33 6 1.22 (SD), with a range of 0–6 species. The mean number of contacts per station was 14 6 25 (SD), with a range of 0–186. The mean number of species detected by roost surveys was 0.81 6 0.96 (SD), with a range of 0–5 species. The mean number of bats per roost was 49.7 6 320 (SD), with a range of 0–5,000. The mean number of species detected by mist netting was 1.01 6 1.54 (SD), with a range of 0–9 species. The mean number of bats captured per station was 2.0 6 4.3 (SD), with a range of 0–30.

The species richness detected was significantly higher for bat detectors than for mist-net stations (H 1/4 8.24, d.f. 1/4 1, P 1/4 0.004) or for roosts (H 1/4 33.55, d.f. 1/4 1, P , 0.0001), although no significant difference was detected between mist nets and roosts (H 1/4 0.01, d.f. 1/4 1, P 1/4 0.89). The number of individuals or contacts per station was higher for bat detectors than for mist nets (H 1/4 43.96, d.f. 1/4 1, P , 0.0001) or for roosts (H 1/4 36.85, d.f. 1/4 1, P , 0.0001), although no significant difference was detected between mist nets and roosts (H 1/4 3.25, d.f. 1/4 1, P 1/4 0.07). However, because species richness increases with the number of individuals recorded, we generated individual-based rarefaction curves to compare species richness between sampling methods for the same number of individuals.

FIG. 2.—Standardized residuals after a log-linear analysis performed with the 3 guilds based on summer roost preferences and the 3 sampling methods (interaction of guild _ method: G 1/4 9,679, d.f. 1/4 4, P , 0.0001). Positive residuals: oversampling of a guild; negative residuals: undersampling of a guild. All the residuals were significantly different from zero.

Mist nets had the highest richness per number of individuals sampled, followed by bat detectors and then roost surveys (Fig. 4).

DISCUSSION

The combination of sampling methods used in our Mediterranean study area during the 6 years of sampling detected 22 species of bats. This number agrees with the total number of bat species known to be present in the area (Flaquer et al. 2004; Palomo and Gisbert 2002; Serra-Cobo 1987) and represents 85% of species belonging to the very rich Iberian bat fauna (Palomo and Gisbert 2002). Overall, 77% of the species were detected by acoustic monitoring, 77% at roost sites, and 59% with mist nets. Our results confirm that combined survey techniques are required for thorough bat inventories (Barclay 1999; O'Farrell and Gannon 1999), as has been found for terrestrial small mammals in the same area (Torre et al. 2004).

Although the sampling effort was intense, the rarest species in the study area (*P. nathusii, M. nattereri, M. capaccinii, P. auritus*, and *N. noctula/N. lasiopterus*) were detected by only 1 method, a fact that indicates that rare species may be easily overlooked if only 1 inventory technique is used. On the other hand, common species such as P. pygmaeus were identified by all the methods used. As noted by O'Farrell and Gannon (1999) and Murray et al. (1999), the number of species detected by bat detectors was significantly higher than that detected by mist nets, whereas roost inspections yielded the same species richness as bat detectors. Nevertheless, mist nets and roost surveys had a higher proportion of sampling stations with negative records and in almost half of the stations our sampling efforts were fruitless; in these localities, detectors were a more efficient method.

Of all methods, mist nets detected the highest species richness per number of individuals sampled, probably because of biases related to the location of sampling stations near ponds or rivers, especially suitable habitats for bats in the Mediterranean region (Russo and Jones 2003). Species-rich sites were found in dry regions wherever nets were located near the isolated ponds or rivers and at 1 station we detected 9 different species on a single night, the highest number of species detected by any sampling method at a single station in this study.

According to our results, the most viable method for assessing species richness of cavity-roosting bats (especially Rhinolophus) is to find their roosts, a limitation that should be taken into account in studies where only mist nets and bat detectors are used. On the other hand, roost-finding techniques under represent crevice- and tree-roosting bats. We ruled out the use of climbing as a means of examining tree roosts (Ruczyn´ski and Bogdanowicz 2005) because this method is highly time consuming and requires specially trained researchers. Furthermore, the Catalan forests lack old trees bearing natural roosting sites as a consequence of forest management practices that emphasized timber extraction until the middle of the 20th century (Flaquer et al. 2007, and references therein). In light of the results from wetlands in the study area (Flaquer et al. 2005, 2006), it is likely that the lack of old trees in the study area with suitable roost sites will increase the importance of bat boxes (Flaquer et al. 2006; Ruczyn´ski and Ruczyn´ska 2000).

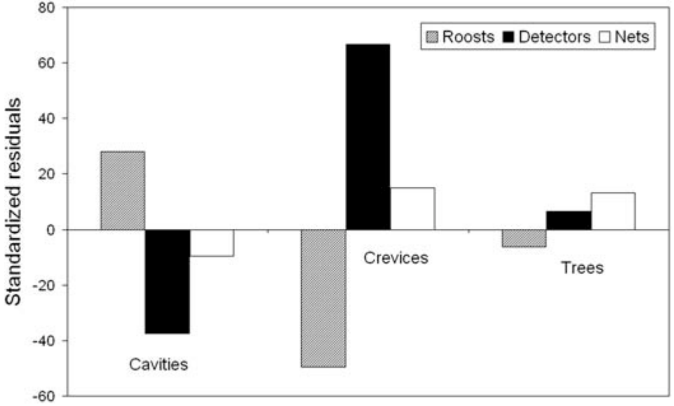


FIG. 3.—Frequencies of occurrence of stations with 0–9 species detected by all sampling methods. Statistical differences between methods for all categories were assessed by means of a log-linear analysis with sampling methods (3 categories) and number of species detected (9 species; interaction of species richness _ method: G 1/4 47.45, d.f. 1/4 18, P , 0.0001). Significant differences between categories are shown by P-level.

Field surveys based on captures in mist nets and harp traps provide the opportunity to collect biological and morphological data that cannot be obtained with bat detectors (Duffy et al. 2000; O'Farrell and Gannon 1999). Furthermore, some species are easier to capture in mist nets than with other capture methods. We believe that annual bat-capture programs based on intensive small-scale trapping in mist nets and harp traps (Mitchell-Jones and McLeish 1999) would be a useful tool for sampling bat communities.

Although some European research has focused on analyzing changes in bat populations (Ransome and Hutson 1999; Walsh et al. 2001), little is known about bats in the Mediterranean region (Russo and Jones 2003). We documented that a combination of capture and bat detector techniques is effective (Duffy et al. 2000; O'Farrell and Gannon 1999), although cavity-roosting bats and some rare species often are underrepresented. Without roost-survey techniques we would have missed 3 of the 22 species encountered. Therefore, roost surveys are essential for assessing bat species richness in Mediterranean areas; finally, although not studied here and as an untested recommendation, we believe that the lack of old trees could make the use of bat boxes useful in bat surveys in this region. We recommend combining all the methods described above in future surveys and monitoring programs for Mediterranean bats.

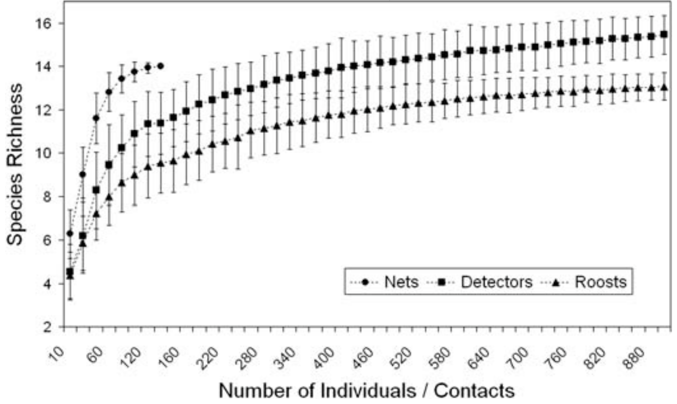


FIG. 4.—Rarefied species accumulation curves showing number of species (mean 6 SD) versus number of individuals or contacts detected by each sampling method.

RESUMEN

Entre los an˜os 1999 y 2005, la fauna de quiro´pteros de Catalun˜a (NE Espan˜a, regio´n Mediterra´nea) fue inventariada usando 3 me´todos de muestreo (detectores de ultrasonidos, redes de niebla y visitas a refugios) obteniendo informacio´n sobre las 22 especies de quiro´pteros presentes en la zona. Doce especies y 5 grupos acu´sticos (_5 especies diferentes) fueron identificadas usando detectores de ultrasonidos, 17 especies fueron detectadas durante la inspeccio´n de refugios, y 13 especies fueron capturadas usando redes de niebla. No obstante, la rarefaccio´n demostro´ que las redes de niebla tuvieron la mayor riqueza relativa al nu´mero de individuos capturados. Comparamos las frecuencias de aparicio´n de las especies identificadas con los 3 me´todos de muestreo y observamos que ciertas especies eran sobre muestreadas o infra muestreadas dependiendo del me´todo de muestreo usado. Tambie´n se agruparon las especies en 3 gremios definidos por la preferencias en el tipo de refugio utilizado durante el verano. Una correlacio´n altamente significativa entre el gremio y el me´todo de deteccio´n fue encontrada y los quiro´pteros de cavidades quedaron infra representados cuando solamente los detectores de ultrasonidos y las redes de niebla fueron utilizadas. Por otro lado, los quiro´pteros que utilizan grietas en rocas o en infraestructuras humanas, y los que utilizan refugios en a´rbol, quedaron infra representados cuando solamente se inspeccionaron refugios. Creemos que para determinar la riqueza de las comunidades de quiro´pteros es necesario utilizar diversas te´cnicas y recomendamos la combinacio´n de todos los me´todos descritos arriba en futuros estudios sobre las comunidades de quiro´ pteros.

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Temporal Variation in Activity of Bats and the Design of Echolocation-monitoring Studies

by John P. Hayes

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I used Anabat II bat detectors to monitor echolocation calls of bats over two streams in the Oregon Coast Range for a total of 195 detector-nights. Activity of bats was positively correlated with biomass of insects and minimum nightly temperature, and was negatively correlated with length of night; activity levels at the two streams were positively correlated. Activity of bats was not significantly correlated with either hours of moonlight or with phase of moon. Level of activity within a night generally peaked shortly after sunset with a second, smaller peak in activity shortly before sunrise, but patterns varied substantially among nights. Total nightly activity at a site also varied substantially among nights, sometimes varying several-fold on consecutive nights. To assess the implications of temporal variation in activity of bats on sampling, I randomly sampled subsets of the data using from 2- to 12-night sample periods and calculated mean levels of activity for each subset. For subsets with seven or more nights, > 60% of the subsets had means that were within 20% of the mean of the entire dataset. Less than 50% of the subsets had means within 10% of the mean of the entire dataset for any number of nights subsampled. When comparing activity between sites, use of blocked or paired designs improved sampling efficiency by 20%. Failure to account for temporal variation in activity of bats when designing research projects and monitoring programs could result in biased estimates of activity of bats.

Key words: bat detector, activity of bats, echolocation, activity patterns, temporal variation, sampling, statistical design

Recently, there has been a surge of interest in studying habitat relationships of bats by monitoring echolocation calls using bat detectors (Barclay, 1991; Burford and Lacki, 1995; Crampton and Barclay, 1996; Erickson and West, 1996; Hayes and Adam, 1996; Krusic and Neefus, 1996; McAiney and Fairley, 1988; Parker et al., 1996; Thomas, 1988). This interest has been spurred, in part, by technological improvements in relatively low-cost bat detectors. Use of bat detectors holds promise for addressing questions concerning patterns of activity and use of habitat by bats, but the technique has limitations. One important limitation is that it is not possible to estimate population abundance using bat detectors; however, data collected using bat detectors can provide estimates of activity of bats. In addition, experimental approaches have not been standardized and considerations for design of studies have not been fully evaluated.

Temporal variation in activity of bats may influence the design and interpretation of studies and monitoring programs using bat detectors. Activity patterns of bats may vary on a daily or seasonal basis in response to a variety of exogenous and endogenous factors, including abundance of insects (Anthony et al., 1981; Avery, 1985; Barclay, 1991; de Jong and Ahlen, 1991; Taylor and O'Neill, 1988), moonlight (Adam et al., 1994; Crespo et al., 1972; Fenton et al., 1977; Morrison, 1978; Reith, 1982; Usman et al., 1980), air temperature (Anthony et al., 1981; Audet, 1990; Avery, 1985; Kunz, 1973; Lacki, 1984; Maier, 1992; Ruedi, 1993; Rydell, 1991; Whitaker and Rissler, 1992), heavy rainfall (Bell, 1980; Fenton, 1970; Fenton et al., 1977; Kunz, 1973; Reudi, 1993), wind (Adam et al., 1994; Avery, 1985; O'Farrell and Bradley, 1970; O'Farrell et al., 1967; Rydell, 1991), relative humidity (Adam et al., 1994; Lacki, 1984), metabolic water balance (Hays et al., 1992; Speakman and Racey, 1989), energetic demands imposed by pregnancy (Anthony et al., 1981; Ruedi, 1993; Swift, 1980), and interspecific competition (Kunz, 1973; Reith, 1980). Factors that are correlated with activity level differ among studies and may be area- and species-specific.

If experimental and sampling designs do not adequately account for temporal variation, estimates of activity for an area could be biased, and apparent differences or similarities among areas could be an artifact of temporal variation. By understanding patterns and correlates of variation in activity of bats, design of research and monitoring programs can be improved. In this paper I present information on temporal patterns of variation in activity of bats in two riparian areas in the Oregon Coast Range.

Materials And Methods

Field methods. I monitored activity of bats in riparian areas of two third-order streams in the Oregon Coast Range; Bark Creek (T11S, R7W, Sec. 30) and Buttermilk Creek (T10S, R8W, Sec. 31). The streams are ca. 14.5 km apart. Overstory vegetation in monitored areas was dominated by red alder (*Almus rubra).* Forest canopy cover was 100% in most areas, and branches of alders interdigitated, creating the appearance of a tunnel of air space over the stream.

I monitored activity of bats for 94 nights at Bark Creek and for 101 nights at Buttermilk Creek between 29 June 1993 and 12 October 1994 using the Anabat II bat detector system according to methods described by Hayes and Hounihan (1994). Echolocation calls were recorded on audio tape as bats flew over or near a monitoring station. I defined each sequence of one or more echolocation pulses with < 1 s between sequential pulses as a pass by a bat (Fenton, 1970). Calls were recorded along with the time of day and a calibration tone to aid in later analysis. Bat detectors were set at a sensitivity of six to minimize stream and insect noises and to eliminate detections of bats flying in adjacent habitats. Each monitoring station was within 3 m of the edge of the stream with the microphone of the bat detector facing parallel to the main axis of the stream.

I sampled populations of insects for 89 nights at Bark Creek and for 87 nights at Buttermilk Creek between June 1993 and October 1994 using 10-watt black light traps (Bioquip, Santa Monica, CA) powered by 12-volt gel cells. Traps were set to operate for a 3-h period beginning 30 min after legal sunset using a 12-volt timer (Real Goods, Ukiah, CA). Insects were collected in alcohol, oven-dried $ 24 h, and weighed. Preservation of invertebrates in alcohol decreases their dry weight biomass (Leuven et al., 1985), and, thus, estimates of dry mass may be biased and only should be considered as indices. I monitored minimum nightly temperatures at the bat-monitoring stations using Hobo-Temp monitors (Onset Instruments, Pocasset, MA).

Analysis of activity levels and environmental correlates. An analysis of 1,879 passes recorded during 10 randomly selected nights at Bark Creek and at Buttermilk Creek revealed that > 99% of identifiable calls had characteristics typical of species of *Myotis* (Hayes and Adam, 1996). Because of similarities in characteristics of echolocation calls among species of *Myotis* in this geographical area, I did not attempt to categorize calls to species in this study.

I used an index of activity (IA) as a measure of activity levels. For nights when bats were successfully recorded throughout the night, IA is the total number of passes recorded. During nights with highest levels of activity, audio tapes were filled with calls of bats before the end of the night. To determine the IA for these nights, I assumed that the best estimate of total activity was a function of the number of passes recorded, the proportion of the night elapsed when the tape was filled, and the proportion of the total number of passes expected to occur during that portion of the night. This approach is not ideal, as patterns of activity can vary among nights. However, this approach should provide a general index of activity that is acceptable for use of rank-order statistical procedures. To determine patterns of activity within nights for use in calculating IA and for assessment of temporal pattern, I determined each night at Bark Creek for which audio tape were not completely filled with calls before the end of the night and for which at least 175 passes were recorded *(n* = 24 nights). I restricted the analysis to these night because I assumed that the pattern of activity in these nights with relatively high levels of activity ($ 175 calls) would most closely reflect the pattern of activity on nights for which the tapes were filled with calls prior to the end of the night. To account for differences in length of night, activity was partitioned into 20 equal-time intervals from sunset to sunrise these intervals varied from 26 to 41 min (0 = 29.7 min). The proportion of passes recorded in each interval was determined and the mean proportion for all these nights was calculated. For nights when the tape was filled with calls of bats before the end of the night, the IA was calculated by dividing the number of passes recorded by the mean proportion of passes recorded in that proportion of the night.

I tested for correlations between nightly IA at Bark and Buttermilk creeks, and between IA at each site and length of night, hours of moonlight, phase of moon (expressed as a percentage of full moon), dry mass of insects captured at the site, and minimum nightly temperature at the site using Spearman's *p*. I also examined correlations between dry mass of insects and minimum nightly temperature. I determined statistical power of tests that resulted in non-significant results using tables in Kraemer and Thiemann (1987). Because of significant correlations among variables, I examined partial correlations of activity of bats with dry mass of insects and with minimum nightly temperature.

Effect of number of nights sampled. As activity of bats generally is greatest and most sampling typically occurs during the summer months, I examined data from June, July, and August at Bark Creek (1993, *n* = 24 nights; 1994, *n* = 22) and Buttermilk Creek (1993, *n* = 28; 1994, *n* = 18) to determine the influence of number of nights sampled on estimates of activity of bats. I randomly sampled from 2- to 12-nights subsets 100 times each from each of the four datasets and determined the mean nightly IA for each random sample. I then determined the proportion of each 100 random samples that had means within 10, 20, 30, 40, and 50% of the mean computed using the corresponding complete dataset. All sampling and analyses were performed using the SAS statistical software package for personal computers (SAS Institute, Inc., 1985).

Comparison of paired and independent sample designs. The number of samples necessary to achieve the same statistical power with paired and unpaired designs is a function of the variance estimates for the two designs. An unbiased estimate of the variance for the paired design is the sample variance for the paired data, S^2_D. An unbiased estimate of the variance for the unpaired design is:

$$2S^2_p - (S^2_p - S^2_D)/(2n-1).$$

where,

$$S^2_p = (S^2_1 + S^2_2)/2,$$

S^2_p is the pooled sample variance of the two populations, n is the sample size of each population, and S^2_1 and S^2_2 are the sample variance of the two populations (Snedecor and Cochran, 1980).

I compared the relative efficiency of paired and independent sampling designs by examining the ratio of variances for the two designs. To account for differences in degrees of freedom in the two experimental designs, I compared variances adjusted for degrees of freedom by multiplying the variances by $(v + 3)/(v + I)$, where v is the number of degrees of freedom of the experimental design (Snedecor and Cochran, 1980). I determined S^2_p and S^2_D using the IA-values for all nights when activity of bats was recorded at both sites. To eliminate the potential influence of low levels of activity in winter months on estimates of variance, this analysis was repeated omitting data collected from November through April.

Results And Discussion

Temporal patterns of activity. Levels and patterns of activity varied substantially within nights, among nights within seasons, among seasons, and between sites. Mean activity within a night had a bimodal distribution with a peak of activity shortly after sunset and a second, smaller peak just before sunrise (Fig. 1). This pattern is typical of many species of insectivorous bats (Erkert, 1982; Kunz, 1973; Maier, 1992; Taylor and O'Neill, 1988) and probably results from a period of initial foraging and drinking after emerging from day roosts, reduced activity during the middle of the night when bats are at night roosts, and a final bout of foraging and commuting activity before returning to day roosts (Kunz, 1974; Kunz et al., 1995).

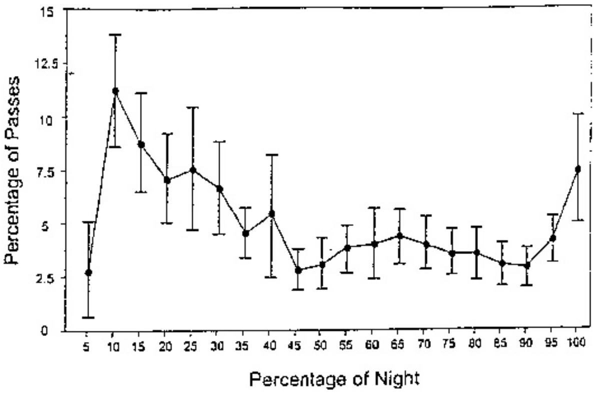

Figure 1

Although distribution of nightly activity tended to be bimodal, patterns of activity varied substantially among nights. Distributions of activity were bimodal on some nights (Fig. 2a), but frequently the second peak of activity was missing (Fig. 2b). On other nights, activity persisted at moderate levels throughout the night with multiple peaks (Fig. 2c), and occasionally there was little activity early in the evening, with increased activity later in the night (Fig. 2d). The reasons for this variability are not clear, and may be related to changes in abundance of insects, meteorological conditions, social factors, energetic needs of the bats, or some other factor. Variability in nightly patterns suggests that caution should be employed when interpreting data collected during small portions of the night. Variability due to changes in distributions of activity will increase sample variance, requiring larger samples for precise estimates, and increases the probability that incorrect inferences will be drawn if sites are inadequately sampled. Total activity also varied substantially among nights (Fig. 3). Levels of activity varied seasonally, but sometimes levels of activity on consecutive nights also differed by several-fold.

Bats were active throughout the year, but activity during winter months was uniformly low (Fig. 3). Low levels of activity during winter is typical for bats (Arlettaz, 1990; Avery, 1985; Brack and Twente, 1985; Hays et al., 1992; Speakman and Racey, 1989; Whitaker and Rissler, 1992). Reasons for activity in winter are controversial, and probably vary with species and conditions, but include feeding (Avery, 1985; Brigham, 1987), drinking (Speakman and Racey, 1989), or changing hibernacula (Whitaker and Rissler, 1993).

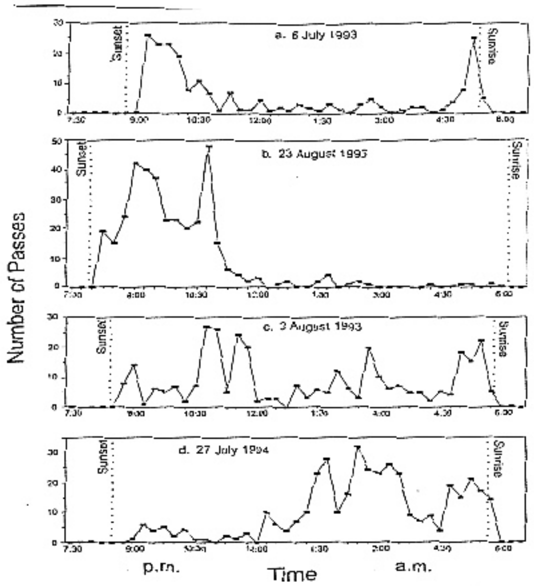

Fig. 2. Temporal pattern of passes recorded at Bark Creek on 6 July 1993 (194 passes; a), 23 August 1993 (363 passes; b), 3 August 1993 (329 passes; c), and 27 July 1994 (387 passes; d). Sunrise and sunset are denoted by vertical dashed lines. All times are Pacific Daylight Savings Time.

Number of passes of bats recorded at Bark Creek (0 = 260.0 " 58.2) averaged 4.8X greater than at Buttermilk Creek (0 = 54.2 " 11.4). Despite these large differences, levels of activity at the two study sites were highly correlated (p = 0.613, n = 82, P < 0.001). Given the separation of the two streams (14.5 km) and the abundance of water sources and potential roost sites in the central Oregon Coast Range, bats using Bark and Buttermilk creeks probably represent independent sets of individuals. Positive correlations in activity between the sites are likely the result of responses to similar environmental conditions at the two sites.

Environmental correlates of levels of activity. Activity of bats was positively correlated with minimum nightly temperature at both Bark Creek (p = 0.643, n = 86, P < 0.001) and Buttermilk Creek (p = 0.456, n = 94, P < 0.001). The relationship between minimum temperature and activity of bats was non-linear. Activity decreased dramatically when minimum temperatures dropped below 4EC at Bark Creek or 0EC at Buttermilk Creek (Fig. 4). Although less pronounced, the IA was positively correlated with temperature when only nights with minimum temperatures > 4EC were considered (Bark Creek: p = 0.321, n = 63, P = 0.01; Buttermilk Creek: p = 0.289, n = 66, P = 0.02). These findings are consistent with those of previous studies documenting the influence of temperature on activity of bats (Anthony et al., 1981; Audet, 1990; Avery, 1985; Kunz, 1973; Lacki, 1984; Maier, 1992; Ruedi, 1993; Rydell, 1991; Whitaker and Rissler, 1992). Activity of bats was negatively correlated with number of hours in the night (Bark Creek: p = !0.513, n = 94, P < 0.001; Buttermilk Creek: p = !0.342, n = 101, P < 0.001), reflecting seasonal changes in levels of activity (Fig. 4).

Activity of bats was positively correlated with dry mass of insects collected (Bark Creek: p = 0.481, n = 70, P < 0.001; Buttermilk Creek: p = 0.388, n = 73, P < 0.001). Rautenbach et al. (1996) also found a significant relationship between abundance of insects and activity of bats. Dry mass of insects was significantly positively correlated with minimum nightly temperature (Bark Creek: p = 0.581, n = 85, P < 0.001; Buttermilk Creek: p = 0.698, n = 78, P < 0.001). Partial correlation coefficients for activity of bats and temperature while holding biomass of insects constant (Bark Creek: p = 0.509; Buttermilk Creek: p = 0.279) were higher than those for activity of bats and biomass of insects while holding temperature constant (Bark Creek: p = 0.172; Buttermilk Creek: p = 0.110). This suggests that the relationship between levels of activity and temperature is stronger than that between level of activity and biomass of insects, and that the apparent relationship between level of activity and biomass of insects may be due to the correlation of both with temperature. The distribution of partial correlation coefficients depends on the multi-variate distribution function of the variables, and consequently P-values can not be determined for non-normal distributions (Conover, 1980).

Activity of bats was not significantly correlated with P either phase of the moon (Bark Creek: p = -0.007, n = 94, = 0.95; Buttermilk Creek: p = -0.007, n = 101, P = 0.94) or number of hours of moonlight (Bark Creek: p = -0.122, n = 101, P = 0.24; Buttermilk Creek: p = -0.115, n = 101, P = 0.25). The statistical power of the tests s > 0.90 to detect correlations of p = 0.35 (at " = 0.05). Lack of statistical significance despite acceptable power suggests that any influence of moonlight on activity was slight in comparison with other factors. The absence of detectable relationships between activity of bats and moonlight contrasts with several studies (Adam et al., 1994; Crespo et al., 1972; Fenton et al., 1977; Morrison, 1978; Reith, 1982; Usman et al., 1980). I did not consider cloud cover in my analysis; cloud cover may have confounded any relationship with phase of the moon, although I do not have evidence to support this hypothesis. Alternatively, dense canopy cover, such as that at Bark and Buttermilk creeks, may minimize the influence of moonlight on activity of bats (Reith, 1982).

*Number of nights required for sampl*ing. The large variation in levels of activity has consequences for sampling design that were evident from the results of subsampling the data (Table 1). As fewer nights are sampled, there is increased probability of obtaining mean estimates of activity that differ greatly from the mean values calculated using large datasets. For example, when subsamples consisted of only 2 nights, < 50% of the subsamples had mean numbers of passes within 30% of means calculated using the full dataset, whereas when subsamples included 7 nights this proportion increased to ca. 80%.

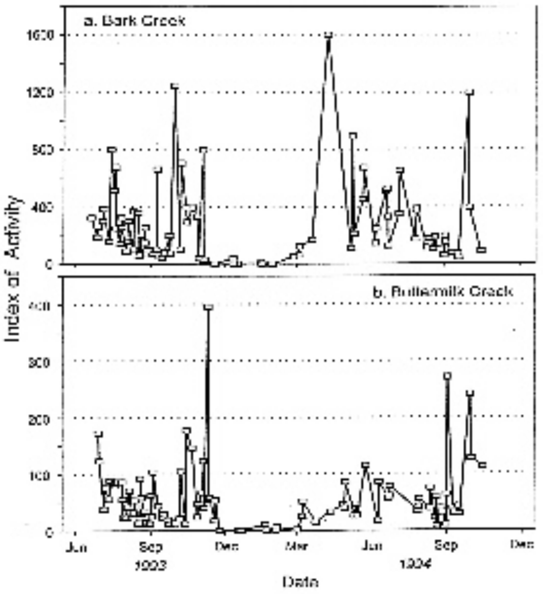

Fig. 3. Index of activity of bats at Bark Creek (a) and Buttermilk Creek (b) from June 1993 to October 1994. Scales for the two streams differ

About 3X more activity was recorded at Buttermilk Creek on 31 August 1994 (IA = 270) than on any other night at Buttermilk Creek during that season (on 8 June 1994, IA = 85), substantially increasing the observed variability in activity at Buttermilk Creek. Having 1 night with an unusually high or low level of activity in the sample decreases the proportion of subsets with means similar to means calculated using the full dataset. As a result, mean values of IA for subsampled data lacked precision and accuracy for the dataset for summer 1994 from Buttermilk Creek. To obtain less-biased estimates of activity, more nights need to be sampled when variation is high. Although the occurrence of 1 night with atypical levels of activity strongly influenced analysis of this dataset, it may not be unusual, and may result from unusually large hatches of insects or other factors that increase local levels of activity.

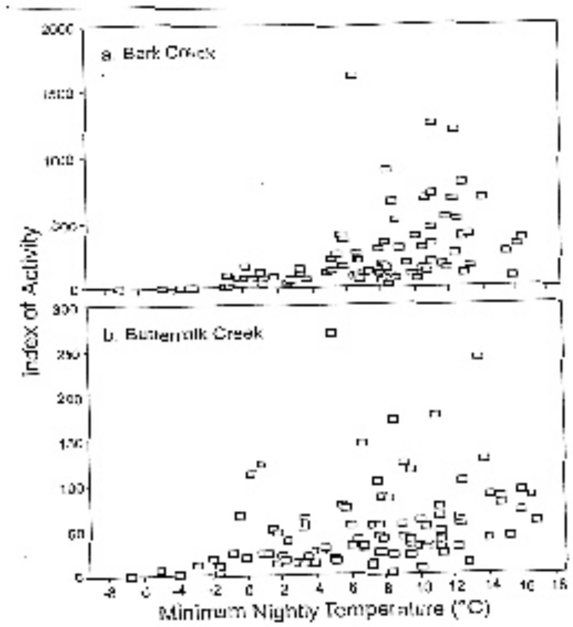

Fig. 4. Relationship between activity of bats and minimum nightly temperature at Bark Creek (a) and Buttermilk Creek (b). Scales for the two streams differ.

Assuming the means calculated from the full datasets represent the best available estimate of activity for a site during a particular season, low-intensity sampling can result in under- or overestimates of activity levels. Accurate and precise estimates of levels of activity derived using bat detectors will only be obtained through intensive sampling efforts. Results may differ regionally or in different habitats, but results from this study indicate that sampling a site fewer than 6 to 8 nights is likely to result in biased estimates of activity.

Comparisons between sites. Although there are times when an estimate of mean activity at a site is useful, research often focuses on comparing levels of activity between two or more sites or types of habitat. For these comparisons, experiments can be constructed to test the null hypothesis that level of activity does not differ among sites; two typical designs to address questions of this type are completely randomized designs and randomized blocked designs. In a completely randomized design with two sites, a researcher randomly chooses nights to sample each site. In a randomized blocked design (or in the two-site case, paired design), a researcher randomly chooses nights, but then samples each site on the same night and compares the difference in level of activity between sites on a night-by-night basis. High correlation between levels of activity at Bark and Buttermilk creeks and the response of activity of bats to environmental factors suggest that designs that incorporate blocking or pairing may reduce experimental error and, therefore, be more efficient than completely randomized designs.

Calculations of statistical power for completely randomized and randomized blocked designs differ only by the variance estimate used. The ratio of unbiased variance estimates resulting from these two designs, adjusted for differences in degrees of freedom in the analyses, can be used to determine the relative efficiency of the designs. Using a randomized-blocked design to compare levels of activity between Bark and Buttermilk creeks was 20% more efficient than a completely randomized design for analyses of the entire dataset (adjusted variance estimate for completely randomized design = 87,920, for paired design = 73,216, n = 82) and for analyses excluding data collected during winter months (adjusted variance estimate for completely randomized design = 64,373, for paired design = 53,958, n = 65). Thus, 20% fewer nights need to be sampled for a paired design to have the same statistical power as a completely randomized design. The paired approach also has the benefit that there is no assumption that variances of the two populations are equal, unlike the *t*-test for independent samples (Snedecor and Cochran, 1980). Design of studies monitoring activity of bats must weigh the advantages of paired designs against the logistical difficulties imposed by collecting data from more than one site during the same time periods.

Because of high temporal variability, statistical tests comparing levels of activity among sites are likely to have poor statistical power to detect small differences. As a result, a researcher may incorrectly fail to reject a null hypothesis and erroneously conclude that activity at two sites is not different. The risk of this improper inference is tempered somewhat by the fact that habitat structure can have dramatic influences on amount of use by bats, resulting in several-fold differences in levels of activity between habitat types (Hayes and Adam, 1996; Thomas, 1988). If subtle differences in levels of activity are of interest, differences may only be detectable with intensive sampling efforts. Use of statistical power analysis will be helpful in determining the sampling effort required for any particular study.

Applicability to other regions. All of the data used for this study were collected at two riparian areas in the Oregon Coast Range; the importance of temporal variation may differ in other regions or habitats. However, in the absence of extensive, site-specific sampling to examine levels of temporal variation in activity, the prudent approach is to assume that temporal variability is a substantial source of variation in levels of activity. Inadequate temporal replication can result in inaccurate and misleading findings. Sampling designs for echolocation-monitoring studies need to account for this variation to yield scientifically accurate, defensible results.

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Table 1. Percentage of random samples having mean indices of activity (IAs) within 10-50% of the mean of the entire dataset. Values represent means and ranges (in parentheses) for datasets partitioned by site and year (*n* = 4); data were randomly sampled 100 times for each 2- to 12-night sample period for each site and year. For each dataset, comparisons were made with the mean IA for all nights at the site and year.

Percentage deviation from mean estimate calculated from full datasets

Number of nights in subsample	# 10	# 20	# 30	# 40	# 50
2	19.0 (13-21)	31.8 (23-36)	47.8 (40-54)	57.8 (47-67)	72.5 (67-79)
3	20.5 (19-26)	43.2 (40-48)	58.0 (53-61)	73.0 (65-76)	82.2 (76-86)
4	21.2 (17-24)	41.3 (39-45)	62.8 (56-69)	77.0 (72-85)	86.2 (78-93)
5	27.2 (24-32)	48.8 (39-59)	69.2 (52-78)	83.8 (74-93)	88.2 (85-99)
6	31.0 (22-36)	52.2 (38-63)	63.8 (54-84)	86.0 (76-94)	94.2 (85-99)
7	29.8 (14-40)	61.2 (55-69)	80.5 (70-90)	91.8 (90-94)	97.8 (96-100)
8	30.5 (14-38)	62.8 (42-78)	83.2 (70-96)	97.0 (92-100)	99.0 (97-100)
9	33.0 (12-42)	67.8 (43-84)	91.5 (82-96)	98.5 (96-100)	99.8 (99-100)
10	39.5 (14-50)	68.2 (51-80)	90.8 (96-98)	98.0 (94-100)	100 (100)
11	33.5 (17-42)	76.0 (58-84)	96.5 (94-98)	100 (100)	100 (100)
12	46.8 (29-58)	85.8 (80-94)	97.5 (96-99)	100 (100)	100 (100)

Transmitter Attachment for Small Insectivorous Bats (< 30 g)

by Dr. Mark Brigham and Holohil Systems Ltd.

Retrieved from: http://www.holohil.com/bd2att.htm (March 17, 2008)

A commonly used "rule" for working with flying animals is to keep the mass of the transmitter AND adhesive below 5% of body mass. This means that the smallest tag currently produced by Holohil (0.35g - LB-2N) should not be attached to bats weighing less than 7.0g. This rule may be bent (slightly) for the purpose of finding roost sites as there is little question that bats can carry heavier loads. However, for studies of roost preference, foraging behaviour, etc. it is my opinion that the 5% rule should be used. See Aldridge and Brigham, 1988 J. Mammalogy. It is important to emphasize that the rule represents a maximum transmitter load and in reality the smaller the transmitter, the less likely it is that an animal's behaviour will be affected.

Transmitters should be attached to the area between the shoulder blades so that the bats cannot use their hind feet to pull off the tag. The adhesive I find works best is Skin-Bond® (see note below). For bats with short fur (e.g., Eptesicus), transmitters seem to remain attached best if the fur is not clipped. The length of the fur, rate of growth, oiliness and even geographic location all seem to contribute to successful attachment. I suggest that at the beginning of a study, attach several tags with and without clipping fur to see what works best.

When applying the adhesive use a very thin layer on both the transmitter and the bat. Remember that adhesive also contributes to the mass of the transmitter package. Let stand for about 5 minutes until the glue bubbles, then affix the tag and hold it for a further 5 minutes. Frost the fur around the edge of the transmitter. At this point the initial setting of the glue will have occurred. It is now important to prevent the bat from scratching at and potentially loosening the tag before the glue fully sets. I recommend holding the bat for another 10 - 30 minutes to make sure that the glue has set completely before releasing the animal.

Note: Skin-Bond® has recently changed its formulation and is no longer suitable for use. It's bonding time is much less than the original formulation. Do NOT use the surgical skin bond which is a methacrylate adhesive (Crazy Glue).

We now suggest using Torbot Bonding Cement. Its adhesive properties are similar to the original Skin-Bond® recommended by Dr. Brigham above. It can be ordered through their website at: www.torbot.com.

Another latex based adhesive that can be used is Eyelash Cement. Instead of a hexane solvent base, this material has a proprietary aqueous solvent base. A flexible formulation of woodworking contact cement is being used by Australian researchers with good results in extremely wet conditions.

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Injuries to *Plecotus townsendii* from Lipped Wing Bands

by Elizabeth D. Pierson and Gary M. Fellers.

Bat Research News, Vol. 34, No. 4, pp. 89-91

In two occasions, the Pacific western big-eared bat, *Plecotus townsendii townsendii*, has been banded as part of an ecological study in Marin County, California. We found that 3-mm lipped bands, of the design used extensively in Britain and known to be suitable for other North American species, caused significant and potentially fatal injuries to > 11% of the recaptured sample. Our data also indicate that bands may cause a decrease in survivorship. We stopped using these bands on *P. townsendii* and have removed bands from all recaptured animals.

Introduction

Banding has been an important research tool in bat population studies for over 75 years (Hitchcock, 1957) and has been a source of continuing investigator concern. Initially when unlipped, metal, bird-leg bands were the primary option, attention focused on the wing-injury rate of *Tadarida brasiliensis* and several other species (Hitchcock, 1957; Davis, 1960; Herreid et al., 1960). Although there appeared to be fewer wing injuries after introduction of lipped bat bands (Herreid et al., 1960), some populations, particularly in hibernacula, showed significant declines in apparent response to the disturbance caused by banding activities (Davis and Hitchcock, 1965; Stebbings, 1969, 1978; Tuttle, 1979; Barclay and Bell, 1988).

Although many bat researchers still observe the informal ban on disturbing hibernacula, increasing numbers of biologists are banding bats during summer, yet there is little discussion addressing the unresolved consequences of banding per se. Serious difficulties with banding a *P. townsendii* population in California lead us to suggest that there is the need for more dialogue on the effects of banding, particularly comparative assessments of different band materials and shapes (e.g., metal vs. plastic bands) and evaluations of species-specific responses to banding.

Methods and Results

On 9 October 1992, a total of 118 *P. t. townsendii* was captured at a roost site, which had been under study for six years. This number represented approximately 95% of the bats present. Each bat was sexed, weighed, measured for forearm length, and evaluated for tooth wear and reproductive condition. Each bat was fitted with a 3-mm, lipped, alloy band issued to the British Mammal Society by Lambournes Ltd. of England. The band was placed over the forearm and manually squeezed shut (without banding pliers) so that it would slide freely along the arm. The band was not loose enough, however, for the metacarpals to slip under the lips and become caught when the wing was folded.

On 21 September 1993, 30 bats were netted in the evening as they exited the roost. One of these had been banded in 1992. As before, each bat was sexed, weighed, measured, and evaluated for tooth wear and reproductive condition. All bats that had not been banded previously were fitted with similar lipped bands (2.8-mm diameter–the new equivalent to 3-mm bands) obtained directly from Lambournes Ltd. There was no sign of wing injury to the single bat that had been banded the previous year.

On 8 October 1993, 111 bats were captured at the same roost. As in 1992, this represented approximately 95% of the bats present. Of the bats captured, 51 were recaptures from 1992 and 11 were recaptures from the previous month. All bats were processed as before. We found seven bats that had wing injuries associated with bands. One of these had been banded only 17 days before. This represented an injury rate of 11.8% (6/51) for the 1992 recaptures and 9.1 % (1/11) for the 1993 sample.

For the one bat that had been banded 17 days before, the band was lodged at the distal end of the forearm. There was no swelling, but the skin under the band was abraded and had been bleeding. There was a somewhat roughened wing area, proximal to the band that held the band in place. It appeared that the band would not have come free on its own, and quite likely, the injury would have progressed.

The five injured bats originally banded in 1992 had considerable swelling around the band and adjacent 2-4 mm of forearm. The area was infected, and even modest movement of the band caused puss to be expressed. Each band was carefully removed, revealing an area devoid of skin. In one case, the band had become embedded at the proximal end of the forearm, whereas the others were at the distal end. In three cases, the band had caused a small hole in the wing with the lipped portion penetrating the membrane and allowing the band to completely encircle the forearm. Although penetration of the wing membrane occurs with some frequency in banding studies, such injuries frequently are reported as having healed or callused over (Heffeid el al. 1960). This was not the case for any *P. townsendii* that we observed. All animals were carefully inspected for signs of earlier band injury (such as scarring) that had healed or injury from bands that had somehow been removed. No such sign was detected.

Discussion

The most direct way to evaluate impacts from banding is to assess the percentage of a recaptured sample that shows wing injury. In our case, not only did an unacceptably high percentage (11.8%) of our recaptured sample show injury, but all injuries were active and thus judged to be potentially fatal. The fact that no bats had scarring to indicate healed wounds added support to the hypothesis that the bats do not recover from these injuries. Although most animals had been banded for a year, the six wounds we observed were in various stages of infection, suggesting an ongoing problem and an annual mortality rate that is likely much higher than the observed injury rate.

We had reason to believe that band injuries would be minimal. Lambournes' bands were used because they were lighter-weight and smoother-edged than any others available. Also Lambournes' bands had been used with virtually no sign of injury on large numbers of *Myotis yumanensis* (3.0-mm size) and *Antrozous pallidus* (4.0-mm size) (W. E. Rainey and E. D. Pierson, unpubl. data). Though there are suggestions in the literature that some species are more sensitive to banding than others (e.g., Hitchcock, 1957), this matter has been give little attention.

Reports of band injuries with *P. townsendii* are variable. Davis (1960) suggests that *P. townsendii* may be among those species most prone to band injury. This view is supported by the experience, in Oregon, of S. Cross and M. Perkins (pers. comm.), who banded very few individuals but experienced a sufficiently high injury rate with lipped U. S. Fish and Wildlife Service bands that they ceased banding *P. townsendii*. On the other hand, Pearson et al. (1956) had very low injury rates (< 2%) using unlipped U. S. Fish and Wildlife Service bands (O. P. Pearson and A. K. Pearson pers. comm.). P. Leitner (pers. comm.), using 4.0 min (size 2) unlipped USFWS bands, had comparably low injury rates on another *P. townsendii* study in northern California, with 7 out of 391 recaptures (1.8%) having embedded bands. Likewise, Stebbings (1966) had high (> 70%) survivorship and almost no sign of wing injury using Lambournes' 3.0-mm lipped bands in England on *Plecotus auritus*–a crevice-dweller that shows marked behavioral differences from its North American congener.

Why *P. townsendii* may be more prone to band injury than some other species from lipped metal bands is not clear, but we offer several observations that may provide a partial explanation. First, *P. townsendii* does not appear to gnaw on bands as other species do. We found no tooth marks nor other signs of wear on the bands and no differential tooth wear on the bats that could be attributed to band chewing. Chewing behavior, while having potentially negative consequences, such as accelerated tooth wear, may be advantageous in keeping bands from lodging on the forearm. Our observations indicate that *P. townsendii* may not attempt to dislodge bands that are stuck. In one early-stage infection, the band moved with only a slight application of pressure and could almost certainly have been dislodged by the bat with only a modest amount of chewing.

Additionally, *P. townsendii* seems to have especially thin wing membranes. Though we have not quantified this, the wings appear to be more delicate than those of other bats we have handled, including almost all genera present in the western United States. If this is an accurate perception, injuries from bands that penetrate the wing membrane might be more likely in this species. Also, the wings have a sticky quality we have not observed in other bats. The bands on recaptured animals and the wings of all animals were covered with a sticky orange substance, which when removed with a cotton swab, appeared identical to secretions from the rostral glands. The stickiness of this secretion may play some role in inhibiting free movement of the band.

An injury rate of > 11% is clearly too high for any species. It was of special concern for this colony because it represents one of only four known for *P. t. townsendii* along the California coast. This subspecies is a Category 2 Candidate for listing under the Federal Endangered Species Act. Our results lead us to conclude that, unless contrary data are available, other workers should not use this band type on P. townsendii. Whether some other banding protocol could work needs to be explored. D. Saugey (pers. comm.) has been using plastic bird-leg bands (A.C. I. Hughes), individually filed to increase the gap, on P. rafinesquii. Preliminary results suggest acceptably low injury rates. He and coworkers, however, observed embedding when unfiled plastic bands were used. This is congruent with observations by one of us (EDP) of an embedded band on an individual that had been banded with a plastic band in southern California. We also note that R. E. Stebbings (pers. comm.) discontinued use of plastic bands over 20 years ago due to high injury rates (partly due to band shrinkage over time) for all species tested. We suggest that before initiating a banding study using plastic bands investigators contact both R. E. Stebbings and D. Saugey.

One of us (EDP) and W. Rainey tried and subsequently rejected the use of bead necklaces (Barclay and Bell 1988) on another population, because the combined weight of the chain and band exceeded the 5% rule. Transponders may offer a viable alternative to banding, though the large size of even the smallest implants needs to be considered.

We are open to the possibility that our banding technique was somehow at fault, although the absence of similar problems for other taxa banded in the same manner argues against investigator error. It is also possible that we should have used a larger size (3.5-mm) band. The 3-mm band is used routinely, however, on comparably sized *Plecotus* in Britain and appeared to fit well on our study animals–moving freely, with space around the forearm. Since it seemed to be the lip that first became lodged, it is not clear that a larger band, which is more than twice as heavy (105 vs. 43 mg), would have alleviated the problem.

We recommend that until it can be established that a particular band causes no more than minimal injury, banding of *P. townsendii* and other potentially sensitive species be limited to studies in which the impacts of banding can be evaluated directly. Since rates of recapture are generally low for bats netted in foraging areas, studies would probably need to focus on bats at known roost sites. Such research would need to be designed carefully to reduce the possibility of undue disturbance, especially for *P. townsendii*, which is known to be so sensitive to human disturbance.

Acknowledgments

We thank P. Winters and C. Scott for their assistance in nursing injured animals back to health. J. Fellers and W. Rainey provided helpful comments on the manuscript. Banding was carried out under a permit and Memorandum of Understanding issued to E. D. Pierson by California Department of Fish and Game.

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Educational Guidelines

by Amanda Lollar and Barbara Schmidt-French

Reprinted with permission from: *Captive Care and Medical Reference for the Rehabilitation of Insectivorous Bats*, 1998. Bat World Publications, Mineral Wells, TX. 329 pages.

Educating the public is one of the most outstanding contributions that can be made towards the conservation of bats as a whole. The use of live bats for educational programs has substantial value in influencing public opinion. However, a healthy balance should be established during these programs between teaching the importance of bat conservation and fully communicating to the audience the potential dangers of handling wild animals. Rabies in wild mammals is of particular concern. It is important that both children and adults understand the possible consequences of handling potentially infected wildlife. North American bats are very small, possibly making them appear harmless to adults and children who might pick them up. Every year incidents are reported throughout the United States involving people (particularly children) who have inappropriately interacted with grounded bats. Although the majority of bats are not rabid, a certain percentage of those handled by the public will have contracted the rabies virus. Public hysteria following some incidents involving human/bat interactions has resulted in the destruction of entire bat colonies. For these reasons, the principal purpose of educational programs should be to deliver accurate information about bats in a manner that protects both bats and humans.

PROTOCOL

1. The use of live bats for educational purposes should be limited to licensed wildlife rehabilitators, educators, and research biologists. The authors recommend that these individuals be previously immunized against rabies and receive boosters when appropriate so that they maintain an acceptable titer. The audience should also be informed that the presenter has received the recommended pre-exposure rabies immunizations in order to work with mammalian wildlife.

2. The presenter should strive for a well-groomed, professional appearance.

3. Bats should never be treated in any manner consistent with generally recognized treatment or care given to domestic pets. Petting, kissing or similar demonstrations of affection towards bats during public programs is highly inappropriate.

4. Presenters should always refer to themselves as the bat’s “handler” rather than its owner.

5. Wildlife rehabilitators, educators, and researchers utilizing indigenous species of bats in educational programs should be permitted or licensed to handle bats by their state wildlife agency. Those using non-indigenous species in educational programs should have an USDA exhibitor's license. It is recommended that permits and/or licenses be prominently displayed during all programs.

6. Presenters should strive to produce a program that is both educational and entertaining. An interactive question-and-answer program is often more conducive to learning than a lecture. To create a pleasant atmosphere, presentations can include amusing and humorous bat facts in combination with more serious ones. Laughter combined with learning may help to relax apprehensive audiences unfamiliar with bats. Entertaining and/or amazing bat facts are perhaps those most likely to be remembered by the audience and recounted to others, thereby furthering your educational efforts.

SUGGESTIONS FOR DISPLAYS

1. Include a display board depicting both indigenous and non-indigenous bat species. Photographs and information about local bat species will be of particular interest to your audience.

2. All displays should include a message on the importance of not approaching wild animals. Any literature to be distributed that addresses the benefits of bats should also include a warning to never touch bats.

3. Display cages, display boards, and literature

placed on tables should be arranged neatly. Keep the area uncluttered during presentations. Literature that will be available to the audience should be placed on a separate table from the one where display cages are situated (or in the area farthest from the display cages if a separate table is not available). This precaution minimizes stress to the bats by reducing traffic near their cages.

4. The use of a cam-corder, RF modulator, tripod, and television is of great value for educational bat programs, particularly when dealing with large audiences and/or limited space. The image of a bat can be enlarged when it is projected onto a television screen. The cam-corder also serves to permanently record programs for both critical self-review and documentation that animals were not touched by the public during presentation.

BATS USED FOR EXHIBITION

1. Bats used for educational programs should either be non-releasable indigenous species or non-indigenous species. Non-releasable status is assigned to orphans, captive born bats, and non-suffering permanently injured bats. Although they may be caged with other bats, indigenous bats should have resided in captivity for at least one year without being exposed to any new bats during that time. Bats should not be on display for more than 30 minutes a day. (It is not humane to subject insectivorous bats to permanent display.)

2. Use of both foliage-roosting and crevice-dwelling insectivorous bats, as well as frugivorous bats, is beneficial for demonstrating ecological diversity (e.g., differences in body size, shape, color, and how this is related to roosting and dietary habits). However, excellent presentations can be given utilizing only one or two individuals of the same bat species when a variety is not available.

3. Bats should be familiar with their handler and should have developed a sense of trust before being utilized for public presentations. Bats that trust their handler will respond to and relax at the sound of their handler's voice during times of stress. Bats that have not become accustomed to their handler will be noticeably frightened during educational programs and should not be used for public viewing.

4. Bats used for display should be conditioned prior to the presentation. Conditioning should include familiarizing the bat with both the display cage and transport carrier. Food rewards can be used throughout the conditioning period so that the bats develop positive associations with display cages.

5. Solitary bats (like many of the foliage-roosting species) can be conditioned and displayed singly during presentations. It is preferable, however, that colonial species be accompanied by permanent roost mates both during the conditioning period and educational presentations.

6. Bats should be left in the transport carrier and placed in an area inaccessible to the public after reaching the program area. Bats should remain undisturbed in the carrier in this area while displays and handouts are organized. Bats should be removed from the carrier and placed into a covered display cage before the audience arrives for the presentation. When the cage is uncovered for viewing, the bat may be given food rewards. After public viewing, display cages should be covered again.

7. Although educators have displayed bats by hand for many years during presentations, it is preferable that audiences view bats that are contained within a display cage. Bats that have been conditioned to being displayed by hand over a long period of time may not adjust to confinement in display cages, however. Some authorities recommend that gloves be worn if bats are displayed by hand because a conflicting message may be sent to the audience if wild animals are handled with bare hands.

8. Presenters should remain next to the cage while bats are being viewed by the audience. Close up viewing of the bat works best if allowed only at the conclusion of a presentation. Encourage the audience to file by for viewing and to leave about one foot of space between them and the table. In addition, they should be told to not lean against the table towards the cage or to touch the cage. Children should be told to keep their hands in

their pockets or behind their backs as they walk by. During this time, a distance of two feet should be maintained between the display cage and the audience. This can be accomplished by placing the cage in the center-back area of the table so that l-foot (30cm) or more of empty table space is created along the front and sides of the cage.

9. Never allow anyone to touch a bat in any way whatsoever. A bat that has been touched by an unauthorized individual may be subject to euthanasia and rabies testing by local health authorities regardless of the nature of the contact or the period of time the bat has remained in captivity.

10. Bats must never be permitted to fly or otherwise be loose during public programs.

TRANSPORT CARRIERS AND DISPLAY CAGES

1. Use a transport carrier, rather than the display cage, for transporting bats to and from facilities where presentations will take place. Carriers should be appropriately modified so that they can be secured in vehicles with a seat belt. Carriers should be padded on the inside and covered with a cloth on the outside. Neither transport carriers nor display cages containing bats should be handled by anyone other than the presenter.

2. Display cages should have surfaces that allow bats to hang upside down. If a plexiglass animal case is used, three of the four sides and the ceiling should be covered with nylon or plastic (not wire) screen to provide appropriate roosting surfaces. (Bats are unable to grip plastic surfaces and may slip and fall, causing wrist or wing injury.) Screened, wooden frame display cages should be “double screened” with nylon or plastic screen with no more than a 1/6" (4mm) mesh for small insectivorous bats. For larger bats such as flying foxes, ½" (13mm) plastic mesh should be used for the inner layer only. There should be a 1" (25mm) space between the two layers of screen. This space and the small mesh used for the outer layer will ensure that bats hanging close to the inside screen or mesh wall cannot be secretly touched from the outside by a curious individual.

3. Display cages should be designed so that bats can remain somewhat hidden without being totally obscured from view. This may be accomplished with the use of either natural or artificial materials including fabrics, silk foliage, tree bark, or small tree branches that can be used to simulate natural habitat, depending on the species. These materials should be secured against cage walls and kept clean and free of odors, sharp areas, dirt, and parasites.

4. Areas within the display cage that are in public view where bats have urinated and/or defecated should be inconspicuously cleaned (if possible) with tissue. The tissue should then be put in a plastic bag brought along for that purpose, and placed out of sight until after the presentation when it can be disposed of appropriately.

EDUCATING CHILDREN

While educational programs about bats should attempt to instill a child with a healthy respect for wild animals and their habitats, such a program should begin by emphasizing the importance of never touching a wild animal. A stern message regarding handling of bats and other wild animals should be leveled at children. These messages must be especially emphasized if presenters handle bats during presentations. It is also necessary to be redundant when delivering messages to children. The following examples have proven successful for Bat World*.

1. Children should be told that grownups who handle wild animals must have “special shots” and special training in order to work with wild animals. They should also be told that the bats being used for the presentation are tame and familiar with the handler, whereas bats in the wild are very different and will bite in self-defense when handled.

2. When giving the bat a food reward during programs, allow children a clear view of the bat’s face and teeth as the bat chews. A cam- corder with a modulator hookup will project this image clearly onto a TV screen for si-multaneous viewing by the audience. Rather than hand feeding the bat, food rewards can be placed into the display cage in a way that enables the bat to find and eat the food naturally (e.g., small pieces of apple can be secured onto branches for

frugivorous bats; mealworms can be placed in shallow dishes camouflaged by leaves or grass for insect-eating bats). While the bat eats, explain that a bat uses its teeth to eat food in the wild, but will also use its teeth for protection against predators, including people who may try to touch it. A strong visible image can be created while the bat feeds by describing how it uses its teeth for protection.

3. Children should be told that if a bat is found within reach, something must be wrong with it. Remind them to never touch the bat because it might be sick. Let them know that if they do touch the bat, it will probably bite them and that the bat will need to be killed so that it can be tested for rabies. If the bat has rabies, they will have to have a lot of shots that don't feel good and cost a lot of money. They should be told that touching the bat will prevent them from helping it. Explain that even if they touch the bat and it flies away, they will still have to get shots. Explain that the only way they can help save the bat is to get an adult. If there are other children or domestic pets with them, they should send a friend for an adult so they can stay behind and make sure that other children or pets stay away from the bat until the adult arrives. Finding a bat will probably be both exciting and frustrating for a child who has learned about that animal. Let them know that they can help the adult who comes by telling him or her to use a can, dustpan, or thick gloves (never bare hands) to scoot the bat into a box that can be covered. If no one had contact with the bat, they can tell the adult to call their state wildlife department, local animal control division, humane society, or wildlife rescue organization for further assistance.

4. Children should be reminded that even though bats are small, they are wild animals. They should be told that it is against the law to keep them as pets and, in addition, they would not make good pets anyway because they need special cages, food, temperatures, and sometimes the company of an entire colony of bats, or they will not survive.

5. Relate a story about a child who found a bat, picked it up, was bitten, and had to receive shots. Then ask the children what they would have done differently if they had found the bat. Encourage and reinforce the proper answers (e.g., don't touch it, tell an adult, etc.).

**Bat World Sanctuary and Educational Center is a licensed facility,*
and Amanda Lollar is a permitted wildlife rehabilitator.

Bat World in Mineral Wells, Texas, (about two hours west of Dallas) is open for scheduled tours from September through June. Tours are held on the second Saturday and the third Sunday of the month. Advance reservations are required, preferably a week ahead: (940) 325-3404.

Adults $8.00, children $4.00, seniors $6.00, under 3 free. The facility closes completely during July and August to care for orphaned and injured bats. For more information, visit www.batworld.org or write to:
Bat World Sanctuary
217 N. Oak
Mineral Wells, TX 76067.

Bats in the Classroom: A conceptual Guide for Biology Teachers

W.T. Rankin and Norma G. Lewis

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The purpose of this article is to present a group of organisms as an instructional tool for introducing a variety of biological concepts. We find bats particularly useful as a gateway to biological concepts for several reasons. First, bats are among the most widespread mammals in the world, and frequently coexist with human beings. Second, the natural history of bats can be very different from human beings, allowing teachers to compare and contrast evolutionary adaptations to different environments. Third, many people do not understand bat biology, lending an aura of mystery to these animals. Students are frequently fascinated by animals they view as mysterious. As a result, bats may serve as a bridge to biological concepts that may otherwise be viewed as remote and esoteric.

Our goal is to present a list of biological concepts that can be introduced or illustrated using bats as examples. We have used these concepts in both traditional and nontraditional venues, for students from middle school through college. The concepts include the following:

Classification & Phylogeny

Bats are the subject of a long-running controversy. Traditionally, bats have been placed into a single order, implying a common evolutionary ancestry. Bat biologists argued that complex adaptations such as flight and echolocation could only have evolved once, meaning all bats must have evolved from a common ancestor.

Bats can be readily separated, however, into two distinct groups. Microbats enjoy a global distribution and are the only bats native to the New World. Microbats are typically several inches long (head and body) and have wingspans less than a foot. They have small eyes and the small, sharp teeth characteristic of insectivores. All microbats echolocate, creating high-pitched sounds in their larynx and using these calls to guide their flight the same way submarines use sonar. Most North American microbats eat insects, but neotropical microbats are just as likely to eat nectar and fruit, and often act as pollinators for flowers and dispersal agents for seeds. Microbats also tend to roost in caves, trees, and attics.

The Old World tropics contain a second group of bats, the megabats. As the name implies, megabats are often larger than microbats: the largest megabats are 18 inches long (head and body) with wingspans over five feet. Megabats have large eyes and navigate through visual clues. A few species do echolocate, but unlike microbats, megabats echolocate by clicking their tongue against the roof of their mouth. None of the megabats is exclusively insectivorous — most eat fruits or nectar. Megabats rarely roost in caves, preferring tree branches.

The two groups of bats are so distinct that many bat biologists believe they represent two evolutionary lines. If this is true, it would mean complex adaptations such as bat flight and echolocation evolved twice — once in microbats, and once in megabats. It would also suggest the two groups should be placed in separate orders.

Speciation

One of the current models of speciation is based on the rapid evolution of small, isolated populations. Bats, the only mammals capable of sustained flight, have colonized isolated islands throughout the world — bats, for example, are the only mammals native to Hawaii. Bats dispersing across the islands of the Pacific Ocean apparently formed a large number of small, isolated populations that underwent rapid evolution. Many Pacific islands now contain endemic species of bats.

Co-evolution

Co-evolution is evolutionary change in one species in response to evolutionary change in a second species. Insectivorous bats locate their prey through echolocation, and insects have evolved adaptations to confuse their predators. Many moths are covered with thick, soft hairs that absorb echolocation signals. The signals do not bounce off the moth and the bat is unable to locate the insect. Other insects have ears tuned to the frequencies at which bats echolocate. When these

Figure 1. The lesser long-nosed bat, *Leptonycteris curasoae*, pollinating a saguaro flower. Note theclose fit between the shape of the flower and the head of the bat. Bat flowers tend to be large, lightly-colored, and open at

insects hear echolocation, they fold their wings and fall to the ground, emulating falling leaves. Still other insects attempt to distort signals by producing false signals of their own — in effect, jamming the bat's sonar.

A second example of co-evolution can be found in bat-pollinated flowers. Flowers pollinated by bats exhibit several characteristics. For example, most bat-pollinated flowers are nocturnal, matching the activity patterns of the bats. The flowers tend to be white or light-colored, increasing their visibility at night, and are often characterized by strong, unpleasant odors. In addition, the flowers are often large and cup-shaped — the shape may reflect the echolocation calls of microbats, allowing bats to hear the flowers more distinctly than surrounding vegetation. Bats are important pollinators of the saguaro and organ pipe cacti of the Sonoran Desert in the American southwest (Figure 1).

Physiological Adaptations

An adaptation is any trait that increases the survival of an organism. Bats exhibit several distinctive traits that can be interpreted as adaptations for their unique lifestyle. For example, virtually all bats roost upside down; this has profound effects on their physiology. For example, blood flow through a mammal is controlled by valves throughout the circulatory system. If a human being is held upside down, blood rushes to its head because the valves in the circulatory system are designed to move blood forward when the person stands erect. In comparison to a human being, the circulatory valves of bats are upside down. A bat hanging upside down probably feels as comfortable as a person standing erect.

A second set of physiological adaptations is associated with sanguivory — the consumption of blood. Vampire bats are the only mammals exclusively sanguivorous. Blood contains a high concentration of proteins and is therefore a very nutritious food, but it also poses problems for a small, flying mammal. Blood is mostly water and therefore quite heavy; a vampire who has just consumed a large meal may be too heavy to fly. When a vampire feeds, it produces large amounts of very dilute urine, effectively purging the water in its meal. When the bat returns to its roost however, it faces a different problem. Digesting a high protein meal requires a large amount of physiological water to flush urea from the body. Vampires are small bats that do not contain much water. Although vampire kidneys can produce very dilute urine, they can also be extremely efficient at reclaiming water from urine. As a result, roosting vampires produce one of the most concentrated urines known from mammals.

Altruistic Behavior

Vampires also engage in one of the few examples of altruistic behavior known in mammals. Sanguivory is a difficult procedure, and many vampires are unsuccessful in any given night. When successful vampires return to their roost, they will regurgitate blood meals to unsuccessful vampires who are genetically unrelated. Truly altruistic behavior is of special interest to evolutionary biologists because it seems to violate the tenants of natural selection — altruistic animals appear to voluntarily lower their own fitness in comparison to the animals benefiting from the behavior.

Morphological Adaptations

Bats exhibit a second unique feature associated with roosting. If a human being is hung from a wall by the heels, that person would hang with its back to the wall. If a bat is hung from a wall by its heels, the bat is hanging with its stomach to the wall. Beginning at the hip, the legs of a bat are rotated 180°. The knees of a bat face sideways, and the feet face backwards. This is an adaptation for flight. A person hanging from a wall must turn around to flap its arms. A bat, however, merely releases his toes and begins to fly.

Figure 2. The frog-eating bat, *Trachops cirrhosus*, attacking an unsuspecting frog. The fingers on the hand are evident in the wing, beginning with the claw-like thumb, the short index finger at the leading edge of the wing, the middle finger extending to the tip of the wing, and the third and fourth fingers forming the points along the trailing edge of the wing. The fingers radiate from the bat's palm, and the elbow is evident midway between the palm and body.The knee is also evident, flexed in the plane of the wing. And, unlike human beings, the soles of the feet hand downward, facing the ventral surface of the bat.

Flight

Bats are the only mammals capable of sustained flight. The wings are formed by two layers of skin stretched across the bones of the fingers and attached along the side of the body — the term 'Chiroptera', the order in which bats are placed, means 'hand wing'. Bat wings are translucent: the bones of the hand and the blood vessels supplying the wing can be clearly seen through the skin. Because the blood cells can be viewed medical research to study the effects of drugs on the flow of blood through capillaries.

Homology

Homology applies to traits shared by species due to descent from a common evolutionary ancestor. For example, mammals share the same bone structure in their hands because they evolved from a common ancestor with those characteristics. Despite dramatic modifications towards different purposes, bat hands have the same bones as human hands (Figure 2). This can be readily demonstrated in class using photographs of flying bats.

Echolocation

Echolocation is a form of sonar: the bat emits high-frequency sounds that bounce off objects and return to the bat. Bats use these high-frequency echoes to find prey and navigate through caves and forests. Bats that echolocate often have disproportionately large ears — the ears of the spotted bat, for example, are two-thirds as long as the bat's body. Echolocation also allows bats to navigate in complete darkness.

Echolocation appears to be primarily a means of foraging. Echolocation is most characteristic of bats that hunt flying insects; many bats that eat fruit do not echolocate. The most sensitive echolocation, however, belongs to the fishing bat of Central America. It can detect the dorsal fin of a fish only a few millimeters above the surface of the water. The bat flies over the water and locates a fish when it breaks the surface.

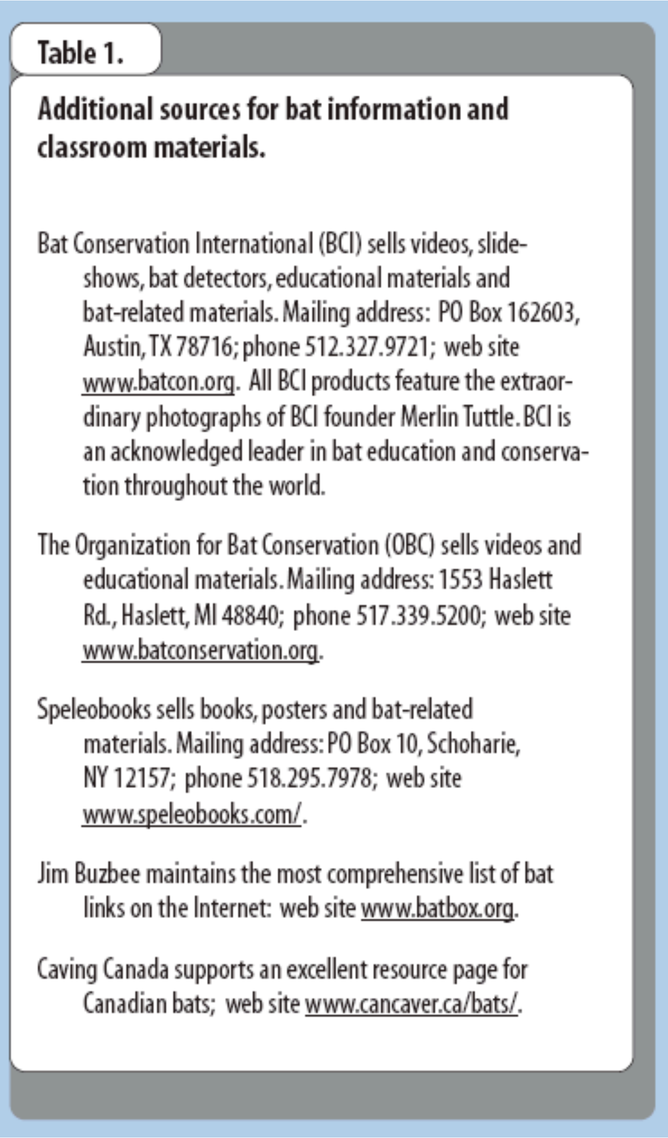

Table 1.

Additional sources for bat information and classroom materials.

Bat Conservation International (BCI) sells videos, slide-shows, bat detectors, educational materials and bat-related materials. Mailing address: PO Box 162603, Austin, TX 78716; phone 512.327.9721; web site www.batcon.org. All BCI products feature the extraordinary photographs of BCI founder Merlin Tuttle. BCI is an acknowledged leader in bat education and conservation throughout the world.

The Organization for Bat Conservation (OBC) sells videos and educational materials. Mailing address: 1553 Haslett Rd., Haslett, MI 48840; phone 517.339.5200; web site www.batconservation.org.

Speleobooks sells books, posters and bat-related materials. Mailing address: PO Box 10, Schoharie, NY 12157; phone 518.295.7978; web site www.speleobooks.com/.

Jim Buzbee maintains the most comprehensive list of bat links on the Internet: web site www.batbox.org.

Caving Canada supports an excellent resource page for Canadian bats; web site www.cancaver.ca/bats/.

Using the long claws on its feet, the bat then scoops the fish out of the water and eats it (see page 417).

Human Biology

Because they frequently share the same habitat, bats and people have enjoyed a long and colorful history. People have surrounded bats with myths (see Sidebar), conscripted them into the military, and boiled them in coconut milk for dinner.

The most common interaction between bats and people is pest management. Several species of North American bats will roost in buildings. The attics of buildings often provide ideal conditions for bats: attics are dark, dry, and offer a variety of temperatures. Most bat problems occur in the fall, when young bats explore inappropriate habitats, and the winter, when hibernating bats may seek warmer environments. Bats can be readily excluded from attics using simple exclusion devices that allow bats to leave the attic, but prevent bats from returning. Before attempting an exclusion, however, please contact an experienced bat person or organization — improper exclusion can expose people to unnecessary health risks.

Side Bar I: Bat Myths

Bats are often the subjects of unfounded myths. Among the more common myths we have encountered:

All bats are rabid (and therefore should be destroyed).

This misconception stems, in part, from faulty research in the 1940s. At the time, rabies were assayed by injecting suspect blood into rabbits; a dead rabbit was considered a positive test for rabies. Unfortunately, bats have a high incidence of Rio Bravo disease, a disease that does not affect humans but does kill rabbits. The high incidence of Rio Bravo produced data that suggested a high incidence of rabies. Better diagnostic techniques have revealed that bats are no more likely to carry rabies than any other mammal. Any mammal, however, can carry rabies. To be safe, people should never touch or handle wild mammals, including bats.

Bats get caught in people's hair.

This myth may stem from medieval Europe, when women had large hair and the streets may have been filled with foraging bats. A bat intent on capturing an insect may have occasionally blundered into a woman's hair. We have never met anyone who actually had a bat caught in her hair. We have, however, tried to catch wild bats using mist nets – very fine nets that are very difficult to see. Most bats avoid the nets through ecolocation. If a bat can discern fine nylon threads designed to catch him, he can easily discern the head of a human being.

Bats attack people.

This myth probably stems from the observation that bats, insects and people occasionally share the same habitat – for example, a fishing pond or swimming pool in the early evening. The bats are hunting the insects attracted to the water and probably don't care how close they come to people; people may misinterpret a close flight pattern as an attack. Bats are small animals that eat insects; people are large animals that eat, among other things, bats. A one-ounce bat attacking a human being is roughly equivalent to a man attacking a large pride of lions armed only with his teeth. Good luck!

Bats drink blood.

Of the 980 species of bats in the world, only three feed on blood, and two of those species are rare. The remaining species is the common vampire bat, a microbat native to Central America. Vampires feed primarily upon livestock, nicking the soft skin around the hoof or ear with their front teeth, then lapping the blood as it runs from the sore. An anticoagulant in the saliva of the vampire keeps the wound bleeding freely. In large numbers, vampires can be serious agricultural pests. Vampire attacks on human beings, however, are rare and preventable.

Bats are blind.

This myth may stem from the observation that blinded microbats can still maneuver and forage through ecolocation. In addition, many microbats have small eyes, often hidden by thick fur. A cursory examination of a bat may not locate the eyes. All bats, however, have functional eyes.

Bat myths are easy to refute, but changing the perceptions of the general public is much more difficult. Unfortunately, bat myths are often the rationale for senseless acts of slaughter, or the manipulation of home owners by unscrupulous exterminators. One homeowner we interviewed, for example, had been told that bats were most likely to become tangled in the hair of blonde women. Other home owners have purchased costly and dangerous treatments to remove bats when bats can be inexpensively and harmlessly excluded from their homes.

Bat problems can provide excellent learning opportunities. Mary Engles, a biology teacher at Vincent High School (Vincent, Alabama), found herself in the midst of a bat problem when bats began flying through the halls of the school. Mary was forced to answer questions about the presence of the bats, the safety of the students, and the management options for excluding the bats. As part of the management program, Mary's students researched and built bat houses to provide alternative roosting sites. We have found bat house construction to be a useful, hands-on activity that allows students to take a personal involvement in bats.

Our goal has been to illustrate some of the possibilities associated with the use of bats as a teaching tool. Additional information on bat biology is available from several organizations specializing in bat education (Table 1). Several organizations offer workshops on bat biology, which are designed for both teachers and conservation professionals — for example, Bat Conservation International leads week-long workshops in several locations each summer. Perhaps the best opportunity for classroom teachers, however, are weekend workshops offered by the Lubee Foundation in Gainesville, Florida (lubeebat@aol.com).

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Rabies

by Amanda Lollar and Barbara Schmidt-French

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HUMAN EXPOSURE

Rabies is a viral infection of the central nervous system resulting in fatal inflammation of the brain and sometimes, the spinal cord as well. Despite the fact that more than 30,000 humans die from rabies each year worldwide, very few of these deaths can be attributed to rabies of insectivorous bat origin. Since 1953, only a few dozen cases of human deaths due to rabies have been attributed to insectivorous bats, 35 of these having been documented in the United States as of December 31, 1998. Although the majority of these cases were formerly attributed to a variant of virus believed to be associated with the silver-haired bat (*Lasionycteris noctivagans*), many of these cases are now being attributed to a variant believed to be associated with the eastern pipistrelle (*Pipistrellus subflavus*). Researchers are trying to unravel what role these bats play in the epidemiology of human exposure. Although modern technology allows for the identification of the specific variant of the virus, it identifies only the original host; it does not provide identification of any possible intermediate hosts such as terrestrial mammals or other bat species.

Exposure to rabies virus typically results from bites of an infected animal. Less common modes of exposure include direct contact of open wounds, cuts, or abrasions with saliva or nervous tissue of an infected animal, contact of mucous membranes (e.g., eyes, nose, mouth) with infected saliva or nervous tissue, and inhalation of aerosolized virus. Although some of the recent human cases attributed to bat variants of the virus report no evidence of a bat bite, it is not possible to eliminate a bite as the mode of exposure. In some cases, the individuals were known to have actually handled bats or there was a report of a bat having been present in the victim's home some time prior to the onset of clinical signs of disease. In addition, by the time the disease was diagnosed, some victims had already died or were too ill to provide specifics regarding the kind of contact they had or may have had with a bat or other wild animal. In such cases, medical professionals were forced to rely on whatever information could be provided by family members or friends. Although the authors have found that bat bites are certainly felt, they do not always leave readily detectable marks on the skin. While victims of bites from terrestrial mammals such as raccoons are likely to seek medical treatment, this may not be the case with victims of bat bites. Unfortunately, the lack of a visible bite mark may have led some victims to dismiss such an encounter as insignificant.

Denny Constantine, formerly with the California Department of Health Services in Berkeley, California, studied rabies in bats extensively. According to Constantine, "Increasing numbers of bats were tested after 1953 as a consequence of increasing awareness of the problem . . .The infected bats were among many thousands of bats submitted for testing, usually because the bats, either disabled or dead, had been captured by pets or children, and bites were known or suspected to have occurred. About ten percent of the bats submitted in this manner for testing in the United States prove to be infected, a proportion that has not changed over the years. It should be emphasized that these bats represent a highly biased sample, because nearly all of them were ill or dead at the time of collection." This explains why health department statistics can vary significantly from those of wild bat populations and why comparisons of wild to suspect-submission rabies prevalence is of limited value.

No survey methods are likely to be entirely unbiased. Because sick bats are more easily caught than healthy ones, surveys taken in roosts may overestimate the frequency of infection in the population in general. Daytime surveys of night roosts may contain only incapacitated individuals (i.e., those unable to return to daytime retreats). Constantine indicates that such surveys may lead to mistaken impressions of rabies outbreaks, but that, " . . . nothing resembling an outbreak or large-scale rabies destruction of a bat colony has been detected, despite careful seeking" (Constantine, 1988). He goes on to state that, "The most reliable and useful survey samples are of bats capable of flight, such as bats issuing from cave entrances. From such sampling, it has been learned that only a small proportion (<0.1 to 0.5 percent) may be infected . . . " (Constantine 1988). While surveys of bats issuing from cave entrances would not include bats that are clinically ill and no longer able to fly, they would include infectious bats in pre-clinical stages.

Despite low rates of infection in wild populations, there is likely to be a much higher frequency of infection in the sick and injured population rehabilitators treat. They handle a highly suspect population similar to the population many health departments receive for testing. For example, 72 bats received at the French rehabilitation facility that either died or that were euthanized between 5/16/96 and 6/27/98 were tested for rabies in a collaborative study with Charles Trimarchi, DVM, of the New York State Department of Health. One bat was untestable due to physical trauma. Of the remaining 71 bats, six (approximately 8%) tested positive for rabies. (Percentages varied from one species to another, ranging from 0% to 19%.) This emphasizes the importance of pre-exposure immunization for bat handlers.

According to the U.S. Centers for Disease Control and Prevention (CDC), post-exposure prophylaxis is indicated following a bite or scratch from a confirmed rabid bat or from one that is not available (or suitable) for testing. The authors have found that some people are reluctant to admit to such encounters. Although this is sometimes due to a concern for the welfare of the animal (i.e., they don’t want it killed for rabies testing), more often it is due to a reluctance to admit to inappropriate behavior (i.e., catching or otherwise handling a wild animal). This may be particularly true of children. It is, therefore, important that rehabilitators carefully inform persons turning bats over to them of the potential consequences of untreated exposure to an infected animal. The CDC recommends that a bat be tested for rabies if it is found in a room with a person who cannot be considered an accurate historian (i.e, a person who may not be able or willing to give accurate information about potential contact with the bat such as a child, or a mentally disable, sleeping, or intoxicated person).

Concern has frequently been voiced about the potential threat of aerosolized rabies virus. Brass (1994) summarizes instances in which rabies have occurred in humans and animals as a result of inhalation of aerosolized virus. Only two human cases of aerosol transmission of bat rabies have been suspected, both in the 1950's. Brass (1996) suggests that misquotes, misunderstandings, and information carried out of appropriate context have resulted in reports that are misleading about this issue. In truth, aerosol transmission is suspected only within the unique conditions that exist in a small number of caves in the Southwest that house large nursery colonies of Mexican free-tailed bats (*Tadarida brasiliensis*). Rabies virus has been isolated from the air of such caves and sentinel animals placed in them have developed rabies without direct contact with bats. The unique atmospheric conditions resulting in caves housing these large maternity colonies (i.e., the presence of hundreds of bats combined with poor ventilation) may have played a contributory role in aerosolized transmission of rabies (Constantine, 1967). Viral entry points could have included skin wounds, the alimentary tract or respiratory mucosa. Brass (1996) points out that aerosolized virus was not detected in subsequent studies of caves housing large bat colonies in Oklahoma, Alabama, and Tennessee, and that rabies researchers do not believe that caves in the northern temperate zone are conducive to airborne transmission. Neither are such conditions found in buildings housing typical bat colonies.

Brass (1994) discusses this issue at length, providing specifics about each of the human cases. In so doing, he states that the evidence that the two deaths in the 1950's resulted from inhalation of aerosolized virus remains questionable. In particular, one victim, an entomologist with the Texas State Health Department who died in 1956, reported no bites but was known to have actually handled thousands of bats as a member of a rabies investigative team. An area of chronic skin irritation might also have had a contributory role in this particular case. The second victim, a consultant mining engineer who died in 1959, reported no bite although one report indicated he had been “nicked” in the face by a bat.

These facts led Brass to conclude that the risk of inhalation exposure to cavers exploring caves other than the aforementioned nursery colonies in the Southwest is virtually nonexistent: “This mode of transmission should not be of even remote concern to either the general public or the vast majority of the caving community, since it is a phenomenon known only from the research laboratory and possibly the exploration of certain unique underground environments” (Brass, 1996).

Brass (1994) also notes that there has been no report of bat-inflicted rabies in a caver secondary to a bite sustained while underground despite the hundreds of thousands of man hours spend underground annually by members of the National Speleological Society. Nonetheless, the author does note the possibility of direct contact with bats during cave exploration despite the fact that conscientious cavers try to avoid disturbing bats. He empathizes prevention and promotes treatment as follows: ". . . the caver's best possible protection derives from common-sense caution in handling bats and from prompt wound care and post-exposure rabies prophylaxis in the unlikely eventuality that a bite from a rabies bat (or from one unavailable or unsuitable for testing) is sustained."

Only laboratory testing of brain tissue can positively identify rabies infection in bats. Rabies infection cannot reliably be excluded by antemortem testing (i.e., testing of a live animal for rabies). This is to say, a positive diagnosis of rabies testing in a living animal is conclusive, but a negative test is not. As previously indicated in this manual, bats that have human contact should always be submitted to animal control or local health departments who will determine if rabies testing is warranted.

BAT BITES

Bites or scratches from the claws of North American bats may or may not leave marks on the skin. All bats are capable of inflicting bites that leave marks despite the fact that they may not always do so. Visible bite marks can range from simple indentations in the epidermis that disappear within moments, to tiny scratches (that can occur when a bat jerks its head while biting), to deeper puncture marks that may or may not result in bleeding. Bites from species found in the United States and Canada are frequently visible as two to four tiny puncture marks, often spaced about 4mm to 5mm apart, depending on the species. The punctures are caused by the canines, either the upper and lower canines on one side of the jaw leaving two puncture marks, or the upper and lower canines of both sides of the jaw leaving as many as four puncture marks.

Bites are commonly received on the fingers or hand by people who handle or otherwise touch a bat. Bites can also result on various parts of the body when a person brushes against or has other bodily contact with a bat because he/she was unaware of the bat's presence. For example, a bite could occur if an individual sat on a chair that a grounded bat had crawled onto. Marks generally fade quickly and are frequently no longer visible after only one or two days. Some bites may be visible for a longer period of time, although seldom more than a week or two. Bites that actually puncture the skin can be painful when received (a sensation similar to that experienced from a needle jab).

Because bats do not always release their bite immediately, they must sometimes be encouraged to do so. Attempting to pry their teeth apart with a pencil or other object is inappropriate (and time-consuming). Blowing in the face of the bat will often cause it to release its hold. When all else fails, make one quick flick of the wrist while the hand is open and held above a soft surface. This action startles the bat, causing it to release its hold.

CLINICAL SIGNS OF RABIES IN INSECTIVOROUS BATS

The incubation period is the interval between exposure to viral infection and the appearance of the first clinical sign of disease. An incubation period of at least 209 days was reported in a naturally infected big brown bat (Moore and Raymond, 1970 [cited by Brass, 1994]). There are also reports of incubation periods of over one year (Kaplan, 1969 [cited by Brass, 1994]; Trimarchi, 1978 [cited by Brass, 1994]).

Although the authors have observed a number of clinical signs in bats testing positive for rabies, ***lack of observable clinical signs of disease cannot be used as a basis for determining if a bat is or is not infected with the rabies virus***. Even clinically normal bats are of unknown infection status. Although the authors have found that bats infected with rabies frequently die within a few days (often within 24 to 48 hours) after being obtained by a rehabilitator, the maximum period of viral shedding (the period of time during which the virus is present in the saliva and the disease can be transmitted to others) prior to the onset of clinical signs in bats (and most other wild animals) is unknown. Virus has been detected in bat saliva as much as 12 days prior to the onset of clinical signs of disease (Baer and Bales, 1967; Baer, 1975; Constantine, 1998). Therefore, even bats that appear to be healthy could be shedding virus and thus be capable of transmitting it to people or other animals.

Clinical signs of rabies infection in Mexican free-tailed bats (*T. brasiliensis*) documented by Constantine (1967) are predominantly paralytic rather than furious in nature. Irritability or depression, weakness, anorexia, hypothermia, and paralysis may characterize the disease in this species. Clinically ill individuals sometimes flap their wings and squeak loudly when people approach, although they are unlikely to attack observers. They do sometimes bite at objects near them, but generally appear focused on their own debilitated state. Squeaking and buzzing have also been reported by other researchers (Centers for Disease Control, 1954 [cited by Brass, 1994]; Bell et. al., 1955 [cited by Brass, 1994]; Moore and Raymond, 1970 [cited by Brass, 1994]; Schowalter, 1980 [cited by Brass, 1994]; Haagsma, 1989 [cited by Brass, 1994]). These bats may be dehydrated, emaciated, hypothermic, and are often found roosting alone (Sullivan et. al., 1954 [cited by Brass, 1994]; Constantine, 1988). They are sometimes observed flying during the daytime and may collide with objects (Bell et. al., 1957 [cited by Brass, 1994]; Constantien, 1967; Price and Evard, 1977 [cited by Brass, 1994]). However, some species of bats normally fly in the late afternoon. Healthy bats will also fly out of roosts during the day if sufficiently disturbed.

The authors often observe aggressive biting and incessant chewing by rabid bats on items that come into contact with them, including inanimate objects such as caging materials. Incessant chewing on inanimate objects in particular is not typical of healthy bats, with the exception of mating males of some species, such as *T. brasiliensis*, in captive colonies. These males do sometimes exhibit aggression towards intruders (i.e., handlers or bats, males or females, that enter their territories – Lollar, 1994). Rabid bats often do not show an interest in exploring or moving around within their environment. Rather, these animals often seem to prefer to remain exposed in one spot with eyes closed or half closed, only responding when anything approaches them. They do not seem to aggressively seek out objects or other animals, but rather bite at whatever materials (or people) that happen to touch them. Verified reports of unprovoked bat attacks are exceedingly rare. The authors frequently receive reports of "attacking bats" from individuals who are surprised by a bat that inadvertently flies into their home through an open door or over their head at a porch light. These people can be quite insistent that the bat in question is attempting to attack them until rescue personnel arrive on the scene and give them the opportunity to see that although the bat will continue to fly around the room, it does not actually jump onto or attack the rescuer. They often express surprise at this observation. French has also observed sick or injured foliage-roosting species, such as red bats (*Lasiurus borealis*), spread their wings and release their grip from their roost when startled. Because they are too weak to fly, they subsequently flutter to the ground. It is understandable that a rare encounter with such a bat would be mistaken for an attack.

The authors have found that, while not always a reliable indication of rabies infection, uninjured crevice-dwelling bats with rabies are often found in exposed areas during daylight. Do not assume that injury precludes rabies infection, however. In fact, rabid bats may sustain injury once they have become sick enough to be grounded. On the other hand, illness and injury does not necessarily mean rabies.

Any injured bat that has become grounded may squeak and flap its wings in an attempt to escape capture. However, the authors have also observed continuous wing-flapping and repeated vocalization in rabid bats. We have also observed the following neurological signs including uncoordinated movements, spastic paralysis of the hind legs, seizures, a hunched back, and legs clamped up against the abdomen in bats testing positive for rabies (although similar signs may also accompany other conditions including pesticide poisoning and back injuries – Lollar, 1994; Clark, et al., 1996).

We have also found that the presence of dirt and/or other foreign substances in or around a bat's mouth may be another indication of rabies infection, possibly resulting when an infected animal bites at the ground or other surroundings. In addition, rabid bats may refuse to eat or drink and become dehydrated. However, rehabilitators should not consider dehydration in itself as being diagnostic of rabies, since many unrelated conditions may also lead to dehydration. Alternatively, we have found that although it is not common, some rabid bats will readily accept both food and water.

Rabies infected bats may also exhibit signs of respiratory distress. French observed bleeding from the ears and mouth of one rabid bat that appeared unable to move its head and neck. Although observation of signs in a single bat have no statistical significance, we feel it is important for rehabilitators to be aware of all of the signs we have observed in bats that have tested positive for rabies. This bat had no other obvious injuries. It is possible that bleeding could have been associated with a head or other injury sustained as the result of a crash or fall due to weakness or the kind of erratic flight that often characterizes rabies in bats. Bleeding from the ears, nose, or mouth may also be associated with pesticide poisoning (Clark, et al., 1996) and heat stroke.

Rabies is a fatal disease for people as well as bats. Rehabbers should protect themselves and humanely euthanize bats demonstrating signs of rabies infection. In case of an animal bite and/or scratch or contact with saliva or nervous tissue from a suspect animal, consult your family physician immediately. Animals involved in such instances must be turned over to authorities for rabies testing. (Care should be taken to prevent physical damage to the brain of an animal that must be tested for rabies.) If you do not have access to a physician, contact your local or state health department. These officials will direct you to the proper emergency medical professionals in your area who have access to the required vaccine. If local or state health department personnel are unavailable, call the Viral and Rickettsial Diseases Division of the U.S. Centers for Disease Control and Prevention at (404) 639-1075 weekdays, or at (404) 639-2888 nights, weekends, or holidays.

There has been little research in the area of rabies vaccination for bats, as vaccination of large, wild populations may not be a feasible undertaking. However, Charles Trimarchi, DVM, with the New York State Department of Health states that, “While most health agencies neither endorse nor prohibit extra-label use of rabies vaccines in wildlife, modern vaccines may protect wild species and because they are killed-virus vaccines, do not pose a risk of vaccine-induced rabies infection.” (Trimarchi, 1996.)

French and Lollar vaccinate bats taken in from the wild that will be added to captive study colonies in order to minimize the potential of disease transmission to other captives. These bats are vaccinated annually with the Imrab 3 rabies vaccine. Each bat is injected subcutaneously with 0.05ml. However, Trimarchi notes that, “. . . if an animal so vaccinated ever bites or otherwise potentially exposed a human or domestic animal, the vaccination will not be recognized as pertinent by health agencies; (ii) if the animal is in contact with a known rabid animal, it will still have to be confined for six months or euthanized; (iii) if the animal develops CNS disorder, rabies must still be immediately suspected” (Trimarchi, 1996).

It is also important to note that a negative test on one captive bat in a cage does not necessarily reflect the rabies status of another bat housed in the same cage.

Human rabies cases in the United States believed to be associated with the following bat species, or viral variants:

Scientific Name	Common Name	Incidence
Pipistrellus subflavus	Eastern pipistrelle	15
Lasionycteris noctivagans	Silver-haired bat	8
Tadarida brasiliensis	Mexican free-tailed bat	5
Eptesicus fuscus	Big brown bat	2
Myotis species	Plain-nosed bat species	2

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Use of Artificial Roosts by Forest-Dwelling Bats in Northern Arizona

By Carol L. Chambers, Victor Alm, Melissa S. Siders, and Michael J. Rabe

Wildlife Society Bulletin 30(4):1-7, 2002

Forest-dwelling bats often use snags and live trees as maternity and bachelor roost sites. These roost sites can be destroyed or altered by natural events (e.g., wildfire) or forest management activities (e.g., prescribed fire, thinning, harvesting). To determine whether artificial roost structures could supplement natural roost sites, we tested 2 types of artificial structures for use by bats: resin (n=10) and wood (n=10) roosts. Artificial roosts were placed on snags in 6 ponderosa pine (*Pinus ponderosa*) stands and compared with use of nearby natural roost snags (n=10). We monitored the 3 roost types (resin, wood, natural) approximately every 2 weeks for use by bats for 2 summers (1999 and 2000). Over the 2-yr period, bats used 17 of 20 artificial roosts (8 resin and 9 wood), using both artificial roost types in about equal proportions. Bats used 5 of the 10 natural snags monitored. Resin roosts were camouflaged to match tree bark, have a >20-year lifespan, and cost US $42 each after construction of a $250 mold. They can be resigned to resemble any tree species. Wood roosts cost about $5 each, were more visible, and likely have a shorter lifespan than resin roosts. Both roost types might require some annual maintenance (recaulking tops and edges). Maintaining and managing for natural roosts should be a priority for resource managers since artificial roosts might not provide the same microclimate as natural roosts. However, artificial roosts might be useful temporary habitat under site-specific conditions. Artificial roosts could also be useful as research tools.

Key words: Arizona, artificial roosts, bats, fire, *Pinus ponderosa*, ponderosa pine, roost habitat, snags, Southwest

Many forest-dwelling bats in ponderosa pine (*Pinus ponderosa*) ecosystems (e.g., long-eared myotis [*Myotis evotis*], fringed myotis [*Myotis thysanodes*], long-legged myotis [*Myotis volans*], Allen's lappet-browed bat [*Idionycteris phyllotis*], and big brown bat [*Eptesicus fuscus*]) rely on large (>69-cm-diameter at breast height [dbh]) ponderosa pine snags as primary roost sites (Rabe et al. 1998, Barclay and Brigham 2001). Roosts often are located under large pieces of loose, exfoliating bark that provide insulation and allow bats to move during the day to seek optimum temperatures. Because of their reliance on large snags, forest bat populations are likely sensitive to roost-site destruction.

Forest management treatments (e.g., thinning, prescribed burning) are being implemented in response to the increased threat of wildfire in the southwestern United States (Covington et al. 1997, Swetnam et al. 1999). However, these management treatments might reduce the availability of snags. Thinning might inadvertently remove snags, and prescribed fire or wildfire might incinerate or alter snags (Horton and Mannan 1988, Dwyer and Block 2000, Randall-Parker and Miller 2002) that serve as roost sites for bats. Although prescribed fire or wildfire also creates snags (Gaines et al. 1958, Boucher et al. 1999), live trees killed by fire generally are small in diameter and therefore not effective replacements of large snags selected by bats, nor do they have exfoliating bark that is used by bats for roost sites (Rabe et al. 1998). Horton and Mannan (1988) found that large (>30-cm-dbh) and more decayed ponderosa pine snags were more flammable, therefore more likely to be lost to fire. This loss of large dead wood might be particularly detrimental to bats, since bats select larger snags (>69 cm diameter) and replacement of large snags could take a long time (e.g., >200 years for a ponderosa pine to reach 50 cm dbh under normal stocking, site index 70 [Meyer 1961]).

In situations where roosts snags are altered or removed, artificial bat roosts might enhance or maintain bat-roost habitat (Fenton 1997). In Thetford Forest, England, the population of brown long-eared bats (*Plecotus auritus)* doubled after 10 years when artificial bat boxes were added. Population increase was attributed to recruitment rather than immigration, suggesting that roost sites had been limiting (Boyd and Stebbings 1989). Other successful uses of box-type artificial roosts have been documented in Europe (Luger 1977, Ziegler and Ziegler 1991).

To test the value of artificial roosts in ponderosa pine forests of northern Arizona, we studied the effectiveness of 2 designs. The first roost was made of a polyester resin shaped and painted to resemble exfoliating bark found on ponderosa pine snags. The second type was hand-constructed of tempered hardboard (wood) that served as a less expensive alternative to the first design. Our objectives were to determine whether 1) forest bats would use artificial roosts and 2) forest bats selected between artificial roost types.

Study area

We placed artificial bat roosts in 6 16-ha stands in the Fort Valley Experimental Forest located northwest of Flagstaff, Arizona (Township 22N,Range 6E, Section 24; Township 22N, Range 7E, Sections 19 and 29, Gila and Salt River Meridian) (P. Fulé,T. Heinlein, and A. Waltz, Northern Arizona University, unpublished report). We selected 3 unharvested stands and 3 treated ponderosa pine stands for roost placement. In unharvested stands ponderosa pine averaged 1,201 trees/ha; in treated stands trees had been thinned to 172/ha. Trees were <80 cm diameter in all stands (P. Fulé, T. Heinlein, and A. Waltz, Northern Arizona University, unpublished report). Treated stands were thinned in 1999 prior to artificial roost attachment, and burned in 2000 after roosts were introduced. Prior to thinning, all stands were similar in ponderosa pine density.

Methods

We used 2 types of artificial bat roosts: 1) wood roosts made of tempered hardboard (which had 1 smooth and 1 rough side and was specially treated to create extra water resistance, surface hardness, rigidity, bending, and tensile strength [Phillips Plywood Company, Inc. 2002]; we used the rough surface as the interior of the roost [Figure 1*a*]), and 2) polyester resin molds shaped and painted to resemble exfoliating bark found on ponderosa pine snags (Figure 1b).

We constructed wood roosts from a 0.6 × 0.6-m piece of 0.3-cm-thick tempered hardboard and wooden wedges fabricated from 5 × 10-cm pine lumber. The wooden wedges, which hold the hardboard away from the snag, could be made to any size. We cut wedges so that openings at the bottom of roosts were approximately 5 cm wide to allow bats easy access. We attached wedges to hardboard with weather-resistant, self-tapping (pointed, with self-cutting threads) deck screws and finish washers (beveled to countersink the screw head). Holes were predrilled in each roost for ease of attachment to snags in the field. Wood roosts (Figure 2*a*) cost US <$5 each, making them an inexpensive alternative to resin roosts.

Resin roosts were made of flexible isothalic polyester resin and reinforced with fiberglass mat, manufactured by Wesco Enterprises (Rancho Cordova, Calif.). They were 100% ultraviolet-stable. We inserted 3 decay-resistant (e.g., redwood, *Sequoia sempervirens*) wood partitions inside each roost to increase the number of roost sites for bats (Figure 1*c*). Resin roosts cost $42 each with an initial $250 charge to create the rubber mold (Figure 2*b*).

Both resin and wood roosts could be attached to snags

Figure 1. Artificial and natural roost types monitored for bat roosting activity in ponderosa pine forests during summer 1999–2000, northern Arizona. *a:* wood roosts; *b:* resin roosts; *c:* interior of resin roost showing 1 decay-resistant wood insert.

of varying size (from 46–90 cm dbh for our study). Both artificial roost types measured 0.6 × 0.6 m and were secured to snags with 3 15-cm deck screws across the top of the artificial roost and 2 down each side. We used grommets between screw heads and the artificial roost to prevent damaging the roost. We used brown caulk to seal the top and sides to prevent moisture from entering the roost, and left the bottom open for access by bats.

In 4 (2 unharvested, 2 treated) of the 6 stands, we selected 2 groups of snags in each stand to serve as substrates for artificial roosts and as areas to check for natural roosts (controls). In each of the remaining 2 stands (1 unharvested, 1 treated) we selected only 1 group of snags per stand because few of the snags present were of adequate size. Each snag group consisted of 3 ponderosa pine snags that were >31 cm dbh and <75 m apart. From each group we randomly chose 1 snag for attachment of a resin roost and 1 for a wood roost; 1 was left as a natural (control) roost (exfoliating bark present). We attached artificial roosts (resin or wood) to the trunk 2–4 m above the ground. Aspect of roost attachment was constrained by available attachment sites on each snag. We made no attempt to randomize roost aspect. Ten roosts of each of the 3 types were placed (artificial) or chosen (natural) for a total of 30 roosts in 6 stands. We left roosts in place for the duration of the study and sampled the same roosts each year, except for 1 control snag that fell and 1 snag and its wood roost that were destroyed by a prescribed burn. We did not monitor the 2 destroyed roosts after 1999.

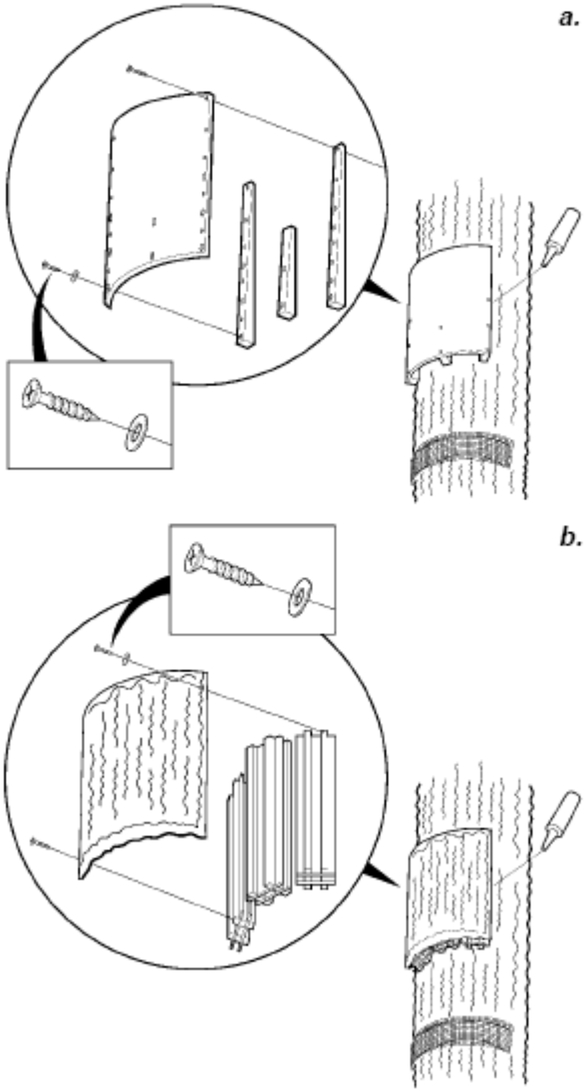

Figure 2. Two artificial roost types monitored for bat roosting activity in ponderosa pine forests, summer 1999 and 2000, northern Arizona. *a:* wood roosts; *b:* resin roosts.

We monitored all roosts for use by bats 3–4 times (approx. every 2 weeks) between 19 July and 26 August 1999 (Year 1) and 10 July and 8 August 2000 (Year 2). We determined use of roosts by the presence or absence of guano (*n* >1 pellet; *x* -=96 pellets per roost, range = 1–1,700 pellets) found in wire mesh catch nets attached to the snag approximately 0.6 m below the roosts (Figures 2*a* and *b*). We monitored natural snags by attaching netting around the base of each. We did not infer abundance, density, or species of bats from guano deposits; however, if bats were present in roosts, (visual or aural confirmation), we identified them to species when possible.

We selected large-diameter snags based on prior observations of bat use in the area (Rabe et al. 1998). For each snag, we recorded height, dbh, and decay class (adapted from Maser et al. 1979). Snags averaged 63.5 cm (SE=2.5 cm) dbh. Snags were in decay classes 3 (*n*=5), 4 (*n*=4), and 6 (*n*=21;Table 1). We compared use among roost types by pooling data from both years. We compared the observed proportion of use to a 95% confidence interval of expected use (chi square goodness-of-fit test, Sokal and Rohlf 1981). Since proportions of available roost types were equivalent, 1 confidence interval was sufficient to compare use of the 3 roost types.

Results

In 1999 bats used 15 of 20 artificial roosts (8 wood and 7 resin) and roosted in 5 of 10 control snags. Ten artificial roosts (5 wood, 5 resin) were in thinned stands and 5 (3 wood, 2 resin) were in unthinned stands. Four of the control snags used were in thinned stands; 1 was in an unthinned stand.

In 2000 bats used 14 of 19 artificial roosts (7 wood and 7 resin; prescribed fire destroyed 1 wood roost) and 3 of 9 control snags (1 had fallen). Nine artificial roosts (4 wood, 5 resin) were in thinned stands, and 5 (3 wood, 2 resin) were in unthinned stands. Two of the control snags used were in thinned stands; 1 was in an unthinned stand.

With years pooled, 17 artificial roosts (9 wood and 8 resin) were used by bats and 5 control snags were used. We did not detect a difference between observed use of the 3 roost types and the expected use ($0.25 < \chi2<0.50$). Ten artificial roosts (5 wood, 5 resin) were in thinned stands and 7 (4 wood, 3 resin) were in unthinned stands. Four of the control snags used were in thinned stands; 1 was in an unthinned stand.

Discussion

Artificial roost use -- Roosts provide bats with cover and concealment from predators and a protected microclimate (Jones et al. 1995, Palmeirim and Rodrigues 1995, Vonhoff and Barclay 1996). Bats in many forest ecosystems select snags for use as roosts (Barclay and Brigham 1996, Rabe et al. 1998, Lacki and Schwierjohann 2001). However, snags are ephemeral and subject to loss through attrition or from forest management practices. Both types of artificial roosts (resin and wood) used in this study were effective as roost sites for some forest-dwelling bats.

We noted use of roosts (natural and artificial) in thinned stands (n =14) and unthinned stands (n = 8), but because of small sample sizes we did not test for differences in use of stand type. If bats selected more open forest conditions, this might have been because of increased availability of foraging and commuting areas (Grindal and Brigham 1998) and flight, navigational, and evasive space (e.g., to avoid aerial predators; Vonhoff and Barclay 1996). However, forest-dwelling bats also might select habitat based on tree density, and dense forest conditions might be important for some species.

In our study, at least 2 species used artificial roosts. We found 2 big brown bats (1 a nonreproductive female; the other evaded capture) in a wood roost in August 2000. In July 2001, we found a maternity colony of long-eared myotis (>7 bats including 3 juveniles and 4 adults) in a resin roost. We suspect other species also used our roosts; however, we could not identify bat species from guano samples, and we did not want to disturb roosting bats during the study period.

We installed artificial resin roosts in 2 other locations in northern Arizona prior to our study. We installed them where bats were known to be present but roost habitat was thought to be limiting (i.e., loss of large snags and lack of replacements for snags). We monitored these artificial roosts only periodically, but bats used artificial roosts at both locations: 1) On the Coconino National Forest in ponderosa pine–Gambel oak (Quercus gambelii) forest, Allen's lappet-browed bats used 2 artificial resin roosts (M. J. Rabe, Arizona Game and Fish Department, unpublished data). We found an active Allen's lappet-browed bat roost under bark on a ponderosa pine snag in 1994; bats also used this roost in 1995. We observed Allen's lappet-browed bats in the resin roost the next two summers, and they also used another resin roost in the same area. 2) We paced resin roosts (n = 67) on live ponderosa pine trees (>60 cm dbh) on the Kaibab Plateau beginning in 1997 in open

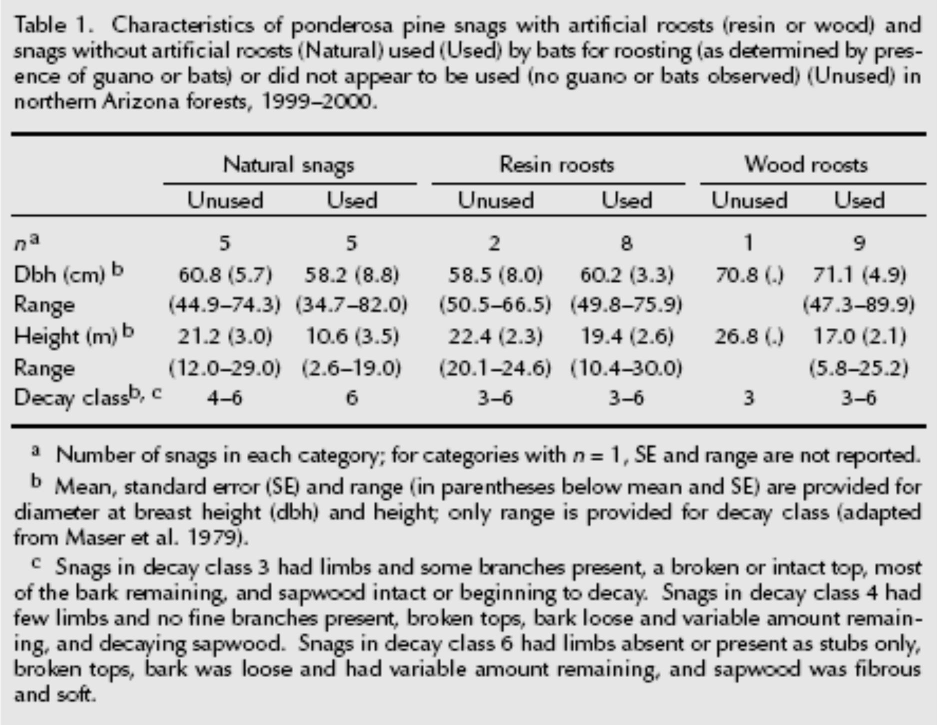

Table 1. Characteristics of ponderosa pine snags with artificial roosts (resin or wood) and snags without artificial roosts (Natural) used (Used) by bats for roosting (as determined by presence of guano or bats) or did not appear to be used (no guano or bats observed) (Unused) in northern Arizona forests, 1999–2000.

	Natural snags		Resin roosts		Wood roosts	
	Unused	Used	Unused	Used	Unused	Used
n^{a}	5	5	2	8	1	9
Dbh (cm) [b]	60.8 (5.7)	58.2 (8.8)	58.5 (8.0)	60.2 (3.3)	70.8 (.)	71.1 (4.9)
Range	(44.9–74.3)	(34.7–82.0)	(50.5–66.5)	(49.8–75.9)		(47.3–89.9)
Height (m) [b]	21.2 (3.0)	10.6 (3.5)	22.4 (2.3)	19.4 (2.6)	26.8 (.)	17.0 (2.1)
Range	(12.0–29.0)	(2.6–19.0)	(20.1–24.6)	(10.4–30.0)		(5.8–25.2)
Decay class[b, c]	4–6	6	3–6	3–6	3	3–6

[a] Number of snags in each category; for categories with $n = 1$, SE and range are not reported.

[b] Mean, standard error (SE) and range (in parentheses below mean and SE) are provided for diameter at breast height (dbh) and height; only range is provided for decay class (adapted from Maser et al. 1979).

[c] Snags in decay class 3 had limbs and some branches present, a broken or intact top, most of the bark remaining, and sapwood intact or beginning to decay. Snags in decay class 4 had few limbs and no fine branches present, broken tops, bark loose and variable amount remaining, and decaying sapwood. Snags in decay class 6 had limbs absent or present as stubs only, broken tops, bark was loose and had variable amount remaining, and sapwood was fibrous and soft.

forest patches (M.S. Siders, North Kaibab Ranger Station, unpublished data). In 1997, 33% of roosts were used, 90% were used in 1998, 45% in 1999, and 61% in 2000 (all determinations of roost use were based on presence of guano; M.S. Siders, North Kaibab Ranger Station, unpublished data). These data indicated that bats were able to locate and use roosts on both snags and live trees.

Artificial roosts might help supplement natural habitat in areas where natural snags have not yet formed suitable roosting structures (loose batk) or replacement snags of adequate size are lacking (e.g., through natural attrition or destruction by natural disturbances such as wildfire), altered or removed (through forest management activities). However, artificial roosts might not effectively replace natural snags. Natural snags might offer different microclimates or roosting substrates, or provide other functions that artificial roosts do not provide.

Of the 20 artificial roosts we monitored in this study, bats used 15 in 1999 and 14 in 2000. Bats did not appear to select one type of artificial roost over another (both resin and wood roosts were used in about equap proportion), although this might be attributable to small sample sizes or a limited number of natural roosts in these areas. Both resin and wood roosts were purposely designed to attract bats.

Comparison of artificial roosts--Resin roosts required little or no maintenance and were made of durable material expected to last ~20 years. Resin roosts wer also cryptic and not subject to color fading. These roosts were 8 times more expensive than wood roosts, and there was a substantial initial cost ($250) to create the roost mold. Resin roosts on the Kaibab Plateau in northern Arizona have been in place for 5-6 years, have required no maintenance or resealing roost edges, and continue to be used by bats.

Wood roosts would be unlikely to persist as long as resin roosts (wood roosts may function for 10-15 years in dry climates). We noticed that wood roosts weathered (the wood discolored) within 2 years. They also would be subject to decay, especially in wetter climates. Wood roosts were more visible than resin roosts, although the could be painted to more closely simulate tree bark. However, wood roosts could be effective research tools because they are inexpensive and easy to produce.

In our study, we were limited in roost placement because more snags were unsafe to climb. We were also limited in the aspect at which the roost could be attached on a snag. Often, roosts could be placed in only a few locations on the snags. If aspect was important for roosting habitat, selecting snags and trees for roost placement should be carefully considered. It might be possible to design an artificial roost that wraps around the exterior of the tree (360☜) or to place multiple roosts on a tree facing several aspects so that bats could select the best aspect for roosting.

Management Implications

The active use of artificial roosts by forest bats of northern Arizona suggested a viable roosting alternative. In areas of high roost mortality from destructive agents (e.g., fire) or in areas that contain snags without desired roosting traits (e.g., exfoliating bark), artificial roosts might be an important management tool. For example, if natural roosts were destroyed during a prescribed fire, placing artificial roosts on surviving snags or live trees could create habitat that might help maintain a forest bat population until natural roosts develop.

Acknowledgments. This project was sponsored by Northern Arizona University's Ecological Restoration Institute, with funding from the State of Arizona, the Cooperative Ecosystems Study Unit, and the Bureau of Land Management. We thank T. Theimer, P. Z. Fulé, and W.W. Covington for their collaboration on the project and early reviews of this manuscript. We thank D. Garcia de la Cade?a, S. Knox, R. Miller, H. Shanes, G. Vance, J. Waskiewicz, and J. Wood for their assistance in obtaining, installing, and monitoring artificial roosts. The wood roost was designed by M. Rabe, the resin roost by D. Garcia de la Cadea. We also appreciate the comments provided by 2 anonymous reviewers

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“Rocket Box” in Kentucky

by Dan Dourson

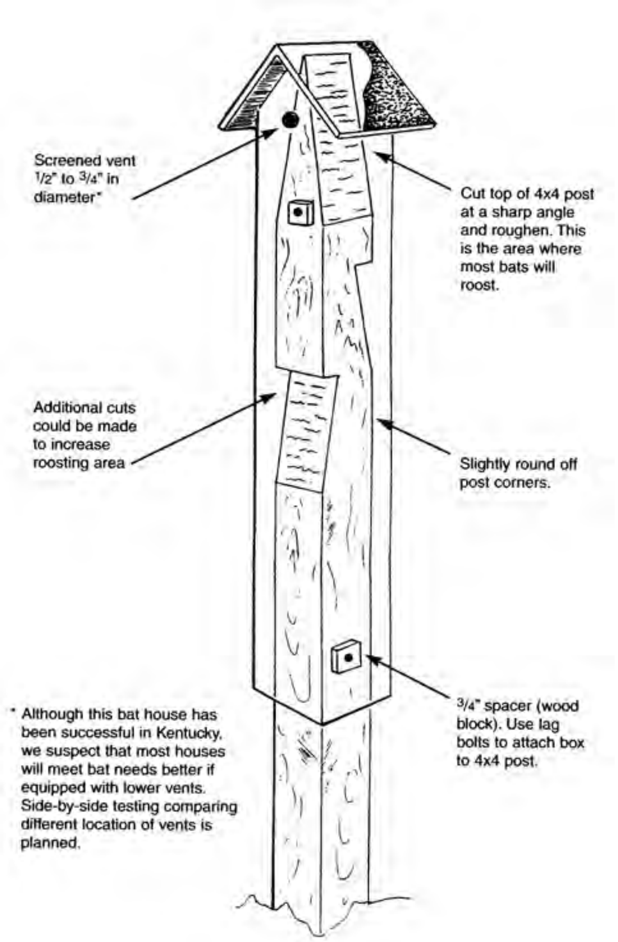
The Bat House Researcher, 5(1): 4 – Spring 1997.

In our work in the Daniel Boone National Forest in Kentucky, John MacGregor and I have been experimenting with a simple bat house design nicknamed the "Rocket Box." The house is basically a covered box that slides over a wooden post inserted in the ground (see diagram). Sixty boxes have been placed in a variety of forest, riparian, and urban habitats. Our best success rate (100%) is with boxes located on ridgetops in prime habitat. About 75% of boxes placed along riparian habitats were used last year, and about 50% of boxes in mixed riparian and urban habitats were used. Use was very low in pure urban areas.

Rocket boxes are designed to be similar to trees with exfoliating bark, one of the most commonly used natural roost sites. Bats can move freely within this design to either cooler or warmer sides of the structure depending on their needs. If predation becomes a problem, predator guards can be added to the 4x4 post.

When building a rocket box, avoid using treated lumber or soft woods for the 4x4 post, since these could be harmful to bats or could decay quickly in the ground. The box itself can be made of a lighter wood since it is not in direct contact with the ground and is partly covered by the roof. Use only galvanized screws to put the bat box together. If you can get the post in the ground at least two-and-a-half to three feet, there is no need to cement it in, although concrete may deter termite damage. Spacing between the bat box and the 4x4 post is critical. Any more than three-quarters of an inch will make it more attractive to mud daubers and paper wasps.

Bats moved into some of these houses in as little as two weeks after installation. Single houses have sheltered up to 15 bats of at least two species, northern long-eared myotis (*Myotis septentrionalis*) and big brown bats (*Eptesicus fuscus*). Many bats have been observed in the bat houses but could not be identified due to the long narrow shape of the house.



* Although this bat house has been successful in Kentucky, we suspect that most houses will meet bat needs better if equipped with lower vents. Side-by-side testing comparing different location of vents is planned.

We had our best results when the bat houses were located in upland forest habitats on south or southwest slopes with open canopy They did well in small openings along forest roads and rights-of-way where they receive more sunlight. We did not place many bat houses close to buildings, and have not painted any of the houses, although caulking and painting could help.

For plans, or more information, contact Dan Dourson, Stanton Ranger District, Daniel Boone National Forest, U.S. Forest Service, 705 West College Avenue, Stanton, Kentucky 40380, (606) 663-2852.

For plans of a double chambered “rocket box”, contact Mark Kiser at Bat Conservation International, P.O. Box 162603, Austin, TX, 78716, (512) 327-9721.

A Two-Chamber Rocket Box

by Mark Kiser

The Bat House Researcher, 6(2): 4-5, Fall 1998.

Building upon the success of Dan Dourson's and John MacGregor's rocket box [TBHR, Spring and Fall 1997], BCI staff designed and tested the first two-chamber rocket box this year. Within three months of installation on Quadra Island, British Columbia, a maternity colony of Yuma myotis moved in. This was also the first rocket box to be installed on a metal pole, which adds strength and longer life. In addition to extra roosting space, the second chamber provides greater temperature diversity, allowing bats to select the most suitable temperatures. We thank the Grant B. Culley, Jr. Foundation for funding this project.

Exterior and bottom views of the new design are provided in Figures 1 and 2, and detailed plans are available upon request. Access ports in the inner shell, near the bottom of each side, enable bats to move between chambers. By extending the length of the inner shell three to six inches below the outer shell, additional landing surface area is created, permitting direct access to either chamber.

Rocket boxes are designed to slide over a wooden 4 x 4-inch post, which serves as both landing area and roosting surface. As an untreated post must be used (treated posts may contain chemicals harmful to bats), service life is shortened because the section of post below ground will eventually decay. By combining a four-foot section of a wooden 4 x 4-inch post (for the landing and roosting surface) with a metal pole, the life span of the bat house can be extended. We suggest using a steel pole with an outside diameter of 1 5/8 to 2 inches.

Starting at one end of the post, cut a 24-inch-long notch down the center with a circular saw. The width and depth of the notch will depend upon the size of the metal pole chosen. Use a jig saw or wood chisel to complete the cut. Secure the metal pole to the wooden post with 3 1/2 -inch screws or bolts and a construction-grade adhesive, such as Liquid Nails. Because the actual finished size of 4 x 4-inch posts varies (typically they are 3 1/2 by 3 1/2 inches), measure the width of the post before cutting the pieces for the inner shell and adjust your measurements accordingly. Build the inner shell first, then measure and cut the pieces for the outer shell. Three-fourths-inch spacer blocks help maintain proper crevice widths.

Eager to try the new design, Honorary Research Associate Kent Borcherding of Hazel Green, Wisconsin constructed his house from BCI's plans this summer. The house was occupied by a colony of 25 little brown bats within several months. Borcherding will test more of these in Wisconsin and Illinois next year, and we plan to test more in side-by-side comparisons with single-chamber rocket boxes.

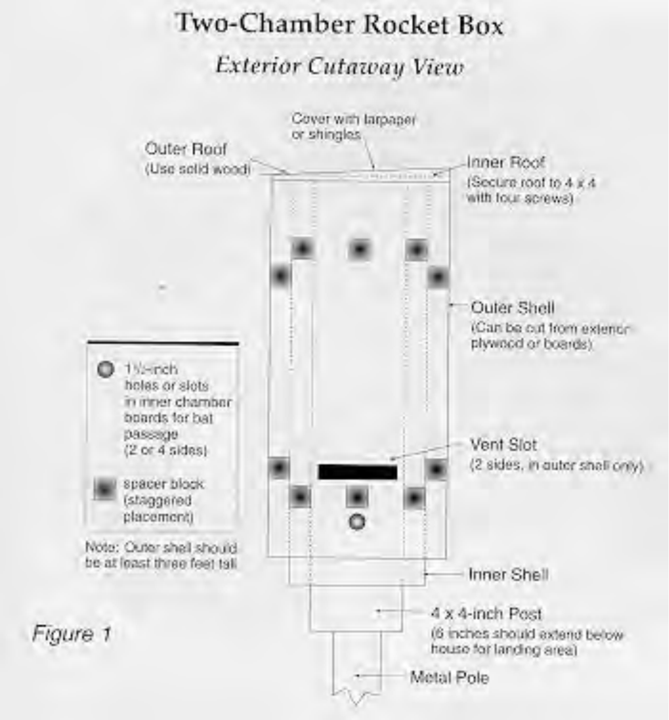


Figure 1

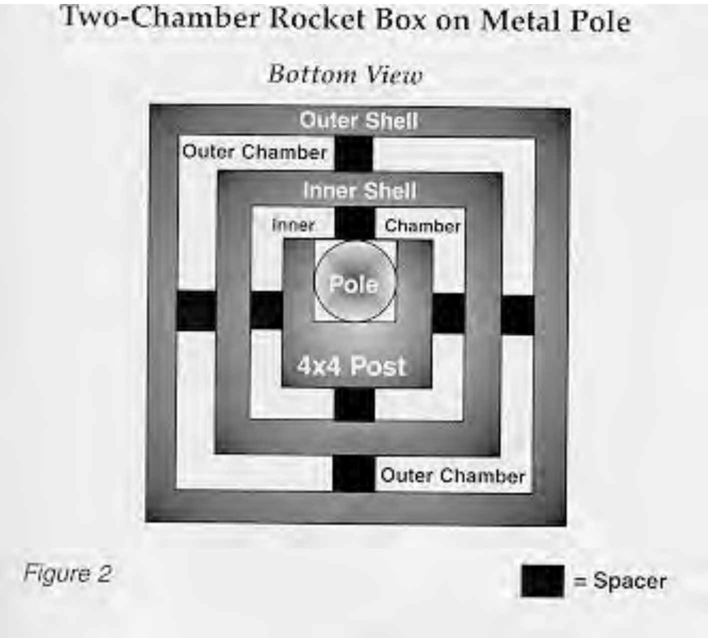


Figure 2

Creating Bat-friendly Bridges and Culverts

A Resource Publication from Bat Conservation International

There are several ways to provide bat-friendly habitat in both new and existing bridges or culverts at little or no extra cost to the tax-payer. During construction planning, it costs nothing for an engineer to specify the appropriate crevice widths of 3/4 to 1-inches (1.9-2.5cm) in expansion joints or other crevices. Retro-fitting bat-friendly habitats into existing structures can be accomplished using the following designs.

The Texas Bat-Abode, Big-eared Bat-Abode, and the Oregon Bridge Wedge bat habitats are designed to provide day-roost habitat in bridges and culverts. In the protected environment of a bridge or culvert, a properly constructed bat habitat made of quality materials will last for years.

The Texas Bat-Abode is a bridge retrofit, designed for crevice-dwelling bat species. *Image 1* depicts the basic structure with an external panel on either side, and 1 x 2-inch (2.5-5.1cm) wooden spacers sandwiched between 3/8 to 3/4-inch (1.3-1.9cm) exterior grade plywood partitionsns (recycled materials such as damaged plywood highway signs are ideal materials). Note that only the external panels need to be cut to fit the internal spaces between the beams. The internal partitions can be square or rectangular shaped and should provide crevices at least 12 inches (31cm) deep. The wooden spacers will produce crevices with the ideal width (3/4ths of an inch {1.9cm}).

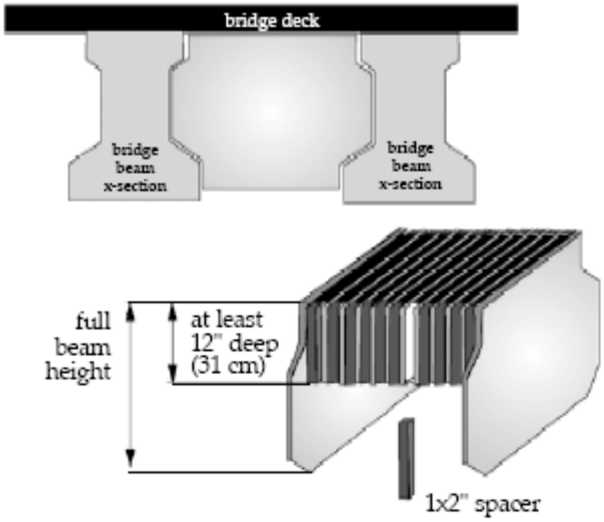


Image 1. Texas Bat-Abode for crevice-dwelling species

To provide foot-holds, at least one side of each plywood partition is roughened (preferably both), creating irregularities every 1/8-inch (0.3cm). Many methods have been used to create foot-holds, such as using rough-sided paneling, nylon screening attached with silicone caulk or rust-resistant staples, mechanically scarifying the wood with a sharp object such as a utility knife or lightly grooving the wood with a saw (do not penetrate to the first plywood glue layer), lightly sand-blasting the wood with rough-grit or by coating the panel with a thick layer of exterior polyurethane or epoxy paint sprinkled with rough grit. Rust resistant wood screws should be used to assemble the spacers and partitions.

Suitable locations for the Bat-Abode include open flight areas (no vegetation within 10 feet {3m}) that are not susceptible to flooding or vandalism and are at least 10 feet above the ground. Measurements of the exact location where the Bat-Abode is to be placed will ensure a proper fit. The number of partitions is arbitrary and limited only by availability of materials and the ability to support the weight of the structure. Because of the weight of the structure, it may be easiest to assemble the cut pieces in the bridge. In wooden bridges, anchor the unit to the structure by using heavy-duty rust-resistant lag-bolts.

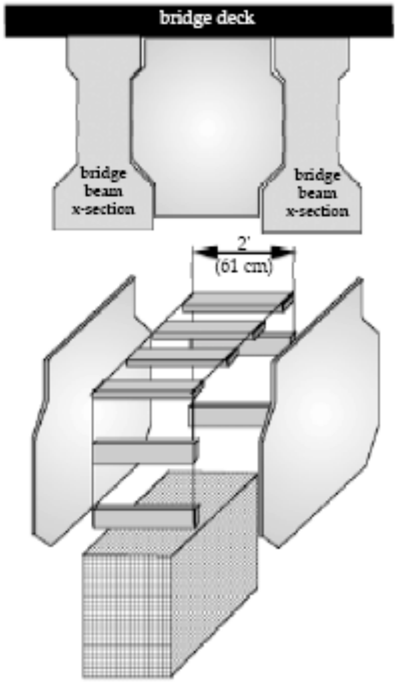


Image 2. Big-eared Bat-abode

Big-eared bats of the genus *Corynorhinus* are frequent bridge users in both the eastern and western United States. They prefer open roost areas such as the conditions created in a large hollow tree, a darkened undisturbed room in an old abandoned house, or between the darkened beams of a quiet stream-side bridge. Although untested, the Big-eared Bat-Abode design mimics these conditions and should attract these bats when properly placed.

For big-eared bats, the Texas Bat-Abode is modified with access from the bottom and spacers that are used as braces to hold the panels together. Lining the interior, nylon screening attached with staples provides foot-holds for roosting bats. (*Image 2*) Unlike crevice-dwelling bats, big-eared bats prefer low bridges with thick vegetation growing alongside. The Big-eared Bat-Abode should be placed at least 6 to 10 feet (2 to 3 m) above the ground in a secluded, vegetated portion of the bridge with care taken not to block access to the fly-way entrance.

The big-eared Bat-Abode can be partially assembled on the ground leaving one end panel off until it is placed in its chosen location. If for a wooden bridge, the unit can be anchored to the bridge using heavy duty lag-bolts. Because big-eared bats are very sensitive to disturbance, it is recommended that units be placed in areas of low activity and painted in such a manner as to avoid attracting attention.

The Oregon Bridge Wedge (*Image 3*) is an inexpensive method of retro-fitting bridges or culverts with day-roost habitat for bats. A single piece of 3/8 or 3/4-inch (1-2 cm) untreated exterior plywood or suitable recycled material (e.g.; damaged highway signs) is cut to the dimensions of at least 18-inches high by 24-inches wide (46 x 61 cm). Backed with three 1 x 2-inch (2.5 x 5 cm) wood strips along the top and sides these panels can then be epoxied to a protected part of a bridge or culvert.

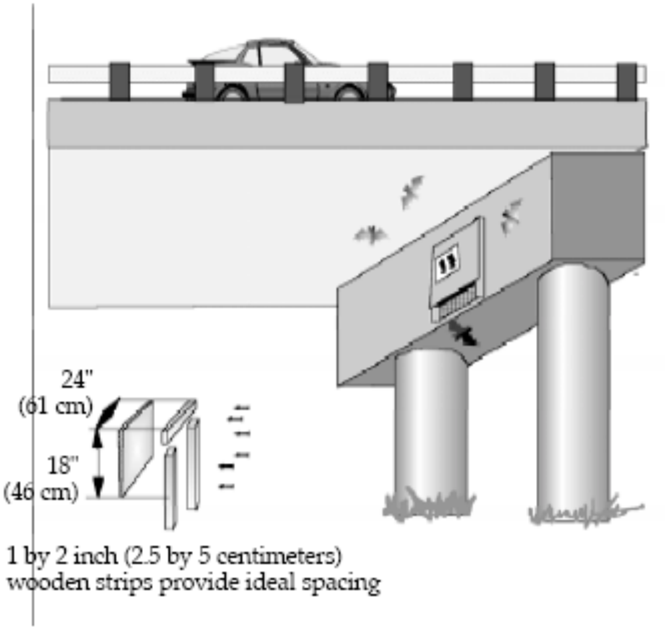


Image 3. Oregon Bridge Wedge. Designs courtesy of David Clayton and Dr. Steve Cross.

Using galvanized wood screws, attach the plywood panel to the wood strips which are cut to fit the top and sides of the panel, leaving an opening along the bottom. Larger or smaller sized panels can be used. Studies have shown that bats prefer crevices 12-inches (31 cm) or greater in depth. If larger panel sizes are used, place the vertical wooden strips every 24 inches (61cm) to support the plywood and prevent warping.

Installation of light-weight (~10 lb {4.5 kg}) Wedges can be done by applying a thick layer of fast-drying environmentally safe epoxy cement (such as 3M Scotch coat 3-12) to the 1 x 2-inch strips. When the epoxy becomes tacky (~20-30 minutes @ 60°F {16°C}) hold the panel in position until it cures enough to support the weight. ***Hint:*** Check the installation site first to make sure the support strips fit flat or nearly so against the concrete surface. Also, to avoid having to hold the entire panel in position while the epoxy cures, the largest support strip can be adhered to the preferred site prior to assembling (a thick layer of clear silicone caulk can be used here). While that piece is curing, assemble the remaining panel, coat it with epoxy and attach it to the pre-adhered strip. If the panel is to be attached to wood, then use appropriate rust resistant wood screws.

Larger sized panels can be used, but additional weight, may necessitate an increase in the support strip width (from 1 x 2-inch strips to 1 x 4 {2.5 x 10 cm} or 1 x 6-inches {2.5 x 15 cm}), thereby increasing the panel-to-bridge epoxy surface area. We also encourage experimentation with the 3/4-inch (2.5 cm) spacing. Although 3/4-inch spaces seem to provide the most versatile bat-friendly widths for North American species, larger species, such as the big brown bat, will use wider crevices. To retain the secluded feeling in the panel, the entrance should remain restricted to 3/4-inches with only the top beveled out-wards. Wedge placement is possible on any adequately sized, flat concrete or wood surface. However, it is recommended that the panels be placed nearest to the sun-warmed road slab (preferably as high as possible between heat-trapping bridge beams), at least 10 feet high (3 cm), with a clear flyway (at least 10 feet) , and out of view or reach of potential predators or vandals. Ideal bridge locations include, but are not limited to, columns, bent-caps, diaphragms, and the sides of beams. The Wedge can also be installed in the middle sections of appropriately sized culverts (> 5 feet (1.5 cm) in height). It is not recommended to place a Wedge in any structure that has the potential for flooding. As a precaution, a 1.5-inch (3.8 cm) gap can be left between where the side and top support strips join to act as an escape route in the event of fast-rising water.

The Bat-domed culvert (*Image 4*) is a modified concrete box culvert designed to provide a secluded bat-friendly "domed" ceiling. The dome has several bat-friendly characteristics; the height is increased, warm air is trapped, and the light intensity and air movement is reduced.

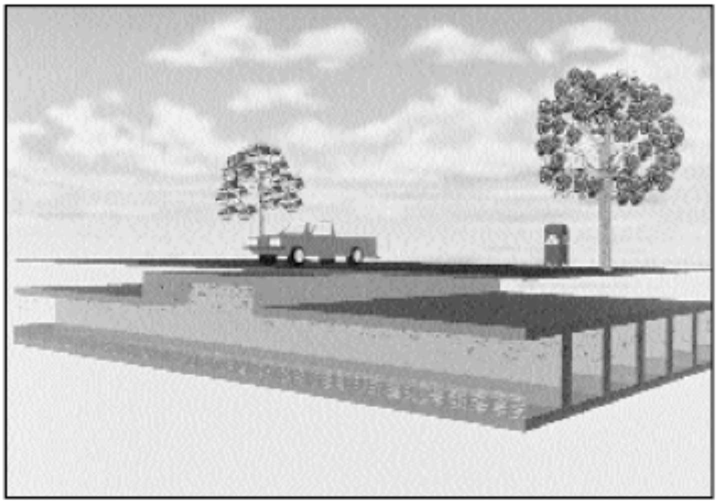


Image 4. Bat-domed culvert. Graphics courtesy of Texas Department of Transportation.

Studies of bat use of concrete culverts indicate that bats prefer long concrete culverts with roughened walls and ceilings greater than 3 feet (0.9 meters) in height. Bat-domed culverts should be constructed from concrete box culverts at least 4 feet (1.2 meters) in height with an additional 2 foot (0.6 meter) raised portion centered in the culvert with the raised area representing 1/4 of the entire length of the culvert. Bat roosts on culvert walls and ceilings are often associated with irregularities. The walls and ceilings of the domed area should be roughened to enhance the value to bats. A method of attaching panels or partitions, such as female threaded inserts, can be incorporated into the dome walls and ceiling for creating opportunities for additional surface areas once the culvert is completed.

The bat-domed culverts should not be placed in areas susceptible to flooding. Consult with the engineers to evaluate the potential for flooding. However, in the event of rising water, it is believed that the dome can serve as a temporary air-trap, preventing water from reaching the roost area for short periods.

This document is also available on the BCI webpage: http//:www.batcon.org

Artificial Roosts and Other Conservation Initiatives for Bats: On-line Resources from BCI

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Various ways to donate

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Go to "http://www.batcon.org/index.php/conservation/topics.html"

Topics Include:

Bat Houses
FAQs
Installation
BCI Certification Program
Community Roosts
Custom Roosts
The Bat House Researcher
Many ***Free Downloads!***
Critera for Successful Bat Houses
Tips for Attracting Bats
Bat House Bats
Bat Houses? Here's How!
FAQs About Bats
I've got bats in my house! Help!
Bats and Public Health
Getting Rid of Wasps
Bats and Mosquitoes
Single Chamber Bat House Plans
Installation Methods
Bat House Researcher Archives
. . . and much more!

Bats & Mines
Conservation Activities – Partial list of bats and mines conservation projects initiated by BCI over the years.
Resources – *Bats and Mines, Resource Publication* and *Bats and Mines* brochure – ***free downloads!***
Upcoming Events – listing of current bats and mines conferences, workshops, and working group activities

Bats & Wind Energy
Link to the "Bats and Wind Energy Cooperative (BWEC) site with an overview of research, products, resources, events, and featured technical and scientific publications about bats and wind energy concerns.

Bats in Bridges
Bats in American Bridges, Resource Publication – ***free download!***

Cave Conservation
Protection and Resoration information about underground environments for bats.
Resources: Field Guide to Eastern Cave Bats and Cave Conservation and Restoration

Water for Wildlife
Water for Wildlife, Resource Publication – ***free download!***
And a complete listing of the Goals and Objectives, Research and Conservation, Collaboration and Training, and Bibliography and Links for more information about bats and western water concerns.

Glossary of Scientific Names Given to Bats

After: Barbour, R.W. and W.H. Davis, 1969. *Bats of America*. University Press of Kentucky, 286 pp.

Antrozous (an-tro-**zoh**-us) – cave animal
Artibeus (ar-**tib**-ee-us) – hanging from the tibia
auriculus (a-**rick**-u-lus) – the external ear
austroriparius (**aus**-troh-rye-**pare**-ee-us) – frequenting southern stream beds
blossevillii (bloss-a-**vill**-ee-eye) – rusty furred
borealis (bor-ee-**al**-is) – of the north; northern
brasiliensis (bra-**zill**-ee-**en**-sis) – belonging to Brazil
californicus (cal-a-**forn**-a-cus) – proper name: California
Choeronycteris (**care**-o-**nick**-ter-is) – nocturnal pig
ciliolabrum (**sill**-ee-oh-**lay**-brum) – hairy lips
cinereus (sa-**near**-ee-us) -- ash-colored
Corynorhinus (core-ee-no-**rine**-us) – club-nosed
curasoae (cur-a-**soh**-ee) – proper name: Curacao
ega (**ee**-ga) – proper name: Ega
Eptesicus (ep-**tess**-a-cus) – flying
Euderma (you-**derm**-a) -- good skin
Eumops (**you**-mops) – good bat
evotis (ee-**voh**-tis) – good ear
femorosaccus (**fem**-oh-row-**sock**-us) -- sack on the thigh
fuscus (**fuss**-cuss) – brown
glaucinus (glau-**sine**-us) – silver, gray, gleaming
grisescens (gri-**sess**-sens) – beginning to gray
hesperus (**hes**-per-us) – the land west; western
humeralis (hume-er-**al**-is) – pertaining to the humerus
Idionycteris (id-ee-oh-**nick**-ter-is) – distinct or peculiar and nocturnal
intermedius (in-ter-**meed**-ee-us) – intermediate; occupying the middle
jamaicensis (ja-may-**ken**-sis) – proper name: Jamaica
keenii (keen-ee-**eye**) -- proper name: Keen
Lasionycteris (lay-zee-oh-**nick**-ter-is) – hairy and nocturnal
Lasiurus (lay-zee-**your**-us) -- hairy tail
leibii (**lee**-bee-eye) – proper name: Leib
Leptonycteris (lep-toh-**nick**-ter-is) – slender and nocturnal
lucifugus (loo-**ciff**-a-guss) – fleeing light
macrotis (ma-**crow**-tis) – large ear
Macrotus (ma-**crow**-tus) – large ear
maculatum (mac-you-**lay**-tum) – spotted
megalophylla (meg-a-low-**file**-lah) – large leaves
melanorhinus (mel-an-oh-**rye**-nus) – black nose
mexicana (mex-a-**can**-a) – proper name: Mexico
molossus (mow-**loss**-sus) – mastiff
Mormoops (more-**moops**) – monster bat
Myotis (my-**oh**-tis) – mouse ear
nivalis (ni-**val**-is) -- snowy
noctivagans (nock-**ti**-vah-**gans**) – night wandering
Nycticeius (nick-**tee**-zee-us) – night hunter
Nyctinomops (nick-**tin**-oh-mops) -- night bat
occultus (oh-**cult**-tus) – hidden, obscure
pallidus (**pal**-id-us) -- pale
perotis (per-**oh**-tis) – maimed ear
phyllotis (fye-**low**-tis) – leaf ear
Pipistrellus (pip-a-**strell**-lus) – a bat
Plecotus (pla-**coh**-tus) – twisted ear
rafinesquii (raff-a-**nesk**-kee-eye) – proper name: Rafinesque
sanborni (**san**-born-eye) – proper name: Sanborn
seminolus (**sem**-a-**nole**-us) – proper name: Seminole
septentrionalis (sep-**ten**-tree-oh-**nal**-is) – belonging to the north; northern
sodalis (so-**dal**-is) – a comrade
subflavus (sub-**flave**-us) – somewhat yellow
Tadarida (ta-**dare**-a-dah) – withered toad
thysanodes (**thigh**-sa-**noe**-dees) – with a thing like a fringe
townsendii (town-**send**-ee-eye) – proper name: Townsend
underwoodi (**un**-der-wood-eye) -- proper name: Underwood
velifer (**vel**-if-fer) – bearing a veil
volans (**voh**-lans) – flying
waterhousii (wa-ter-**house**-ee-eye) – proper name: Waterhouse
xanthinus (zan-**thigh**-nuss) – yellowish
yumanensis (**you**-ma-**nen**-sis) – belonging to Yuma (Arizona)

ACOUSTIC INVENTORY DATA SHEET

Location: ______________________________
Lat (N): ________ Long (W): ________ UTM (E): ________ UTM (N): ________
Date: ______________________ Time: ______________________

Recorder: ________ Temp: ________ Wind: ________ Sky: ________
Sunset: ________ Moon: ________ Moonrise ________ Moonset: ________

Stationary Monitoring

Habitat Description:							
Time:							
Passes:							

Stationary Monitoring

Habitat Description:							
Time:							
Passes:							

Stationary Monitoring

Habitat Description:							
Time:							
Passes:							

Walking/Driving Transect

Habitat:							
Time:							
Distance:	0.00						
Passes:							

Walking/Driving Transect

Habitat:							
Time:							
Distance:	0.00						
Passes:							

Walking/Driving Transect

Habitat:							
Time:							
Distance:	0.00						
Passes:							

Notes:

SPECIES	REPRESENTATIVE FILENAME	COMMENTS

BAT CAPTURE DATA FORM

STAFF: ____________

Location (state, county, town): ____________

Date: ____________ **Start Time:** ____________ **End Time:** ____________ **Recorder:** ____________

Lat/Long: ____________ **Start Temp:** ____________ **End Temp:** ____________ **%clouds:** ____________

Habitat:____________

Capture Technique: (# and type)
____2.6m net ____12m net
____6m net ____ Harp Trap
____9m net __________ Othe

Set Over/Near Water: YES/NO – If "yes" dimensions of Pool-size: ___W x ___L and of "swoop-zone": ___W x ___ L (*put diagram on back*)

Please use separate data-forms for net-caught vs. trap-caught bats; or otherwise indicate bats caught with different methods.

TIME		SPECIES	SEX (M/F)	AGE (J/A)	REPRODUCTIVE STATUS (M:S/NR) (F:P/L/PL/NR)	FA (MM)	EAR (MM)	WEIGHT (G)	CAP (H/N)	BAND OR MARKING (COMMENTS)
1.										
2.										
3.										
4.										
5.										
6.										
7.										
8.										
9.										
10.										
11.										
12.										
13.										
14.										
15.										

PLEASE DRAW DIAGRAM OF SET-UP ON BACK. NOTES ON BACK: YES NO **PAGE ______ OF ______**

INSTRUCTIONS FOR FILLING OUT BAT CAPTURE DATA FORMS

Fill out a single data form for each site. A “site” can be defined as a single net or trap, or a group of nets and/or traps arranged in tandem (e.g., end-to-end) or in various geometric configurations (e.g., parallel, V-formation, stacked (double-, triple-, or quad-high), etc). Bats that are “net caught” should always be specifically distinguished from those that are “trap caught,” either by recording them on separate data forms or by identifying them with a unique identifier on a single data form (e.g., “N” for net-caught bats and “T” for trap-caught bats). If a single data form is used to record bats from more than one site, then the entire set-up MUST be diagramed on the back of the sheet with each site clearly identified (e.g., A, B, C, or 1, 2, 3) AND then captures from each site clearly identified on the front of the sheet. Specific information about each line-item on the bat capture data form can be found below.

Metadata

STAFF: Each night at least one BCI staff member or wrangler will be designated to assist with a site. This person’s name should be recorded incase questions about the data crop up during analysis or reporting.

LOCATION: Include the two-letter state abbreviation first on this line then consult the STAFF to confirm the county, nearest town, and area. BCI Staff will maintain complete “locality” information for each site.

DATE: Include day, month, and year information. Print out name of month (i.e., do not use an ordinal).

START TIME/END TIME: Use “military time” (i.e., 24-hour clock), and record the time at which the set-up is complete (not the time at which the first bat is caught) as the “start time” and record the time at which nets are closed (or trap bag is removed) as the “end time.”

RECORDER: Include full name of person (people) responsible for filling out data on form.

GPS: Use provided equipment to get an exact GPS location at the net/trap (or from the middle of a complex net/trap setup).

GPS Datum: Record the “datum” used to acquire the GPS location (e.g., NAD27 (preferred), NAD83, WGS84 or specify another convention).

START TEMP/END TEMP: Record temperature both at time of set-up and take-down. Report temperatures in °C.

% CLOUDS: Estimate amount of cloud cover as follows: clear = 0%, partly cloudy <50%, mostly cloudy >50%, overcast/cloudy = 100%.

HABITAT: Describe the habitat within 150 m of the site. Include topography (riverbed, meadow, hilltop, etc.) and vegetation, indicating dominant tree/plant species.

WEATHER/WIND: Include weather data such as fog, mist, intermittent rain, steady rain, thunderstorms, snow etc., and qualify wind conditions as follows: calm (no discernable wind), breezy (leaves rustling), windy (trees swaying).

CAPTURE TECHNIQUE (# and type): Specify net or trap, include numbers of nets/traps and lengths/sizes if multiple nets/traps are used, Indicate if nets are double-, triple-, or quad-high by recording them as 2H, 3H, or 4H respectively. If unique configurations or geometric combinations are used, be sure to diagram the setup(s) on the back of the sheet, identify each set-up of more than one net, trap, or net and trap by number or letter and index each individual caught in that set-up by the same number on the front of the sheet in the **SET** column.

SET OVER/NEAR WATER (pool and swoop zone dimensions): Estimate pool size (width and length) in meters either by pacing off the dimensions or by comparing the pool size to the net length(s) used. Record the swoop zone by calculating the total size of the unimpeded approach to and from the pool.

DIAGRAM OF SET-UP ON BACK: If more than one net is used at a site, the set-up must be diagramed on the back. Multiple set-ups MUST be identified by a unique letter or number for each set-up, with corresponding captures identified for each set-up using the same identifiers on the front of the sheet.

Data Columns

TIME: Capture time for each individual should be recorded as soon as removal begins, using a 24-hour (military) clock. Capture times for trapped bats should be the same for every individual removed during a single checking effort, unless exact capture time is observed.

SET: If multiple nets are set at a single site, then each set-up (of a single net/trap or group of nets/traps) need to be identified and indexed by letter or number in a diagram on the reverse of the form. Captured bats must then be identified by set-up using the same letter or number index.

SPECIES: Species names are recorded using a 6-letter code where the first three letters represent genus and last three letters represent species (e.g., *Myotis lucifugus* = MYOLUC).

SEX: Report sex as “M” for “male” or “F” for “female” (do not use symbols). If an individual is inadvertently released before being sexed, enter “UNK” for “unknown.”

AGE: Age is reported as “A” for “adult, or “J” for juvenile and is determined by the ossification of the metacarpal-phalangeal joints (knuckle bones) in the fingers. Joints appearing bulbous, opaque, and dense indicate adults, and joints appearing elongated, translucent, and undeveloped. This is most easily observed when back-lit by a weak light (e.g., a mini Mag light).

REPRODUCTIVE STATUS: Males are identified as “scrotal” (**s** = epididymis swollen) or “non-reproductive” (**nr** = no visible evidence of reproduction). Females are identified as “pregnant” (**p** = when palpated, abdomen appears distended and skull or forearm of fetus can be discerned, a swollen abdomen without obvious fetal parts indicates a bat with hibernation or migratory fat and is considered non-reproductive), “lactating” (**l** = nipples, located in under-arm region, are obvious, swollen, and milk can be expressed when palpated), “post-lactating” (**pl** = nipples are obvious, hair around them has been rubbed off, yet they are limp and no milk can be expressed), or “non-reproductive” (**nr** = no visible evidence of reproduction).

MEASUREMENTS (FA, EAR, TR*, HF*, WT): Measurements are taken with millimeter rulers, calipers, spring-scales, or digital scales provided. Forearms (**FA**) are measured from the wrist to the elbow joint and are easiest to do on a folded wing. Ears (**EAR**) are measured from the notch at the base to the tip. Long eared bats often curl their ears back and these will have to be un-rolled along the length of the ruler for an accurate measurement (calipers are difficult to use for ear measurements). Tragus lengths (**TR**) are measured from the base to the tip. Hind foot lengths (**HF**) are measured from the ankle joint to the tips of the toes. Weights (**WT**) are easiest to obtain when bats are confined in a bag or tube (which will be provided) it is important to subtract the tare-weight of the container before reporting the actual weight of the bat. All lengths are reported in millimeters (mm) and weights are reported in grams (g). ***important only for T&E or TNW species.***

BAND/TAG/NOTES: If you are asked to permanently band or tag a bat, complete details of the band/tag must be recorded. For bands, this includes the band material (usually metal or plastic), the color, the inscription, and where the band was applied (generally males are banded on the right, females on the left). If a bat has been captured and already has a band or other form of marking, then it is identified as a “re-capture” and the same information above is recorded. If a bat is radio-tagged, then the frequency (in mHz) is recorded. This space can also be used for any other distinguishing characteristics (e.g., molt patterns, injuries, temporary markings, or unusual observations).

Other

DIAGNOSTIC PHOTO AVAILABLE: In cases of Endangered Species, certain “threatened native wildlife” (TNW), or species not known from the area (i.e., range extensions) photographic documentation might be warranted. In these cases, macro or other suitable close-up pictures should be taken of diagnostic characteristics (e.g., calcars, tragi, dentition, fur patterns, bands, etc.) along with a full-face portrait. Images must be indexed to the capture record and filed with permit reports.

NOTES ON BACK: If a diagram of the net-set up is included OR if data or any other information is recorded on the reverse of the form then it is important to indicate as such on the front. This ensures that if forms are copied in the future, information on the reverse is also included.

PAGINATION: If additional pages are needed to record all the data from a site, then they should be numbered sequentially and the total number of pages indicated in the blanks in the bottom right corner. Be sure that at least the Recorder name and the Location information is copied at the top of each additional page so the data does not become confused between sites on a given night.

Echolocation Call Characteristics of Eastern US Bats

	species	f_c	hi f	lo f	f_{maxE}	dur	uppr slp	lwr slp	slp @Fc	total slp	special characteristics
50 to 40 Myotis	*Myotis grisescens* gray bat	***45.7*** ***47*** ***44*** 41-51	***79.5*** ***91*** ***68*** 53-107	***41.8*** ***44*** ***40*** 37-46	***48.2*** ***52*** ***44*** 41-85	***7.2*** ***8.5*** ***5.8*** 2.4-10	***11.5*** ***15*** ***8.3*** 3.6-29	***2.0*** ***3.1*** ***0.9*** 0.5-12	***2.4*** ***4.2*** ***0.5*** 0.0-13	***4.8*** ***7.6*** ***2.0*** 1.3-20	Longer calls (>5ms) typically display a **strong inflection point at the knee, pronounced downward tail ending call**, and an **extended call body with broad amplituded distribution**. Shorter calls (3-5 ms) are typically at a higher frequency than other geographically overlapping Myotis.
	Myotis leebii eastern small–footed myotis	***44.3*** ***46*** ***42*** *38-48*	***95.1*** ***104*** ***86*** *55-115*	***40.6*** ***42*** ***39*** *31-44*	***49.1*** ***52*** ***46*** *40-71*	***3.2*** ***3.9*** ***2.5*** *1.7-5.3*	***33.5*** ***40*** ***27*** *6.9-48*	***9.6*** ***12*** ***7.0*** *2.5-22*	***8.9*** ***12*** ***5.5*** *0.0-28*	***16.9*** ***22*** ***12*** *4.6-36*	**FM sweep a smooth curve** (i.e., no inflection), beginning steeply and then increasing in curvature*. May have a **well defined downward tail**. **Peak power of call typically persists for at least 1 ms on non–saturated calls.** Forage close to ground or vegetation. *some calls may have an inflection, but the smoothly curved variant is diagnostic.
	Myotis austro-riparius south-eastern myotis	***43.6*** ***45*** ***42*** 38-48	***84.3*** ***95*** ***73*** 66-116	***39.6*** ***41*** ***38*** 31-44	***46.4*** ***48*** ***44*** 42-65	***4.6*** ***5.5*** ***3.8*** 2.0-6.2	***17.6*** ***22*** ***13*** 5.9-31	***6.1*** ***8.6*** ***3.6*** 1.8-14	***6.6*** ***11*** ***2.2*** 0.0-22	***9.7*** ***15*** ***4.7*** 4.0-26	**FM sweep a smooth curve** (usually no inflection), beginning steeply and then increasing in curvature*. May have a **well defined downward tail**. **Peak power of call typically persists for at least 1 ms on non–saturated calls**.
	Myotis septen-trionalis northern long-eared myotis	***43.2*** ***47*** ***40*** 32-53	***104*** ***114*** ***95*** 60-12	***37.0*** ***42*** ***32*** 25-50	***51.3*** ***62*** ***41*** 37-95	***3.9*** ***4.6*** ***3.1*** 1.7-6.6	***24.2*** ***30*** ***18*** 8.5-55	***11.7*** ***16*** ***7.4*** 3.0-36	***13.1*** ***18*** ***8.0*** 0.0-37	***18.6*** ***24*** ***14*** 6.5-43	**Calls may have up to 100 kHz of bandwidth.** FM sweep may be nearly linear making f_c difficult to recognize. Quiet but consistent calls. Fly near vegetation, often with a linear flight path when searching.
	Myotis sodalis Indiana bat	***40.8*** ***42*** ***39*** 34-47	***80.9*** ***90*** ***72*** 50-115	***37.5*** ***40*** ***35*** 25-43	***44.0*** ***47*** ***41*** 37-70	***5.8*** ***6.6*** ***5.0*** 1.9-7.8	***16.8*** ***21*** ***13*** 4.1-42	***4.6*** ***5.8*** ***3.3*** 1.0-16	***2.6*** ***4.6*** ***0.5*** 0.0-14	***7.1*** ***9.2*** ***5.1*** 2.3-23	Distinctive longer call type (>4.5 ms) may have a **secondary inflection leading into a “ledge” or flat section <1.3 ms** just prior to terminal sweep or “tail.” Note: some Mylu long calls share this feature. Distinctive shorter call type also has ending ledge, but ~5–15% of shorter Myle & Mylu also exhibit this feature.
	Myotis lucifugus little brown bat	***39.7*** ***41*** ***38*** 34-46	***69.4*** ***78*** ***61*** 47-104	***36.5*** ***38*** ***35*** 27-43	***43.4*** ***47*** ***40*** 38-73	***5.8*** ***6.7*** ***4.9*** 2.0-7.8	***10.5*** ***14*** ***6.7*** 3.0-37	***3.5*** ***4.6*** ***2.3*** 1.0-15	***4.1*** ***6.2*** ***2.0*** 0.0-17	***5.0*** ***6.7*** ***3.4*** 2.2-23	Sometimes with multiple power centers making calls look clumpy. **Longer duration calls recorded in open air are more discriminating**. **Dur >7 and Lwr slp <3 distinctive.**

Echolocation Call Characteristics of Eastern US Bats

	species	f_c	hi f	lo f	f_{maxE}	dur	uppr slp	lwr slp	slp @Fc	total slp	special characteristics
40 nonMyotiS	*Perimyotis subflavus* Tri-colored bat	***42.6*** ***44*** ***41*** 36-47	***57.6*** ***67*** ***48*** 41-106	***41.3*** ***43*** ***40*** 34-46	***43.9*** ***46*** ***42*** 36-50	***7.1*** ***8.4*** ***5.8*** 3.5-12	***7.7*** ***14*** ***1.7*** 0.3-38	***1.1*** ***1.7*** ***0.4*** 0.0-4.9	***0.2*** ***0.7*** ***-0.4*** 0.0-4.2	***2.5*** ***4.0*** ***0.9*** 0.1-12	**Strongly inflected, almost vertical FM changing to low slope below 47 kHz for the majority of the call.** Calls generally consistent across a sequence. Appear hockey stick–shaped in sonogram when FM sweep is present. Some calls exhibit "squiggles."
	Lasiurus borealis Eastern Red Bat	***40.4*** ***44*** ***37*** 29-49	***67.6*** ***81*** ***54*** 29-99	***40.2*** ***43*** ***37*** 28-48	***43.8*** ***49*** ***39*** 29-73	***6.8*** ***9.1*** ***4.6*** 3.2-16	***10.0*** ***16*** ***4.4*** 0.1-25	***2.0*** ***3.2*** ***0.7*** 0.0-10	***0.6*** ***1.6*** ***-0.4*** 0.0-8.1	***4.4*** ***7.1*** ***1.7*** 0.1-17	**U-shaped calls; up–turn at end of call; may exhibit variable f_c across sequence. Power smoothly centered in call.** Low frequency can go as low as 30 kHz.
	Lasiurus seminolus Seminole bat	***40.4*** ***44*** ***36*** 33-49	***62.8*** ***76*** ***50*** 38-87	***39.9*** ***44*** ***36*** 36-44	***42.8*** ***48*** ***37*** 35-52	***7.6*** ***9.7*** ***5.5*** 4.9-11	***7.9*** ***13*** ***3.0*** 0.7-17	***1.5*** ***2.4*** ***0.6*** 0.4-3.5	***0.4*** ***0.9*** ***-0.2*** 0.0-2.3	***3.3*** ***5.3*** ***1.3*** 0.6-8.4	**(In progress)** **U-shaped calls; up–turn at end of call; may exhibit variable f_c across sequence. Power smoothly centered in call.** Low frequency can go as low as 30 kHz. Possibly acoustically indistinguishable from *L. borealis.*
	Nycticeius humeralis Evening bat	***37.8*** ***40*** ***36*** 31-43	***63.0*** ***78*** ***48*** 35-101	***36.1*** ***38*** ***34*** 28-43	***40.0*** ***43*** ***37*** 32-48	***6.6*** ***9.4*** ***3.8*** 3.3-14	***12.5*** ***20*** ***4.7*** 0.5-32	***2.3*** ***3.7*** ***0.9*** 0.0-6.1	***1.2*** ***2.5*** ***0.0*** 0.0-6.5	***4.9*** ***7.9*** ***1.8*** 0.1-13	Sweeping curved calls that may lack any inflection. Calls have more slope in body (lower slope) than do similar-shaped shorter and longer Pisu calls. **Sequences may display f_c alternating up and down.**

How to use this table

This table presents ranges for the general characterizing call parameters of echolocation calls. The boldface numbers display the mean and ± standard deviation of the subset of calls correctly identified using SonoBat automated classification, i.e., the subset of each species call repertoire having the most species-discriminating characteristics, using the default 0.90 discriminant probability threshold. The lower, smaller font numbers display the overall range of all calls in the library of species-known calls used to prepare the SonoBat classifiers. Bold text indicates the most species–discriminating characteristics.

Because of intraspecific variablity and similarity with other species, the parameters presented here will often be insufficient for confident identification. SonoBat extracts more than five dozen parameters that it uses for call and sequence classification.

Analyze 1) well–formed calls, i.e., search phase calls recorded from bats in a steady mode of flight, away from roosts and not accelerating or performing some other maneuver that elicits rapid, short calls, e.g., like that from a hand–released bat, and 2) calls with a strong signal that clearly rise above the background noise level and have little distortion or echoes. It is generally preferable to avoid analyzing calls that saturate, i.e., overload, the detector or recorder. However, saturated call specimens may still be used to interpret time-frequency characteristics, but consider the time-amplitude domain from saturated calls to be unreliable.

Terminology and key

lo f: lowest apparent frequency (kHz), **hi f**: highest apparent frequency (kHz); this can vary depending upon the distance to the bat, f_c: characteristic frequency, i.e., the frequency of the call at its lowest slope toward the end of the call, or the lowest frequency for consistent FM sweeps (kHz), f_{maxE}: the frequency with the greatest power (kHz), **dur**: call duration from the beginning to the end of the call (ms), **upper**: the slope of the upper portion or onset of the call (kHz/ms) from the high f to the knee (listed as HiFtoKnSlope on SonoBat output), **lower**: the slope of the lower portion or body of the call (kHz/ms) from the knee to the f_c (listed as KnToFcSlope on SonoBat output).

FM: frequency modulation, i.e., a change in frequency with time, **flat**: a call or portion of a call with a very low slope or no slope (horizontal), **inflection**: a pronounced change in the slope of a call, sometimes called a "knee," **power**: the amplitude or sound energy of a call or portions of a call, **squiggle**: an S-shaped variation in frequency with time over a portion of the call.

Echolocation Call Characteristics of Eastern US Bats

	species	f_c	hi f	lo f	f_{maxE}	dur	uppr slp	lwr slp	slp @Fc	total slp	special characteristics
30	*Lasiurus intermedius* *northern yellow bat*	***28.4*** ***30*** ***27*** 33-25	***45.5*** ***53*** ***38*** 29-79	***27.9*** ***29*** ***26*** 25-32	***29.4*** ***32*** ***27*** 25-41	***10.5*** ***13*** ***8.3*** 3.7-16	***4.9*** ***7.3*** ***2.4*** 0.5-14	***0.9*** ***1.4*** ***0.4*** 0.2-2.9	***0.06*** ***0.3*** ***0.0*** 0.0-2.4	***1.9*** ***2.9*** ***0.9*** 0.3-6.0	**U-shaped calls; up–turn at end of call; may exhibit variable ƒc across sequence. Power smoothly centered in call.** Low frequency can go as low as 25 kHz. Calls similar in shape and variability to other Lasiurans, but intermediate in frequency range between Labo/Lase and Laci.
	Eptesicus fuscus big brown bat	***27.9*** ***30*** ***26*** 21-33	***49.4*** ***56*** ***42*** 29-69	***26.5*** ***28*** ***25*** 19-32	***30.0*** ***32*** ***28*** 22-42	***8.2*** ***11*** ***5.3*** 2.8-19	***5.8*** ***8.3*** ***3.3*** 0.9-17	***1.8*** ***2.9*** ***0.7*** 0.2-9.4	***1.5*** ***2.9*** ***0.1*** 0.0-8.2	***3.1*** ***4.6*** ***1.5*** 0.3-12	Variable; calls with high ƒ below 60 kHz can be confused with Lano and/or Tabr. **Calls with high ƒ above 65 kHz distinguish from Lano**, even long calls have some FM component, i.e. never flat. The end of calls may hook upward. *** Shorter calls recorded with full detail, i.e., ones that closely approached the microphone, as indicated by the presence of harmonics, exceed 65-70 kHz.**
	Lasio-nycteris noctivagans silver–haired bat	***26.6*** ***28*** ***25*** 23-31	***41.7*** ***51*** ***33*** 26-63	***25.4*** ***27*** ***24*** 14-30	***28.8*** ***31*** ***27*** 24-44	***8.9*** ***13*** ***4.8*** 2.3-24	***5.5*** ***9.3*** ***1.7*** 0.0-22	***1.3*** ***2.7*** ***0.0*** 0.0-8.8	***1.1*** ***2.6*** ***-0.5*** 0.0-8.3	***2.6*** ***4.9*** ***0.4*** 0.0-12	Shorter calls reverse J–shaped; often with a distinct inflection. Some call variants can be confused with Epfu and/or Tabr. **Flat calls ≥26 kHz diagnostic.** Flat Laci calls are lower in ƒ. Low slope calls in the 25–26 kHz range may be distinguished from Laci by the presence of an inflection. Epfu has more FM, typically with smooth curvature (no inflection). *** Shorter calls recorded with full detail, i.e., ones that closely approached the microphone, as indicated by the presence of harmonics, still do not exceed 50-55 kHz.**

Caveats: Please note that the range of characteristics listed in this table overlap among many of the species, and that although compiled from over 11,000 calls, it still represents a finite, noninclusive data set and any individual bat may emit calls beyond the typical ranges and call characteristics listed in this table (and mimic another species). This and the variability of bat echolocation calls renders acoustic classification of bats a probabilistic process and relatively inexact compared to a process like genotyping. For some species, confident species classification can only be achieved on a subset of call types within its repertoire that falls outside of data space shared with another species. As a result many recordings will have ambiguous species classification. Expect that, and seek the most species-discriminating call types on which to make species determinations.

Species classification also depends upon accurate extraction of call parameter data, and that depends upon high quality recordings having clear signals with a high signal to noise ratio and free from distortion and confounding echoes.

Echolocation Call Characteristics of Eastern US Bats

	species	f_c	hi f	lo f	f_{maxE}	dur	uppr slp	lwr slp	slp @Fc	total slp	special characteristics
20	***Corynorhinus townsendii*** **Townsend's big–eared bat**	***23.4*** ***26*** ***21*** 18-32	***42.5*** ***45*** ***40*** 36-51	***21.4*** ***23*** ***19*** 17-30	***31.1*** ***34*** ***28*** 22-41	***4.6*** ***6.3*** ***3.0*** 1.7-11	***7.1*** ***13*** ***1.2*** 0.2-70	***4.9*** ***6.6*** ***3.2*** 1.1-13	***4.2*** ***6.5*** ***1.9*** 0.0-13	***5.0*** ***6.5*** ***3.5*** 1.0-11	Low intensity, difficult to detect; harmonics often present. Call–shape **simple linear FM sweep**, (sometimes with upsweep at onset). *f*max may alternate between fundamental and second harmonic. This species sometimes applies more amplitude in the second harmonic than in the first.
	Corynorhinus rafinesquii **Rafinesque's big–eared bat**	***22.8*** ***25*** ***20*** 23-23	***39.8*** ***42*** ***37*** 40-40	***22.5*** ***25*** ***20*** 22-22	***33.2*** ***37*** ***30*** 33-33	***2.6*** ***5.1*** ***0.1*** 2.6-2.6	***6.2*** ***8.6*** ***3.7*** 6.2-6.2	***7.4*** ***8.9*** ***5.9*** 7.4-7.4	***6.7*** ***8.9*** ***4.4*** 6.7-6.7	***6.7*** ***8.1*** ***5.2*** 6.7-6.7	Low intensity, difficult to detect; harmonics often present. Call–shape **simple linear FM sweep**, (sometimes with upsweep or flat tone at onset before sweeping downward). *f*max may alternate between fundamental and second harmonic. This species sometimes applies more amplitude in the second harmonic than in the first.
	Tadarida *brasiliensis* **free–tailed bat**	***25.5*** ***28*** ***23*** 18-33	***32.3*** ***39*** ***25*** 19-61	***24.1*** ***26*** ***22*** 17-33	***28.0*** ***31*** ***25*** 18-46	***11.5*** ***14*** ***9.5*** 3.5-20	***1.6*** ***3.2*** ***0.0*** 0.0-17	***0.5*** ***0.8*** ***0.1*** 0.0-4.5	***0.4*** ***1.0*** ***-0.3*** 0.0-4.1	***0.7*** ***1.4*** ***0.0*** 0.0-4.8	Variable; FM to flat; can be confused with Epfu, Lano, or Laci. **Long calls that "turn on" power rapidly with high energy at beginning (oscillogram carrot–like).** Calls often **upswing into call and downswing** out of call.
	Lasiurus cinereus **hoary bat**	***20.1*** ***22*** ***18*** 16-32	***26.0*** ***31*** ***21*** 17-58	***19.7*** ***22*** ***18*** 16-31	***20.8*** ***23*** ***18*** 17-49	***11.0*** ***15*** ***7*** 4-26	***2.2*** ***4.1*** ***0.3*** 0.1-14	***0.4*** ***0.8*** ***0.1*** 0.0-5.7	***0.0*** ***0.2*** ***-0.1*** 0.0-4.6	***0.7*** ***1.4*** ***0.1*** 0.0-8.3	**Pronounced or subtle U–shape;** very flat calls may have slight downturn into call or upturn at end. Fully formed (i.e., good quality) calls never get completely flat like a Tabr or Lano, but out of range fragments can appear flat and mimic Tabr. The most flat calls tend to be lower in *f* than flat Lano calls. **Low *f* may vary across sequence, power builds toward center then gradually declines**. Short calls can be confused with Lano, Epfu, or Tabr.

Sources:

Characteristics gleaned from recordings acquired by J.M. Szewczak, Humboldt State University Bat Lab (and Aaron Corcoran, Jean-Paul Kennedy), T.J. Weller, USFS Redwood Sciences Lab, and Patricial C. Ormsbee, USFS Pacific Northwest Research Station, and various contibutors to the Pacific Northwest Bat Grid, and numerous other contributors.

The information presented in the table represents work in progress and is presented with the acknowledgement that it is unlikely to be the definitive description of these species' acoustic characteristics. Please use accordingly.

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