

## Chiropteran Mortality

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### INTRODUCTION

The study of chiropteran mortality is a difficult one because observations concerning mass mortality, predation, and fatal accidents are sporadic and unexpected. Almost every known predaceous animal preys on bats from time to time; but (with one or two rare exceptions) do so only when an occasional opportunity presents itself, and do not specialize in bat predation.

Our knowledge of bat pathology is meager. Mass-mortalities have been reported only from sight observations, and the causative organisms rarely ascertained, because of the unexpected encounter. The relationships between human and chiropteran diseases are becoming much better understood; this study is mostly oriented toward man, and not toward the cause and effect of disease in the chiroptera.

The longevity of certain bats is known to range between 15 and 20 years; but their unique activities make them rather prone to accident. They become impaled on such sharp objects as barbed wire, and locust, burdock, and cactus spines. They fall into water holes and drown, get entrapped in tar pits, get electrocuted on high-power lines, etc., but remain among the most abundant mammals on earth today.

We have attempted to assemble the literature on all known causes of mortality in bats but cannot, of course, cite all noted occurrences.

### MAMMAL PREDATORS

The Common opossum, *Didelphis marsupialis*, is known to include bats in its diet when such are available (Campbell, 1925 and Rice, 1957). Like most other mammalian predators, however, the opossum is probably merely opportunistic, and does not actively seek bats as prey. Capture of live bats by opossum, when they catch any live ones at all, is probably limited to sick individuals, and to bats disabled by accident or weather conditions.

Several mustelids are known predators (Table 1). Hog-nosed skunks, *Conepatus conepatus*, and striped skunks, *Mephitis mephitis*, occasionally prey on free-tailed bats in the Ney Cave of Texas (Constantine, 1948). Since neither are good climbers, it is reasonable to assume that they capture bats that fall from their roost. Mumsford (1969) reported the deliberate attack by a long-tailed weasel, *Mustela frenata*, on a big brown bat (*Eptesicus fuscus*) nursery housed in the rafters of a barn. The weasel killed several adult female bats and their attached young as

the owner looked on and tried unsuccessfully to chase it away. Finally the owner shot the efficient little predator.

Hall (1946) ascertained predation on young *Myotis yumanensis* fallen from the ceiling nursery by a bobcat, *Lynx rufus*. Evidence of this was gained from the presence of the lynx's footprints deep in the cave, and from the remains of the bats in bobcat scats near the cave's entrance. Feral cats, *Felis catus*, have also been known to capture young bats which had fallen to the floor, and then to wait deliberately for the mother as she came to the rescue (Campbell, 1925).

Bat predation is restricted to the birth and nursery season for a number of mammals. Civet cats, *Genetta*, are known to visit bat caves for only a short period during this season (Campbell, 1925 and Rosevear, 1965). The same habit of seasonal predation is known for raccoons, *Procyon lotor* (Campbell, 1925 and Cockrum, 1952), and for dogs (Dwyer, 1962). Taylor (1954) found that ring-tailed cats, *Bassariscus astutus*, regularly include in their diet a small percentage of red bats, *Lasiurus borealis*.

The taking of bats is almost universal among rodents when the opportunity is presented. Squirrels and smaller rodents commonly feed on bats which have fallen to the snow from their hibernacula (Ryberg, 1947). Unlike most carnivores, not all cases of rodent predation are necessarily restricted to accidental falling of bats from their roosts. The pack rat, *Neotoma micropus*, has been known to go to the attack upon seeing bats alight in a crevice (Cockrum, 1952). *Pipistrellus subflavus* remains have been found with the skin turned inside out in typical rodent fashion (Martin, 1961). Since pipistrels hang low on cave walls, this may be a true case of rodent predation. Martin (*op. cit.*) also reported finding a dead prairie vole, *Microtus ochrogaster*, apparently suffocated, with a portion of a *Myotis* wing protruding from its mouth. Other predator-prey combinations include *Rattus rattus* on *Mystacina* (Dwyer, 1962), and *Peromyscus leucopus* on *Myotis* (Hitchcock, 1965).

Ryberg (1947) claimed that predation by opportunistic shrews occurred when bats flew from sun-heated hibernacula into subzero air, and fell to the ground, apparently "cold-shocked" (discussed under Accidents).

Omnivorous baboons find bats easy prey and readily feed on them where they frequent the same rocky areas (Rosevear, 1965).

Man is by far the most efficient predator of bats. In Africa and south-eastern Asia they are taken for food. Locally, the flesh of certain Old World fruit bats is so relished by natives that they are captured and sold in markets (Walker, 1968; Ogilvie & Ogilvie, 1964). In some

areas the fat of fruit bats is considered effective treatment for rheumatism and baldness (Walker, *op. cit.*).

Students of Chiroptera account for a significant annual loss of individuals. Mist nets take by far the greatest toll; but shooting is not uncommon. In some areas bat-shoots are considered a challenging sport, since the darting path of a bat's flight is difficult to follow. Several occurrences of accidental trapping have been reported, but since these were not cases of deliberate predation, they are discussed in the Accidents section.

Man's fear of bats and their diseases locally justifies wanton destruction wherever they are found in large numbers. Cockrum (1952) felt that needless and foolish destruction of bats was common and should be outlawed. Phillips (1966) reported that at Leavenworth, Kansas, fires were deliberately set to rid local caves of large colonies, which not only killed bats but also left the roosts unfit for habitation. To cite the cruelty of fire he described a bat with a severely burned tongue, all the hair burned from its head and shoulders, its ears and forearms crisp from the flames, and its teeth charred to mere nubs.

Another method man uses to rid himself of bats is through the deliberate destruction of flyways by removal of adjacent vegetation. Still another is the use of the hard, round, light-weight seeds of shack-shack, *Leucaena glauca*, in 0.410 cartridge loads, effective on vampires feeding on poultry, without damaging the livestock (Greenhall, 1963).

Strychnine poisoning has also been found to be effective on vampires. A drop or two is placed on a previous wound of the plagued animal, and when the vampire returns for a second meal the next night, it dies within 2 or 3 seconds upon licking the poisoned wound (Greenhall, *op. cit.*). Banana-plantation owners also use strychnine to kill *Carollia*, *Artibeus*, and other frugivorous bats. The poison is injected into the bunch of fruit, and when the bats come to feed on the fruit they are killed instantly.

Among bats the false vampire of India (*Lyroderma*), its relative, *Macroderma* of Australia, *Phyllostomus*, *Vampyrus*, and *Megaderma* of the American tropics are considered natural enemies of bats (Allen, 1939). These appear to be the only mammals that actively prey on bats in nature. It is not uncommon, however, for a number of insectivorous genera in captivity to prey on smaller or weaker bats, or even resort to cannibalism. Ditmars (1935) reported that after a helper placed a *Phyllostomus* in a cage with a mother *Artibeus* and her young all that could be found was a claw of the mother. Other genera reported to prey on weaker bats when in captivity are: *Myotis* (Ryberg, 1947); *Lasiurus*, (Wimsatt, 1959); *Eptesicus*, (Engler, 1943; Krutzsch, 1950).

*Hipposideros* and *Scotophylus* may be considered occasional predators of other bats. The false vampires, megadermatids, and some phyllostomatids often prey more consistently on smaller and weaker bats in nature, and almost any insectivorous bats are potentially dangerous to other bats when stressed by captivity. Cannibalism is unknown outside of captivity.

A list of mammal predators is provided in Table 1.

#### BIRDS

Owls, hawks and falcons are the most common bird predators on bats. Of the 43 instances listed in Table 2, fully half include just five genera, *Falco* (7), *Buteo* (3), *Accipiter* (3), *Bubo* (4), and *Tyto* (6). It is probable that all hawks and owls prey on bats where the predators' roosts are close to large colonies. Falcons appear to prey on bats in aggregation on emergence or on return to the roost (Ryberg, 1947 and James, 1963); or on stray bats flying in full daylight (Wright, 1932 and Orr, 1954).

Sparrow hawks (*Falco sparverius*), duck hawks (*Falco peregrinus*), and the European Kestrel (*Falco tinnunculus*) are the most common predators among falcons.

The diurnal habits of hawks and falcons indicate that they prey on wandering or lost chiroptera which are late in returning to the roost, or are unable to find a roost during migration. Several authors report groups of hawks or falcons working together in a small area with devastating effectiveness on emerging or returning colonies. Stager (1948) gives a vivid description of a group of six duck hawks which habitually met a large colony of Mexican free-tailed bats, *Tadarida mexicana*, on both their evening emergence and morning return. Although none of the hawks was captured, it appears likely that they were at the time feeding almost exclusively on the bats, for they had learned the colony's habits; and their methodical predation was certainly more than just happenstance.

Another interesting aggregation is reported by Taylor (1964), who described predation on *Tadarida brasiliensis* by a group of fifteen Mississippi kites, *Ictinia mississippiensis*. On the return to their roost in the early morning the large colony of tadarids (perhaps numbering a million or more) was attacked repeatedly by the kites. Like the peregrine falcons, the Mississippi kites found the bats easy prey. In both instances the behavior of the *Tadarida* colony in flight did not seem to be affected at all, as if the bats were not aware that they were in danger, and they made no effort to avoid the predators.

The bat-buzzard, *Machaerhamphus andersonii*, a dark-colored cre-

puscular hawk generally distributed over most of Africa, is a constant predator, as the common name attests. When they live in the proximity of caves, bat buzzards perch just outside the entrance, and as a bat appears, the hawks swoop down to seize their prey in their talons; after crushing the victim, the bat is swallowed whole (Rosevear, 1965 and Verschuren, 1957).

Owls, with their crepuscular and nocturnal habits, prey regularly on bats for a good percentage of their food. Predation by only two genera, *Tyto* and *Bubo*, the barn owls and the horned owls, constitutes more than a fourth of the reported instances (Table II). Bat remains are also common in owl pellets; the eight genera listed in Table II are probably but a fraction of the prey. That owls are nocturnal feeders probably explains their high frequency as predators. Rosevear (1965) reports that *Tyto* not only takes bats in flight, but occasionally lives near roosts where it can dive and take bats at its leisure.

The mechanism of capture among raptorial birds presents an interesting study in resourcefulness. Twente (1954) describes predatory chasing by a barn owl, *Tyto alba*, after a Mexican free-tailed bat, *Tadarida mexicana*, near the bat's roost in a cave. The owl soared about twenty feet over the emerging column and went into a stall with its head up and wings spread, falling into the flight pathway of its prey. Several hit the owl's wings and breast, and in each of five consecutive instances, a bat was picked off as it hit the owl's body. Similar capture is reported by Rosevear (1965) for *Tyto*, and by Macy (1939) for *Buteo jamaicensis* (= *borealis*), the red-tailed hawk, preying on *Tadarida mexicana*.

Screech owls, *Otus asio*, prey heavily on the big brown bat, *Eptesicus fuscus*, during the winter in Minnesota, probably securing their prey while the bats hang dormant on the wall of their hibernaculum. These bats commonly hibernate in the open near the mouth of a cave, leaving them vulnerable to owl predation (Beer, 1953).

The New Zealand morepork, *Spiloglaux novae-zealandiae*, a strictly nocturnal owl, has been frequently observed to prey on bats (Dwyer, 1962).

Of the remaining reports of avian predation, at least two are related to territorial defense. In both instances a bat was seen intruding a daytime territory, and several defenders attacked the bat in common pursuit. Swallows have been observed chasing bats in broad daylight (Ryberg, 1947). Similarly, several redwing blackbirds, *Agelaius phoeniceus*, along with a single common grackle, *Quiscalus quisquala*, were observed chasing a little brown bat, *Myotis lucifugus*, into the water over their territory. This observation even suggested that territorial defense by the blackbirds might be a limiting factor in the daytime

activity of the little brown bat in overlapping habitats (Miller, 1962).

Other records of bird predation include bluejays, *Cyanocitta cristata*, on red bats, *Lasiurus borealis* (Allan, 1947 and Elwell, 1962); a single record of a crow (*Corvus*) with bat remains in its stomach contents (Rosevear, 1965); a Brewer's blackbird, *Euphagus cyanocephalus*, on a pallid bat, *Antrozous pallidus* (Orr, 1954); a roadrunner *Geococcyx californianus* on a red bat (Wilkes and Laughlin, 1961); and two European black-headed gulls, *Larus ridibundus*, chasing a common bat, *Vesperugo pipistrellus* (= *Pipistrellus pipistrellus*), although the gulls were unsuccessful (Paterson, 1927). In addition Ryberg (1947) lists titmice as potential predators on cold-shocked bats.

#### REPTILES

Like birds, reptiles are occasionally more than merely opportunistic predators on bats. Although snake predation is commonly known, only sixteen cases have been reported (Table 3), and ten belong to the genus *Elaphe*, the rat snakes, the corn snakes and the chicken snakes.

Snakes of the genus *Elaphe* are excellent climbers, and are often active at night, seeking out small animals for food. Hamilton (1943) credits to a single pilot black snake, *Elaphe obsoleta*, the complete eradication of a colony of *Eptesicus* sp. where the snake had taken up residence in the eaves of a house and fed on bats as they came close enough to be caught.

That rat snakes are extremely heavy predators has been acknowledged by several authors. Rice (1957) even claims that *Elaphe obsoleta* and *Elaphe guttata* are the single most important predators on *Myotis austroriparius* in Florida. Campbell (1925) once killed a chicken snake that had fourteen bats in its stomach.

One reason for the effectiveness of *Elaphe* might well be their ability to locate prey in total darkness, allowing them to seek out actively their prey within a cave. Mankins (1965) reports that a rat snake, *E. triaspis*, was found killing a long-tongued bat, *Glossophaga soricina* by constriction in total darkness in a cave in Honduras. Mankins' is the only report of a snake taking prey in the complete absence of light.

Similarly, another colubrid, *Coluber taeniatus* of the eastern tropics, reportedly takes a heavy toll from caves. This snake has become troglodyte, so that it tends to be pallid-colored, like other cave-haunting vertebrates (Allen, 1939). By deduction, this snake is likely to take its prey in total darkness, like the rat snake, *Elaphe triaspis* mentioned above.

There are but few reports of poisonous reptiles which regularly take bats, although two are known to feed heavily on certain species.

Loveridge (1923) describes the capture of a big-eared orange-winged bat, *Lavia frons*, by a black mamba. The mamba occasionally climbs trees, often in the same area where *Lavia* hangs in its daytime retreat. When approached, these bats betray themselves by constantly moving their long sensitive ears. Such motion is easily detected by a mamba, whereupon it can easily glide to within striking distance. The *Dendraspis* is a deadly poisonous elapid, and except for the mildly toxic lyre snake of North America, is the only poisonous serpent reported to kill bats for food.

The California lyre snake, *Trimorphodon vandenburghi*, is known to feed on *Tadarida* and *Myotis* where these bats frequent the lyre snake's rocky habitat. Killing is probably augmented, especially in quarters too close for constriction, by their mild poison from the grooved rear-fanged teeth of the upper jaw (Krutzsch, 1944 and Stager, 1942).

The only other known snake predator is the Cuban boa, *Epicrates angulifer*, which feeds near cave entrances, and probably strikes at bats, knocking them down as they fly through small openings on emergence in the evening. Killing is by constriction (Hardy, 1957).

Only one instance of lizard predation has been reported. It is not likely that lizards are common predators; the only known predator on bats is *Boiga blandingi*, the Amaga lizard of West Africa. One such was found to have taken eight bats (Rosevear, 1965).

#### FISHES AND AMPHIBIANS

The only known amphibian predators are frogs of the genus *Rana* (Table 4). Holman (1956) was the first to anticipate that cave-dwelling ranids might occasionally feed on young myotids which had fallen to the floor in a cave in central Florida. *Rana pipiens*, the North American leopard frog, and *Rana esculenta* in Europe have been observed killing bats (Kinsey, 1961 and Brosset, 1966).

Kinsey discovered a leopard frog in the act of killing a small *Myotis* when he went to investigate the bat's distress cries. First the frog had a hold on the bat's rump, but the bat escaped, although it did not fly away. The frog attacked again, taking the bat head first. Immediately the frog tried to swallow the bat whole, but it was too big to swallow completely. Later, Kinsey secured the frog, its victim apparently having been suffocated.

Another leopard frog was observed with an evening bat, *Pipistrellus subflavus* (Figure 1-B) in its mouth (Creel, 1963).

But two fishes are recorded as bat predators (Table 5). Ingles (1947) lists rainbow trout, *Salmo gairdneri*, as occasional predators on California bats.

One interesting episode occurred when several men were seining fish in a cave in Texas. When the men passed under a colony of Mexican free-tailed bats, *Tadarida mexicana*, roosting on the ceiling, the bats became disturbed and several fell into the water. On lifting the seine, the men found that a green sunfish, *Lepomis cyanellus*, had captured and swallowed one of the bats, with a wing fluttering and still protruding from the fish's mouth. In this instance, all the animals in the cave, except for the bats, had been trapped there for several months because of drought conditions, so sunfish predation may not be a common phenomenon at all (Jones & Hettler, 1959).

#### INVERTEBRATE PREDATORS ON BATS

Five invertebrates are listed as potential predators on bats, although only the driver ants and cockroaches are known to kill bats for food (Table 5).

American cockroaches (*Periplaneta americanus*) and introduced Australian cockroaches (*P. australasiae*) are said to be second only to the rat snake as important predators of *Myotis austroriparius* in Florida (Rice, 1957). Although the cave-dwelling cockroaches are mostly scavengers, they take a heavy toll of young bats which have fallen to the floor.

Coudenhove (1925), in describing life in Nyassaland, describes raids of the dreaded driver ants (locally known as "Bambesi") upon a colony of bats that lived between the ceiling structures in his house. The armies of ants would climb up posts on the veranda or they would fall from trees and swarm over the bats in their daytime retreat. Young bats were the most common prey. Eventually both Coudenhove and the bats abandoned the house.

Large spiders in the tropics are also potential predators. Bats are sometimes found caught in their large, strong webs, and perish from the entrapment. Once caught, they are vulnerable to attacks from spiders, and it is not unlikely that they are occasional prey. *Heteropoda venatoria*, a big house-spider, was seen to catch a *Pipistrellus* sp. and kill it (Bhattacharya, 1941). The only visible injury was around the neck area where the spider with its strong mandibles had a death grip on the small bat. The bat was not devoured.

Although no specific instances have been reported, Orr (1954) includes scorpions as potential enemies of bats, since their poison is effective on most mammals.

#### DISEASE FACTORS IN BAT MORTALITY

Our knowledge of the role of disease in bat mortality is rather limited. There have been reports of mass mortality; but in most cases no definite



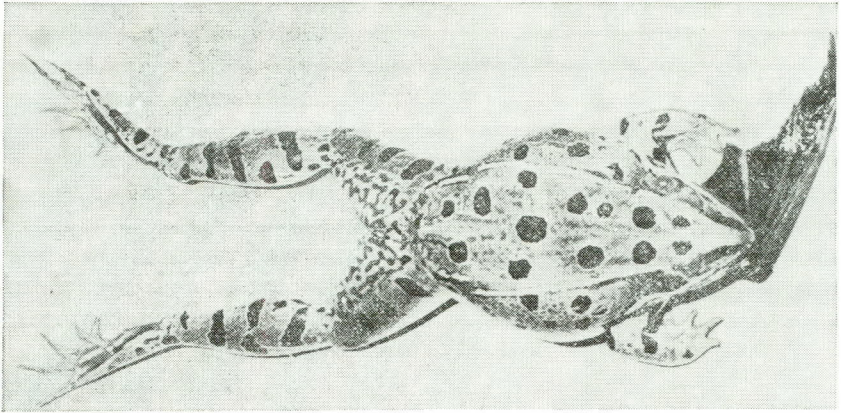


FIG. 1. Leopard frog, *Rana pipiens*, with a pipistrel bat, *Pipistrellus subflavus*, projecting from its mouth (after Creel, 1963).

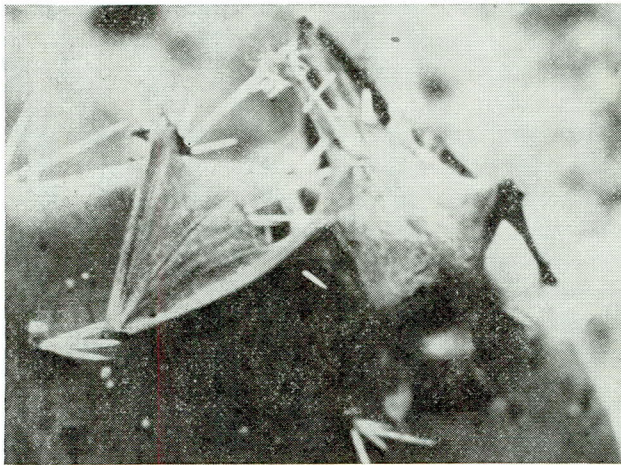


FIG. 2. Mexican free-tailed bat, *Tadarida mexicana*, caught on a prickly-pear cactus (photograph by Pete Lindsley).

reasons are proposed for the deaths. Booth (1965) observed thousands of moribund and dead free-tailed bats (*Tadarida* sp.) in a Mexican cave; but due to the lack of facilities was unable to determine the cause of death. Villa (1955) recorded a large die-off of *Mormoops megaphylla* in northern Mexico, but could not determine the exact cause of death. He suggested that some epidemic virus had spread among the bats, and urged that the causative organism should be deter-

mined in similar situations, in view of the possible importance of such viruses to the economy and health of man.

The protozoan, *Trypanosoma hippicum* is fatal to both host (horses) and vectors, and is one disease known to take a toll of bats. According to Dunn (1932) the vampire bat (*Desmodus*) and some insectivorous bats are vectors for *T. hippicum*. Because of the short and fatal course of the disease, Dunn suggested that insectivorous bats were probably not the most important vectors. *Desmodus* is believed to be the more successful vector, since it lives longer with trypanosomes and readily bites horses and men. *T. hippicum* is morphologically similar to *T. cruzi*, the cause of Chagas' disease in man. This latter species is discussed by Ubelaker (this volume).

Helminths are commonly encountered in bats, but have not been demonstrated as the cause of death. Most helminths that occur in habitats such as the intestine probably have little ill-effect on their hosts. Some larval nematodes, however, occur in the body cavity or in the tissue of the host, and probably contribute to the death of some bats. Additional relationships are discussed by Ubelaker (this volume).

The most important fatal disease of bats is rabies, which is of considerable concern to man. Constantine (1967) describes periods of mass mortality in Carlsbad Caverns and the symptomatic lapse due to rabies. The bats fell to the cave floor doubled up, feet crossed. They grasped their abdomen and sometimes bit their feet during their frenzy. Most of the bats died in the doubled-up position with wings folded and digits extended. The seizure was similar to that of an epileptic fit in man, with death following the cessation of abdominal muscular contractions.

Pawan inoculated *Desmodus* and *Artibeus* with negri-bodies, and found death to occur from nine days to five months later. *Desmodus* was apparently the more tolerant of the two. Courter (1954) confirmed Pawan's findings and demonstrated that *Desmodus* could remain alive and pass infective organisms to 5½ months; while death occurred in *Artibeus* usually within 130 days. Courter also identified six forms of rabies in *Desmodus*: (1) The classical furious rabies in which fury is prominent and is followed by paralysis and death; (2) The typical paralytic form typified by no fury of excitement but paralysis eventually resulting in death; (3) A furious form of rabies predominant with fury but followed by recovery; (4) A furious type which proceeds to death without paralysis; (5) A form found in *Desmodus*, in which death suddenly occurs without previous evidence of illness; and (6) A sub-clinical, or latent, form of infection in which the bat continued to live without any apparent departure from normal, but remained infectious.

Although rabies is often fatal to *Artibeus planirostris*, they have also been observed to survive without ill effects (Malaga-alaba, 1954). The reasons for the extreme variation in the effects of rabies on bats remains ill-understood. Research headway is being made (see Sulkin & Allen, this volume) but occurrences of mass mortality, well studied, are desperately needed.

#### ACCIDENTS

Accidental death is probably the most neglected aspect in mortality-rate and longevity-studies for bats. Although most of the accidents discussed are cases involving single individuals or small groups, several reports indicate that entire colonies are vulnerable to accidental death. This may be especially due to accidents related to climatic factors. Man's presence has certainly rendered bats more prone to accidental injury; for example, barbed wire fences and electric power lines are responsible for a small, though significant toll.

*Adverse climatic conditions.*—In temperate regions, winter severity and duration of cold weather are often the most important factors controlling population-size. Although information is scanty, there is probably a close correlation between number of young and juvenile survival.

Except for some early claims that aged individuals are the most severely affected by winter hibernation, most authors agree that juvenile mortality during a generation's first winter is the single most important mortality factor. Davis (1966) found that in a *Pipistrellus subflavus* population "the high loss of bats between their first hibernating season and their second is most likely due to a failure to survive the winter and not to mortality during the bat's second summer" as he had earlier concluded (Davis, 1957). Similar conclusions can probably be drawn for most populations of bats, since young individuals are not as well primed as are adults for hibernation.

Extensive observations relating mass mortality to climatic factors in Scandinavia indicate that bats hibernating in trees are especially vulnerable to low temperatures. Mass-mortality results when the bats freeze to death in their arboreal hibernacula, and local extermination is often the result. Even when extremely low temperatures occur only a few times in a century, the toll is severe enough to have long-term effects on population size (Ryberg, 1947). Bats enter hibernation heavily laden with fat. Young bats, because they go into hibernation later and start with considerably less stored fat, are particularly susceptible to winter starvation. When a winter is exceptionally long, severe mortality is often the result.

Even in cave hibernacula winter severity is an important factor. A colony of 500–800 cave-dwelling *Myotis* in Vermont was nearly wiped

out by extreme cold. In the chamber where the bats preferred to roost a large entrance and good air circulation resulted in "the formation of huge icicles from seepage water on the walls, room and floor of the cave." The population was reduced to less than fifty by death and emigration (Griffin, 1945).

Surprisingly, some Chiroptera are especially vulnerable to direct exposure to cold. Especially in regions which are not often subject to freezing temperatures, bats resting in unsheltered roosts are likely to be adversely affected by rare cold spells. A hoary bat, *Nycteris cinerea* (= *Lasiurus cinereus*), was found frozen to death while clinging to a stone wall (Gregg, 1937). Ryberg (1947) is the only author to report the phenomenon which we have called "cold shock" already mentioned in the mammal- and bird-predators sections. He acknowledges that awakening from hibernation is a most critical time in a bat's life. When awakening is not correlated with the actual end of cold weather, but rather with short-term warm spells, a bat is likely to find unfavorable conditions. Such occurrences are common for bats wintering in unprotected hibernacula (as in trees, behind shutters, between surface cracks in rocks, etc.). A hibernaculum unprotected from heating can be warmed considerably by direct sunlight, even when the air temperature is well below freezing. A bat awakened under these circumstances is prone to fly out into the cold air, and if still weak from hibernating, the shock of the rapid temperature-change is too much for the bat to endure, and it will fall into the snow, unable to return to the roost. This is "cold shock" and resulting death is not uncommon. Ryberg's evidence shows that bats so affected are often attacked by titmice and other small birds, small rodents, squirrels and shrews even before freezing to death in the snow, as indicated by breast and abdominal peck wounds beneath undamaged wings. Instances of death from cold shock are cited for *Pipistrellus pipistrellus* and for *Nycterobius noctula*.

More than one hundred big brown bats, *Eptesicus fuscus*, were caught by a severe early November snowstorm in Minnesota, and the result was catastrophic. High drifts caught the bats away from their hibernaculum and the entrance to their preferred cave was snowed shut. Although several other caves in the area remained open, the entire colony continued to seek entrance to their favorite cavern; they eventually fell to the ground exhausted, and all died in the snow (Rysgard, 1941).

Thus, excessive exposure, even within roosting caves, and exhaustion, are high-ranking causes of death. Low temperature, as already discussed, is the most common stress factor. Constantine (1967) adds good air circulation in caves as another important cause of stress. Where there

is considerable renewal of the air, which adds to the heat loss by convection and evaporation, the ambient temperature is likely to be lowered. When an already exhausted bat returns to a cold roost, chances of survival are considerably lowered.

Rain and wind are also important. For example, when bats at Carlsbad Caverns were caught in a heavy rain, they returned to their cave completely soaked, and many died (Constantine, 1967). Bats normally avoid flying in heavy rainfall. Although no one has suggested the possibility, there must certainly be an adverse effect on local populations in areas which occasionally experience torrential rainfall. During hurricanes, other unusual or unseasonal climatic changes occur; the obvious effect doubtless would be destruction of normal survival. Likewise, in arid regions where occasional storms might last for several days, local populations which are accustomed to daily feedings are likely to find even a short fast unfavorable. Like cold weather in temperate regions, tropical storms in lower latitudes and occasional, though infrequent, heavy rainfall in arid areas are possible factors controlling local population size.

In Uganda, Africa, giant fruit-eating bats, *Eidolon helvum*, are commonly picked up from the ground during heavy thunderstorms and are locally sold for food. The bats probably fall from their arboreal roosts when they become water-soaked or when high winds blow them out of the trees. On one occasion a candle nut tree was split, apparently from high winds, and twelve bats were killed or maimed by the accident (Ogilvie & Ogilvie, 1964).

Stress during migration is another common mortality factor. Constantine (1967) found that excessive flight exercise in *Tadarida mexicana*, when compounded with cooler roosts, often causes them to become moribund and die. Major changes in aggregation numbers, correlated with increased disorder in the roosts, are often associated with increased mortality in the Carlsbad bats. One of Constantine's passages warrants quoting:

As bat mortality at the cavern became noticeable, railroad bridges were replaced throughout New Mexico that had not been replaced for about a hundred years. The new bridges were not suitable as bat roosts, and they were freshly creosoted . . . Very few bats took shelter in them. The replacement of bridges eliminated numerous stop-over sites for migrating bats and displaced the resident bat populations that probably were necessary to guide migrants to local roosts, disrupting the established migration routes and procedures. The bats would have to find substitute shelters, frequently unavailable in the plains, and suffer exposure to the weather, mortality being greatest in bad weather. This would explain why great numbers of bat deaths had not been observed previously at the cavern.

Thus, even mildly unfavorable climatic conditions, when coupled with exacerbating circumstances, can have a severe effect.

Circumstantial evidence in two instances has mass-drowning as an additional cause of death. Hall (1963) believed that flooding completely eradicated a colony of perhaps 300,000 Indiana bats, *Myotis sodalis*, in Bat Cave, Kentucky. Jegla (1963) likewise blamed apparent drowning as the cause of death for several hundred little brown bats, *Myotis lucifugus*, in a dome-pit in Mammoth Cave, also in Kentucky. Curiously, the concentrated accumulations of skeletons beneath roosts were the primary evidence. With all due respect to Hall and Jegla, we are wondering if these deposits might as well be accounted for by long-term accumulation. The remarkable Pleistocene Reddick Cave vertebrate fauna in Florida contains literally thousands of bones in a cubic foot of deposit, many of which are bat bones (Gillette, personal observation). This deposit supposedly represents the continuous accumulation common in many caves, with running water carrying bones to quiet pools, where the resultant mass is aptly called "bone breccia" by paleontologists.

About forty Mexican free-tailed bats, *Tadarida mexicana*, were found embedded and frozen to death in a trout-line reservoir in the Colorado Desert (Campbell, 1931). In addition there were caught on separate fish hooks a California mastiff bat, *Eumops perotis*, another *Tadarida*, and a horned owl (*Bubo*), all caught by the wings. They had all probably come to drink in the evening and were caught in the surface slush that had been formed by the heat of the daytime sun.

*Natural accidents.*—Reports of natural accidents not related to weather conditions are few. The most common phenomenon is heavy loss of young, which fall to the floor of the cave and there perish from either starvation or by predation. There seems to be little consistency among authors concerning rescue-behavior of mother bats which have lost their young, but most agree that the death toll is considerable. Specific instances of death from falling from the mother are known for the lump-nosed bat, *Corynorhinus rafinesquei*; Tennessee brown bats, *Myotis grisescens*; and Indiana bats, *Myotis sodalis* (Mohr, 1933 and Hamilton, 1943).

That mass-drowning as a result of flooding in caves is a possible mortality factor was discussed above. On at least one additional occasion, drowning is known to have caused many deaths in a single colony. Unlike the accounts previously mentioned, all the drowned were young bats. Where mother fringed-bats, *Myotis thysanodes*, in Carlsbad Caverns were hanging over water during the nursing season, the surface of the water was "littered with the remains of young bats that

had dropped from the ceiling and drowned" (Baker, 1962). Interestingly, where they were roosting over dry floor, no remains were found, indicating that fallen young were indeed rescued.

Although parturition has not often been observed, there might be significant infant mortality at birth in some forms. On several occasions newborn have dropped accidentally from the mother during birth, rupturing and breaking the umbilicus, and eventually perishing from the ordeal (Wimsatt, 1960). In these cases, active participation of the baby during labor probably caused the mother to lose control of the process, perhaps throwing her off balance or causing irregular labor contractions.

Naturally-occurring fires in caves, though rare, occasionally account for mass mortality. With accumulation of guano in caves, fires sometimes start by chemical combustion from heat generated by the decomposing material (Campbell, 1925). In central Texas, ranchers locally call burning caves "smoking holes" where this phenomenon is common. Bats caught in a cave when a fire starts are surely burned, or overcome by smoke, and an entire colony can be displaced for several months while such fires run their course.

An interesting phenomenon was observed by Bob H. Slaughter (personal communication) who saw an entrapped bat in a tar pit at Fort Sill, Lawton, Oklahoma, along with a hawk, several small rodents, and a snake. Presumably the smaller animals were caught as they sought water on the surface of the tar, and the snake and hawk became mired in the tar as they sought easy prey. The bat's presence is curious, however, and this must be an extremely rare occurrence, for no bats are reported even for the remarkable Pleistocene Rancho La Brea tar pits fauna. As the bat skimmed the surface of the water its wings either came in contact with the tar and it became overburdened and fell into the pit, or it might have literally "run out of water" and come to a sudden fatal halt.

Careless or crowded flying account for several instances of bats becoming entangled in plants or on fences. Especially where cave entrances are long and narrow or where they open into heavy overgrowth, the result of emergence is an occasional death by entanglement. An interesting incident occurred at the entrance to Bracken Bat Cave, north of San Antonio in central Texas. A local spelunker, Pete Lindsley of Dallas, found a bat which had fallen into a prickly pear cactus (Figure 1-A) and had died from the wounds. This cave harbors one of the largest *Tadarida mexicana* colonies in the state, and emerging flights are very crowded. The sink entrance, according to Lindsley, is relatively small, about thirty feet in diameter, and is situated about ten

feet below normal ground level. On emergence bats must swirl around at the entrance and spiral out of the cave. Bats commonly fall to the ground at the entrance where the flights are most crowded, and it is not unusual to see several on the ground at once. The cactus plant was some five feet below normal ground level adjacent to the entrance, so it is likely that the bat was caught when it was knocked down by other members of a crowded flight.

A similar instance was sighted by Hal Kirby in 1967. As he and Ned Mudge watched the emergence of cave swallows, he noticed also the emergence of free-tailed bats, *Tadarida brasiliensis*. One of the bats during the confusion of the emergence from the cave became entangled in some grass burs which were growing at the cave's entrance. The more the bat struggled, the deeper the bur became imbedded in its fur. The bat was practically immobilized by the burs stuck between the fur and wing membranes. Kirby gently removed the burs from the bat's fur and wing membranes and set it free. The bat did not die in this instance but speculation could be made that death could be caused by the grass burs or could render the bat helpless against predators (Kirby, personal communication).

One of us (Kimbrough) recently found a *Pipistrellus pipistrellus* impaled on a cactus in the Black Gap Wildlife Refuge of southwestern Texas. Since the cactus was not close to any apparent cave, it was presumed that the bat became careless in its pursuit of an insect and flew into the cactus thorns.

Burdocks are known to have a similar effect. The barbed burs of this thistle weed (*Arctium lappa*) are responsible for at least three deaths (Johnson, 1933 and Lyon, 1925), two involving little brown bats, *Myotis lucifugus*, and one involving a red bat, *Lasiurus borealis*. It is possible that in flying close to the ground these bats did not detect the protruding burs, and their mistakes were fatal.

Like burdocks and cacti, barbed wire fences are also a menace to bats. On three occasions, bats have been found caught by their inter-femoral membranes. In each case the bat was wrapped several times around the fence resulting from struggles to escape. That all three records involve *Lasiurus*, two for the hoary bat, *L. cinereus* (Iwen, 1958 and Hibbard, 1963), and one red bat, *L. borealis* (Johnson, 1933) is significant. Possibly, *Lasiurus* cannot detect fences soon enough to avoid hitting them; and when a fence includes barbs, the result is disastrous.

A more curious entanglement befell a Seminole bat, *Lasiurus seminolus*, which perished when several strands of Spanish moss became twisted around its neck tightly enough so that it was unable to free



itself (Dunaway, 1960). These bats often frequent Spanish moss for shelter; hanging, therefore, may not be at all uncommon.

Electrocution of fruit bats is another manifestation of probable clumsiness in flight. Where electric cables are strung close to fruit trees, a fruit bat is liable to strike the wires on its way to a tree. If both wings contact separate wires a short circuit results in the subsequent electrocution (Rosevear, 1965 and Allen, 1939). Obviously, smaller bats are not subject to such a fate, since they are not long enough to connect two widely-spaced cables.

Accidental trapping by man is not altogether uncommon. Several have been caught in museum special snap traps set for rodents. A pallid bat, *Antrozous pallidus*, was on one occasion killed when it apparently was feeding on insects near a snap trap (Killpack & Goates, 1963). Considering the habits of pallid bats, becoming caught by a snap trap is not unusual. They often feed on scorpions which may be on or near the set traps; or, where they hang in small bushes to eat their prey, a trap might be set beneath for rodents.

Other bats are attracted to bait on the traps (Huey, 1936), and are caught as they seek an easy meal. *Glossophaga* and *Corollia* have been caught in traps baited with bananas (Hall & Dalquest, 1963), which is supposedly not an uncommon occurrence. These bats apparently can smell the banana and are attracted to it. In addition, a silver-haired bat, *Lasionycteris noctivagans*, has been caught in a mouse trap set with cheese for bait (Bartzsch, 1956).

Occasionally, bats are caught in light traps set for insects. In feeding on the prey which are attracted by the light, insectivorous bats are liable to be caught. A red bat, *Lasiurus borealis*, was once caught in a light trap, and the fluorescent black light, with its three to four thousand angstroms of radiant energy, was lethal (Wilson, 1965).

Still another kind of entrapment occurred when a little brown bat, *Myotis lucifugus*, fell into an open china slop jar in an attic, and was unable to escape. Its cries apparently attracted others and the old catch-jar for a leaky roof became a death trap for the ensuing procession of bats coming to the aid of the drowning victim (Hitchcock, 1963).

#### CONCLUSIONS

There seem to be no predators, as a group, that consistently make bats their habitual prey. There are only individual predators that make a consistent diet of the bats. These individual predators include almost all known predaceous animals.

Sight observations of mass mortality are reported by several authors; but no causative organism is offered because of the lack of facilities to handle the moribund bats. The relationship between diseases of bats

and man is becoming better illustrated through research, but data for the effects and causes of disease in the bats themselves are needed.

Bats freeze or starve to death in the winter when the winters are too adverse or too long. Their nocturnal flight activities tend to make them accident-prone. They become impaled on sharp objects such as barbs of barbed-wire, locust and burdock thorns, and cactus spines. The bats fall into water and drown, get caught in tar pits, get electrocuted, and get caught in traps set for other animals.

Though bats have many deleterious habits, it is because of their relatively low mortality rate that they remain one of the most populous animal groups on the earth today.

#### FUTURE WORK

Mortality is probably the least understood aspect of chiropteran natural history. Almost all carnivorous animals occasionally prey on bats but for the most part are merely opportunistic and very few actually specialize in these animals. Accidents and epidemics cannot be predicted, limiting the amount of planning that can go into investigations involving death of bats. The relationship between disease in bats and man has stimulated increased laboratory research on effects of virus on bats but investigations of this sort in the natural habitat is for the most part restricted to parasites.

Of prime importance to a better understanding would be immediate reporting of any encountered mass mortality of bats to the nearest communicable disease center to allow thorough investigation into the causative factors. It is also possible that sustained observations of a single roost over a long period of time would enlighten us to mortality rates and causes. This, of course, is extremely time consuming and guarantees little result.

It is therefore probable that our future enlightenment of bat mortality will require the scientist to be as much of an opportunist as the bat predator; that is, to recognize and follow through on the rare mortality problem that presents itself in the course of other studies.

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TABLE 1  
MAMMAL PREDATORS

<i>Predator</i>	<i>Prey</i>	<i>Reference</i>
<i>Didelphis marsupialis</i> (opossum)	<i>Myotis austroriparius</i>	Rice, 1957
<i>Didelphis marsupialis</i> (opossum)	bats	Campbell, 1925
<i>Mephitis elongata</i>	<i>Lasionycteris noctivagans</i>	Sperry, 1933
<i>Mephitis mephitis</i> (striped skunk)	<i>Tadarida brasiliensis</i>	Constantine, 1948

TABLE 1 (cont.)

<i>Predator</i>	<i>Prey</i>	<i>Reference</i>
<i>Conepatus conepatus</i> (hog nosed skunk)	<i>Tadarida brasiliensis</i>	Constantine, 1948
<i>Mustela frenata</i> (long tailed weasel)	<i>Eptesicus fuscus</i>	Mumford, 1969
<i>Mustela frenata</i> (long tailed weasel)	bats	Quick, 1951
<i>Mustela vison</i> (mink)	<i>Myotis lucifugus</i>	Goodpaster & Hoffmeister, 1950
	<i>Myotis sodalis</i>	
<i>Felis catus</i> (wild domestic cats)	bats	Campbell, 1925
<i>Felis catus</i> (wild domestic cats)	bats	Rosevear, 1965
<i>Felis catus</i> (wild domestic cats)	<i>Mystacina</i> sp.	Swyer, 1962
<i>Felis rufus</i> (bobcat)	<i>Myotis yumanensis</i>	Hall, 1946
<i>Canis</i> sp. (dog)	<i>Mystacina</i> sp.	
<i>Genetta</i> sp. (civet cats)	bats	Rosevear, 1965
<i>Procyon lotor</i> (raccoon)	bats	Campbell, 1925
<i>Procyon lotor</i> (raccoon)	<i>Eptesicus fuscus</i>	Phillips, 1966
<i>Procyon lotor</i> (raccoon)	<i>Tadarida</i> sp.	Eads, 1955
<i>Procyon lotor</i> (raccoon)	<i>Myotis velifer</i>	Cockrum, 1952
<i>Bassariscus astutus</i> (ring tailed cat)	bats	Campbell, 1925
<i>Citellus</i> sp. (squirrels)	bats	Ryberg, 1947
<i>Microtus ochrogaster</i> (vole)	<i>Myotis</i> sp.	Martin, 1961
	<i>Pipistrellus subflavus</i>	
<i>Peromyscus leucopus</i>	<i>Myotis</i> sp.	Hitchcock, 1965
<i>Rattus rattus</i> (black rats)	<i>Mystacina</i> sp.	Dwyer, 1962
<i>Neotoma micropus</i> (pack rat)	<i>Myotis velifer</i>	Cockrum, 1952
shrews	bats	Ryberg, 1947
baboons	bats	Rosevear, 1965
<i>Homo sapiens</i> (man)	bats	Walker, 1968
<i>Antrozous pallidus</i> (pallid bat)	smaller bats	Engler, 1943
<i>Eptesicus fuscus</i> (big brown bat)	smaller bats	Engler, 1943 and Krutzschn, 1950
<i>Hipposideros</i> sp. (Old World leaf-nosed bat)	smaller bats	Wimsatt, 1959
<i>Lasiurus cinereus</i> (hoary bat)	smaller bats	Bishop, 1947
<i>Lyroderma lyra</i> (false vampire)	smaller bats	Allen, 1939
<i>Macroderma gigas</i> (Australian false vampire)	smaller bats	Allen, 1939
<i>Megaderma</i> sp. (African false vampire)	smaller bats	Wimsatt, 1959
<i>Myotis myotis</i> (mouse-eared bat)	smaller bats	Allen, 1939 and Ryberg, 1947
<i>Myotis blythii</i> (mouse-eared bat)	smaller bats	Allen, 1939
<i>Phyllostomus hastatus</i> (spear-nosed bat)	smaller bats	Allen, 1939, Ditmars, 1935, and Wimsatt, 1959
<i>Rhinolophus luctus</i> (horse-shoe bat)	smaller bats	Allen, 1939
<i>Scotophilus</i> sp. (house bat)	smaller bats	Allen, 1939
<i>Vampyrus</i> sp. (spear-nosed bat)	smaller bats	Allen, 1939

TABLE 2  
BIRD PREDATORS

<i>Predator</i>	<i>Prey</i>	<i>Reference</i>
Falcons		
"falcons"	bats	Ryberg, 1947
<i>Falco sparverius</i> (sparrow hawk)	"small bat"	Wright, 1932
<i>Falco sparverius</i> (sparrow hawk)	<i>Antrozous pallidus</i>	Orr, 1954
<i>Falco sparverius</i> (sparrow hawk)	<i>Myotis velifer</i>	Bent, 1938
<i>Falco peregrinus</i> (duck hawk)	<i>Tadarida mexicana</i>	Stager, 1941, 1948 and James, 1963
<i>Falco tinnunculus</i> (kestrel)	<i>Noctilio and Pipistrellus</i>	Bent, 1938
<i>Falco tinnunculus</i> (kestrel)	<i>Vesperugo pipistrellus</i> (= <i>Pipistrellus</i> <i>pipistrellus</i> )	Paterson, 1927
<i>Falco albicularis</i>	bats	Allen, 1939
Hawks		
<i>Buteo lagopus</i> (rough-legged hawk)	<i>Myotis velifer</i>	Twente, 1954
<i>Buteo jamaicensis</i> (= <i>borealis</i> ) (red-tailed hawk)	<i>Tadarida mexicana</i>	Macy, 1939
<i>Buteo jamaicensis</i> (= <i>borealis</i> ) (red-tailed hawk)	bats	Bent, 1937
<i>Accipiter striatus</i> (sharp-shinned hawk)	<i>Lasiurus borealis</i>	Downing, 1961
<i>Accipiter striatus</i> (sharp-shinned hawk)	bats	Orr, 1954
<i>Accipiter velox</i>	bats	Bent, 1937
<i>Machaerhamphus andersonii</i> (bat buzzard)	bats	Rosevear, 1965
<i>Ictinia mississippiensis</i> (Mississippi kite)	<i>Tadarida brasiliensis</i>	Taylor, 1964
Owls		
<i>Bubo virginianus</i> (great horned owl)	bats	Taylor, 1964
<i>Bubo virginianus</i> (great horned owl)	<i>Tadarida mexicana</i>	Twente, 1954
<i>Bubo virginianus</i> (great horned owl)	<i>Antrozous pallidus</i>	Orr, 1954
<i>Bubo virginianus</i> (great horned owl)	bats	Bent, 1938
<i>Tyto alba</i> (barn owl)	bats	Taylor, 1964
<i>Tyto alba</i> (barn owl)	<i>Eumops perotis</i>	Reeder, 1946
<i>Tyto alba</i> (barn owl)	<i>Rousettus aegypticus</i>	Rosevear, 1965
<i>Tyto alba</i> (barn owl)	<i>Tadarida mexicana</i>	Twente, 1954
<i>Tyto alba</i> (barn owl)	<i>Antrozous pallidus</i>	Orr, 1954
<i>Tyto alba</i> (barn owl)	bats	Bent, 1938
<i>Otus asio</i> (screech owl)	<i>Eptesicus fuscus</i>	Beer, 1953
<i>Spiloglaux novae-zealandiae</i> (morepork)	<i>Mystacina</i> sp.	Dwyer, 1962
owl pellets	<i>Eptesicus fuscus</i>	Phillips, 1966
owl pellets	<i>Myotis</i> sp.	Hall, 1964
owl pellets	<i>Lasionycteris noctivagans</i>	Hall, 1946

TABLE 2 (cont.)

<i>Predator</i>	<i>Prey</i>	<i>Reference</i>
owl pellets	<i>Brachyphylla</i> sp.	Allen, 1939
owl pellets	<i>Artibeus</i> sp.	Allen, 1939
owl pellets	<i>Ardops</i> sp.	Allen, 1939
owl pellets	<i>Erophylla</i> sp.	Allen, 1939
owl pellets	<i>Phyllonycteris poeiy</i>	Allen, 1939
Other birds		
swallows and titmice	bats	Ryberg, 1947
<i>Geococcyx californianus</i> (roadrunner)	<i>Lasiurus borealis</i>	Wilkes, 1961
<i>Corvus</i> sp. (crow)	bat	Rosevear, 1965
<i>Euphagus cyanocephalus</i> (Brewer's blackbird)	<i>Antrozous pallidus</i>	Orr, 1954
<i>Agelaius phoeniceus</i> (redwing blackbird)	<i>Myotis lucifugus</i>	Miller, 1962
<i>Quiscalus quisquala</i> (common grackle)	<i>Myotis lucifugus</i>	Miller, 1962
<i>Cyanocitta cristata</i> (blue jay)	<i>Lasiurus borealis</i>	Allan, 1947
<i>Cyanocitta cristata</i> (blue jay)	<i>Lasiurus borealis</i>	Elwell, 1962
<i>Larus ridibundus</i> (European black-headed gull)	<i>Vesperugo pipistrellus</i> (= <i>Pipistrellus</i> <i>pipistrellus</i> )	Paterson, 1927

TABLE 3  
REPTILE PREDATORS

<i>Predator (snakes)</i>	<i>Prey</i>	<i>Reference</i>
<i>Elaphe obsoleta</i> (rat snake)	<i>Lasiurus cinereus</i>	Wiseman, 1963
<i>Elaphe obsoleta</i> (rat snake)	<i>Eptesicus fuscus</i>	Silver, 1928
<i>Elaphe obsoleta</i> (rat snake)	<i>Myotis austroriparius</i>	Rice, 1957
<i>Elaphe obsoleta</i> (rat snake)	<i>Myotis sodalis</i>	Barr and Norton, 1965
<i>Elaphe obsoleta</i>	<i>Eptesicus</i> sp.	Hamilton, 1943
<i>E. obsoleta</i> and <i>E. guttata</i>	bats	Holman, pers. comm.
<i>E. guttata</i> (corn snake)	<i>Myotis austroriparius</i>	Rice, 1957
<i>Elaphe</i> sp.	bats	Campbell, 1965
<i>Elaphe triaspis</i>	<i>Glossophaga soricina</i>	Mankins, 1965
<i>Elaphe laeta</i>	<i>Molossus nigricans</i>	Davis, 1951
<i>Trimorphodon vandenburghi</i>	<i>Myotis velifer</i>	Stager, 1942
<i>Trimorphodon vandenburghi</i>	<i>Tadarida femorosacca</i>	Krutzsch, 1944
<i>Epicrates angulifer</i>	bats	Hardy, 1957
"nocturnal snakes"	<i>Antrozous pallidus</i>	Orr, 1954
<i>Coluber taeniatus</i>	bats	Allen, 1939
<i>Dendraspis</i> sp.	<i>Lavia frons</i>	Loveridge, 1923
Lizards		
<i>Boiga blandingi</i>	bats	Rosevear, 1965

TABLE 4  
FISH AND AMPHIBIAN PREDATORS

<i>Predator</i>	<i>Prey</i>	<i>Reference</i>
<i>Rana pipiens</i>	<i>Pipistrellus subflavus</i>	Creel, 1963
<i>Rana pipiens</i>	<i>Myotis</i> sp.	Kinsey, 1961
<i>Rana esculenta</i>	bats	Brosset, 1966
<i>Rana</i> sp.	<i>Myotis</i> sp.	Holman, 1956
<i>Lepomis cyanellus</i>	<i>Tadarida mexicana</i>	Jones and Hettler, 1959
<i>Salmo gairdneri</i>	"California bats"	Ingles, 1947

TABLE 5  
INVERTEBRATE PREDATORS

<i>Predator</i>	<i>Prey</i>	<i>Reference</i>
<i>Periplaneta americana</i>	<i>Myotis austroriparius</i>	Rice, 1957
<i>Periplaneta australasiae</i>	<i>Myotis austroriparius</i>	Rice, 1957
Scorpions	bats	Orr, 1954
Spiders	bats	Allen, 1939
Driver ants	bats	Coudenhove, 1925