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OF THE

NATIONAL SPELEOLOGICAL SOCIETY

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Contents

CAVE BATS: THEIR ECOLOGY, PHYSIOLOGY, BEHAVIOR, AND FUTURE SURVIVAL

A Symposium with Recommendations

APRIL 1972

NATIONAL SPELEOLOGICAL SOCIETY

The National Speleological Society is a non-profit organization devoted to the study of caves, karst, and allied phenomena. It was founded in 1940 in the District of Columbia. The Society's headquarters are presently located in Huntsville, Alabama. The Society is affiliated with the American Association for the Advancement of Science.

The Society serves as a central agency for the collection, preservation, and dissemination of information relating to speleology. It also seeks the preservation of the unique faunas, geological and mineralogical features, and natural beauty of caverns through an active conservation program.

The affairs of the Society are controlled by an elected Board of Governors, which appoints National Officers. Technical affairs of the Society are administered by specialists in the fields that relate to speleology through the Society's Biology Section, Section on Cave Geology and Geography, and Research Advisory Committee.

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Discussion of papers published in the BULLETIN is invited. Discussions should be 2,000 words or less in length with not more than 3 illustrations. Discussions should be forwarded to the appropriate editor within three months of publication of the original paper.

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Papers in any discipline of speleology or any cave-related topic are considered for publication in the BULLETIN. Papers may be a technical article on some cave-oriented geological or biological research, a review paper on a speleological topic, or a speculative discussion of theory. We particularly welcome descriptive or geographical articles about significant caves or cave areas, especially if comments on speleogenesis, biological surveys, historical significance, etc. are included. Articles on other topics such as cave conservation, history, etc. are also invited.

Articles in the biological sciences should be sent to the Biology Editor, David C. Culver, Dept. of Biological Sciences, Northwestern University, Evanston, Illinois 60201. Articles in the line of geology or geography should be sent to the Earth Sciences Editor, William B. White, Materials Research Laboratory, the Pennsylvania State Univ., University Park, Pa. 16802. Articles not falling in either of these categories may be sent to the Managing Editor, David Irving, Science Applications, Inc., P. O. Box 2351, La Jolla, California 92037.

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Interested contributors, especially those who are not professional scientists or writers, are invited to consult with the editorial staff or the NSS Research Advisory Committee for guidance or aid in the presentation of their material.

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Cave Bats: Their Ecology, Physiology, Behavior, and Future Survival

Robert E. Henshaw,* Moderator

A symposium presented at the annual meeting of the American Association for the Advancement of Science, Philadelphia, December 30, 1971. Co-sponsored by the National Speleological Society and the American Society of Zoologists.

ABSTRACT

Cave bats, with their nocturnal activity, winter hibernation or migration, use of remote caves for colonies, and feeding on noxious flying insects, might be thought to be relatively safe from man-induced ecological destruction. Yet the Indiana bat *(Myotis sodalis)* was recently placed on the Endangered Species List. and other species may be declining. Present understanding of ecology, physiology, and behavior of cave bats may demonstrate their low adaptability and the precariousness of their niche. Because of their Count Dracula public image, bats receive little direct protection in conservation movements. Biologists, speleologists, and spelunkers must play an increasingly important role in protecting these highly beneficial flying mammals.

PREFACE TO THE SYMPOSIUM

This symposium on bat conservation was especially significant. The AAAS conducted a public forum where concerned scientists talked on public issues. Many scientists have observed the rapid disappearance in recent years of the unique order of flying mammals—the bats; few, however, have confronted the likely causes, and fewer yet have proposed solutions. With the exception of Charles Mohr's early warning in 1953, little has been said of man's role in the demise or survival of bats. In committing an entire issue of the NSS *Bulletin* to this symposium, the NSS provides important liaison to many of those to blame and—one-and-the-same—to those who can be most effective in slowing or stopping the extinction of bats.

For at this meeting, bat researchers publicly confirmed their complicity in bat mortality.

Here, spelunkers/speleologists acknowledged publicly the effects of their activities on bat populations resident in cave hibernacula.

Here was documented the part played by cave commercializers in decimation of bat populations.

At this public forum, then, much of the blame was placed where it should have been placed a decade ago—on ourselves. In these papers the components of the bats' ecosystem (Horst, Poulson) are described. Generalizations about the fixity and adaptive value of these characters (Henshaw) lay the groundwork for a definitive statement on current decimation of bat populations and the causes (Mohr). Possible beginning remedies are presented (Mohr, Henshaw). The symposium closes with a list of concrete recommendations.

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The general mood of alarm did not give way to gloom, rather most attendees felt optimistic. Concern and sympathy for control measures were expressed by those who are partially responsible for bat population decline. Their willingness to aid in preparation of legislation and regulations may lead to resolving up to 60% of the problems leading to decline in bat numbers. It was clear that everyone can make contributions whether through a Bat Conservation Task Force or individually. The symposium was adjourned with a feeling of real accomplishment. Two addresses which should be available to all are:

Mr. Charles Mohr
Division of Parks, Recreation, and Forestry
Department of Natural Resources and Environmental Control
Dover, Delaware 19901

Dr. Clyde Jones, Chief, Mammal Section
Fish and Wildlife Service
Bird and Mammal Laboratories
National Musem of Natural History
Washington, D. C. 20560

This symposium, then, should represent to the reader a Call to Action. The rapid decline of bat populations is documented, the causes are indicated, correction and control are in the hands of the informed and concerned, and—maybe—it is not too late.

The Status of Threatened Species of Cave-dwelling Bats

Charles E. Mohr *

ABSTRACT

The reduction of populations of insectivorous bats, reported as early as 1952, has recently reached alarming proportions. One major cave population of *Tadarida*, the free-tailed bat, has dropped to 1% of its number of 10 years ago, while populations of 22 different species have declined in part or in all of their ranges. Mass mortality observations are reported. In the few cases studied, rabies was shown to be negligible. Insecticide poisoning has been proven in thorough laboratory analyses. *Tadarida* suffers extreme exposure to organochlorine pesticides during foraging flights and seasonal migrations. Disturbance by scientists engaged in banding and other research activities and by spelunkers inadvertently is identified as a factor in the decline. Conservation proposals include reduction of banding, severe limitation on visitation to bat caves by scientists and spelunkers, and enactment of legislation for bat protection.

Decline of Bat Populations

In 1815, John James Audubon calculated that a 3-day passenger pigeon flight in Kentucky totalled 2 billion birds. Without doubt, it was the most abundant migratory bird in America, but by 1900, the passenger pigeon was rarely seen, and the last zoo survivor died in 1914. One factor often mentioned in accounting for its rapid decline was its low reproductive rate: two young a year.

The free-tailed or guano bat, *Tadarida brasiliensis mexicana*, might be compared to the passenger pigeon—so abundant that its disappearance could not be conceived. The total population in the U.S. and Mexico has never been even guessed at. In 1936, the flight from Carlsbad Caverns, New Mexico was estimated at 8,700,000 (Allison, 1937). Members of the famous Project X-ray in World II (Mohr, 1948) visited every known colony in a cave or mine in the Southwestern United States, and they found many previously unknown colonies. Their estimate of the U.S. population was 100,000,000.

In the decades following the war, *Tadarida* was the subject of a vast amount of research, and a number of additional bat caves were located. In Texas alone, Davis *et al.* (1962) estimated that 13 caves had 100,000,000. Perry (1965) reported that five Oklahoma caves had about 8 million. The country's largest maternity roost in Eagle Creek Cave, Arizona, was estimated by Cockrum (1969a) to have between 25 and 50 million in June, 1964. He also estimated (Cockrum, 1969b) that the bats in this colony destroyed 40 tons of insects in a single night!

Yet the latest information from a few caves for which there are early records reveals reductions so staggering that *Tadarida* probably should be considered for inclusion in the official list of rare and endangered species. The first alarm was sounded at Carlsbad in 1955 when the first of a series of southwestern bat die-offs was noted. In the investigation that followed, Constantine (1967) found that the population at Carls-

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bad was down from 8,700,000 to about 3,800,000 in 1956. By 1962, according to the estimate of Edgerton *et al.* (1966), it had dropped to about 250,000—about 1 for every 35 that were there 35 years earlier. Even more disturbing is the report from Eagle Creek Cave by Reidinger (1972) where the highest recent count, in June 1970, was 600,000. This would be about 1 for every 100 bats that were present 10 years earlier. In the Devil's Sinkhole, Texas, Mitchell (1970) netted *Tadarida* in a two-census mark-recapture survey and estimated that the present population numbered just 5,000 bats. He questioned the accuracy of earlier estimates that placed the population at levels of 10 to 16 million.

Granted that some estimates of huge cave populations may be unreliable (Davis *et al.* 1962; Humphrey, 1971b) and that current information is limited to rather few of the major cave populations, the concensus of bat experts in the Southwest is that alarming decreases have occurred and that the factors revealed by the few studies reported here probably apply to most if not all of the *Tadarida* populations.

The plight of *Tadarida* is not unique. One bat from the continental United States, *Myotis sodalis,* has been on the list of rare and endangered species since 1966 (Bureau of Sport Fisheries and Wildlife, 1966). A current survey of 100 of the nation's leading bat experts by Clyde Jones (1971) indicates that a total of 22 species or subspecies (out of 78 in the U.S.) are believed to be declining in part or in all of their ranges. Five have been nominated for the revised endangered list.

How reliable are these reports? Might the decline be more apparent than real? Bird watchers know that their success in spotting migrants varies greatly from year to year. Despite a multitude of observers, major movements of hawks and insectivorous birds sometimes go almost undetected. On an annual basis, bird watchers consider this to be disappointing but not, as a rule, alarming.

How is the situation with bats different? In the case of bats, the evidence is based on resident populations since hibernating populations and nursery aggregations generally have been considered to be quite stable in size for long periods of time. In addition, researchers have discovered that great numbers of bats visit certain "transient" caves for brief periods during migration (Glass, 1958; Villa and Cockrum, 1962; Hall, 1962; Davis, 1964; Hall and Wilson, 1966; Constantine, 1967; Hall and Brenner, 1968; and Fenton, 1969). This "swarming" provides an opportunity to net bats at cave entrances, but rapid turn-over of these populations and the uncertainty of comparable captures from day to day and from year to year severely limits the usefulness of the data in assessing population trends. Size of cave-dwelling populations provide most of the information on the present status of cave species. Few such populations are likely to have been overlooked. Since 1932, when sustained banding got underway, banders and other researchers have visited every promising cave and mine in search of bats. Most known colonies have been revisited frequently; only occasionally is a new colony located. Non-cave colonies have been found in a variety of structures, few of which offer permanent security.

Incidentally, as Griffin states and abundantly documents (1970), "The distinction between migratory tree bats and hibernating cave bats is not a sharp and absolute one." Swarming at the caves during migration includes species not ordinarily considered to be cave-dwelling species. This discussion is concerned with all North American bats.

Declines in cave populations were noticed and reported as early as 1952 by Mohr (1952, 1953) on the basis of data from many of the 30 banding cooperators who up to that time had banded 70,000 bats, mostly in caves. By 1952, populations had been reduced at many sites and one species, *Myotis sodalis,* had virtually disappeared from its known hibernating caves in the Northeast. Now there are nearly 70 active banders, a total of possibly 2,000,000 bats have been marked, and mounting nationwide evidence reveals an alarming situation.

Scientists have long recognized that bats comprise a large and important sector of the ecosystem. Now, to a greater extent than previously realized, they are suspected to be indicators of the degree of the chemical contamination of the environment (Cockrum, 1969b; Pimental, 1971). Any documented decline should be a matter of wide concern, calling for corrective action.

HUMAN DISTURBANCE TO BAT POPULATIONS

This symposium was called together by the two groups that should be most aware of the threats to bat populations, groups which should recognize (as Pogo does), that we are part of the problem and that we should be capable of initiating both immediate and long-range steps to relieve certain pressures on bat populations. These two groups are the organized spelunkers in the National Speleological Society and the research biologists. In the opinion of virtually every bat expert (Jones, 1971), inadvertent disturbances of bats by spelunkers, who often are unaware of the effect of their visits, and also by scientists carrying on banding or other research have been responsible for marked reductions in well known cave populations.

When they enter hibernation, insectivorous bats are heavy with fat deposits. They are able to survive the winter-long fast only because of the metabolic economy achieved through dormancy. Higher first-year mortality rates noted among young bats have been interpreted as the inability of many of them to accumulate enough fat reserves to last until spring (Davis and Hitchcock, 1965). Since even minimal disturbance during hibernation may arouse bats to an active state and create a drain on their energy supply, the frequency of unnatural arousal must be kept to a minimum.

Scientific parties from a single university have been known to make 40 trips into a major bat cave in one year. Reidinger (1972) notes that the peak of biologist-bat encounters occurs in the major bat caves in June and July when most bat species are pregnant or rearing their young.

Handling of pregnant females may cause abortion. Gunier (1971) reported that *Myotis grisescens* aborted young, apparently due to their captivity in collecting cages for a short period of time. Novick (1960) and Cockrum (1969a) also reported that pregnant females aborted their young after capture. Humphrey (1969) found that some species are much more sensitive to disturbance than others. In the case of the big-eared bat, *Plecotus townsendii,* "even the simple presence of people causes them to vacate their preferred nursery roost, to move to a new and perhaps less desirable site. Many probably desert the cave altogether."

In many southern caves which serve as nursery roosts for huge colonies, summer visitation appears to increase perceptibly the number of accidents to young bats. When disturbed, many fall from their fairly precarious perches and are consumed by a host of predatory invertebrates and vertebrates (Gillette and Kimbrough, 1970). *Myotis velifer,* the cave bat, reacts unfavorably to disturbance in nursery caves. Humphrey (1969) documents severe population declines that closely followed visits by spelunkers. Myers (personal communication) noted some recovery of populations of *M. sodalis* and *M. grisescens* after he reduced his banding visits to one a year.

Humphrey (1969) notes that *Tadarida* also is intolerant of disturbance. One summer population of 5000 male freetails left an Oklahoma cave in response to a very slight disturbance while handling of females led to a delayed but nearly total desertion. Lactating females remained and "completed parental care before moving elsewhere." They were totally absent for several years, but within 10 years a new colony had formed. Most disturbances created in the big *Tadarida* nursery caves can't be blamed on spelunkers. Humphrey says, "The ammonia produced by decaying guano keeps sensible people out of free-tail caves, bat researchers undoubtedly cause most of the problems for this species."

Though the little brown bat, *Myotis lucifugus,* rarely occurs in colonies of more than 10,000, its range extends from Labrador to Alaska, and it "may be the most abun-

dant bat in the United States" (Barbour and Davis, 1969). Its populations in New England and Canada have been studied over long periods by Griffin (1945), Davis and Hitchcock (1965), and Fenton (1970a), and in the Midwest by Henshaw and Folk (1966) and Humphrey (1971a). In Indiana and North Central Kentucky, Humphrey reports that extermination or bat-proofing of nurseries caused a loss of at least 52% in a decade. Winter populations lost 80%. "Continual declines are expected."

Fenton (personal communication) reports that bat populations (especially *M. lucifugus*) in Ontario are down in most of the unprotected caves and mines, particularly the smaller ones. As for the future, he says, cessation of banding disturbances appears to have been beneficial, but likely "the increased use of snowmobiles is affecting bat populations since people are now able to easily get to relatively isolated hibernacula."

During the long period of hibernation, there may be many visitors—banders, serious spelunkers, curious school boys, and wanton vandals. Over the years, I have several times seen the floor of the mine at Hibernia, New Jersey, littered with hundreds of dead bats. That population is probably reduced by 75%. Perhaps the most vivid description of attacks on bats are from Ralph Ewers of the Cinncinnati Museum of Natural History who reported to me (and a few other concerned persons) on December 30, 1960:

> "At Carter Caves State Park, Kentucky, in the winter of 1957, hundreds of bats were killed by being stoned from the low ceiling. In December of 1958, vandals discharged fire crackers and home-made bombs in the midst of the clusters. On December 26, 1960, three boys, moments before our arrival, tore great masses of bats from the ceiling and trampled and stoned the helpless animals. Thousands fell into the stream which flows through the cavern and were drowned before they could rouse from their torpid state. An estimated 10,000 bats were killed."

As a result, a gate was designed and installed, but insurmountable mechanical problems made it ineffective. Finally, in the fall of 1969, the State of Kentucky fenced the approaches to Bat Cave. Visitation during the hibernation period is now carefully regulated.

A few other state and federal agencies, alerted to the problem by speleologists and biologists, have gated some caves and have restricted access to others, permitting only approved investigators to enter the caves. Recently however, Williams *et al.* (1971) reported that many governmental agencies in the West, where much of the land (86% in Arizona) is in the public domain, are faced with so many "administrative problems of a far higher priority than cave conservation" that obtaining their cooperation "has thus far proved to be frustrating, contradictory, perplexing, and mostly impossible." That even where sincere efforts are made to protect bat populations, ill-considered acts have proved to be disastrous is ironic. Several well-intended but inexpert gating operations by federal agencies prevented free access *by the bats* and resulted in drastic reductions of wintering populations before the situations were discovered and corrected.

Some situations may defy solution. In commercializing Fourth Chute Cave, Quebec, construction eliminated the circulation of cold air in one of the unvisited passages of the cave where the largest known population of *Myotis leibii* in eastern North America hibernated. These bats have been totally dispossessed (Hitchcock, personal communication) as a result of the warmer microclimate produced, and their whereabouts are not known. Other alterations to cave habitats assume greater importance as studies of thermoregulation and microclimatic preferences or requirements of different species are determined (Henshaw and Folk, 1966). An unfortunate event in Marvel Cave, Missouri, endangered one of the major wintering colonies of the gray bat, *Myotis grisescens*. Gunier (personal communication) reports that the burning of debris following construction work in March, 1971, resulted in the death of thousands of bats, including 154 banded individuals in one passage.

Concentration and Hazards to Survival

Two species, *M. grisescens* and *M. sodalis*, since they congregate in larger numbers and in fewer caves than any other vespertilionids, have been subjected to heavy visitation. Populations of *M. sodalis* in the Northeast have disappeared. Several Midwest populations are protected and are considered reasonably stable. Other colonies are reduced. In Wyandotte Cave (commercial) in Indiana, the 15,000-member colony studied by Cope and Mumford in 1951 was down to 1200 in 1969 (Mumford, personal communication). The Carter Caves colony has suffered from vandalism, as already noted, and to a limited extent from flooding, but it probably is still close to 100,000, down from an estimated 125,000.

Some hibernating sites used by *M. sodalis* appear to be especially subject to natural catastrophies such as collapse (of mines)—a particular hazard in Blackball Mine in Illinois—and floods. Hall (1962) stated that *M. sodalis* follows river valleys during migrations. It might be more vulnerable to floods in such places than in safer caves chosen for hibernation. Along the Green River in Mammoth Cave National Park, Kentucky, is a deposit of 300,000 skeletons of *M. sodalis* (Hall, 1962), in a section of the cave that has been inundated as recently as the floods of 1957 and 1964. This represents a colony three times the size of any existing today. A flood in Aitkin Cave, Pennsylvania, experienced by Griffin (1953) in November, 1950, drowned perhaps 90% of a population of 5,000 bats, mostly *M. lucifugus* but including 500 *M. sodalis*. A flash flood that swept through Big Spring, Breckenridge County, Kentucky in early March, 1964 (DeBlase *et al.*, 1965) virtually wiped out the wintering population in Wind Cave. This cave population had been under study by James Cope and his associates for several years. The population three months before the flood was 6,545 bats. Of these almost 60% were *M. sodalis*, nearly 40% *M. lucifugus*. After the flood, 839 banded bats were found among the 1600 carcasses. Surviving in the highest part of the cave, where they had been seen in December, was a cluster of 370 still torpid bats.

Few spelunkers visit the deep, pit-type caves preferred by *M. grisescens*, but unfortunately, several caves occupied by this species have been developed for commercial operation—Marvel in Missouri, Sauta in Alabama, and the Coach-James Cave system in Kentucky, Despite cooperative attitudes by the present operators, the future of these very large colonies is uncertain. In Kentucky (Hall, 1964) some of the colonies could shift to safe hibernacula in Mammoth Cave National Park. Biologists most familiar with the situation support inclusion of *M. grisescens* on the endangered list. Unlike *M. sodalis*, whose nursery roosts have never been found, one winter population of *M. grisescens* is known to scatter widely and to occupy at least 10 nursery caves in Kentucky, southern Illinois, and northern Tennessee (Hall and Wilson, 1966). The recovery of nearly 10% of banded bats from this area in a single Edmonson County, Kentucky cave in winter indicates a "populational home range" of 10,500 square miles. Separate populations evidently hibernate in Ozark caves. In winter, in Marvel Cave, Stone County, Missouri, Gunier (personal communication) has retaken bats banded in Kansas, Oklahoma, Arkansas, and Missouri. Three other hiberating sites in Shannon and Laclede Counties under study by Myers (personal communication) also serve populations from a very large summer range.

This concentration of such a large proportion of the known population into so few caves constitutes the real threat to their survival. In contrast, *Myotis velifer*, in the Southwest and Mexico, congregates in maternity roosts, occasionally numbering up to 15,000 or 20,000 (Twente, 1955; Humphrey, 1969; Hayward, 1970),

but colonies are scattered throughout innumberable caves, mines, and buildings.

Injuries Due to Bat Banding

Recognition of the hazards created by disturbance and handling has come only recently, but within little more than a decade of banding's beginning, injuries to bats were being reported (Griffin, 1945; Trapido and Crowe, 1946). The aluminum bands designed for use on the relatively insensitive legs of birds often damaged the delicate tissues on the wings of bats (Greenhall and Paradiso, 1968).

Tadarida was especially susceptible to injury. Irritation, infection, and swelling was traced to improperly applied bands: too tight, too loose, crooked (Cockrum, 1969b). Bats often chewed the bands until the numbers were illegible or holes were worn completely through the bands. In many cases bands became deeply imbedded in the flesh and even partially into the bone. Perry and Beckett (1966) found that osseous deposits enlarged the developing bones of the forearm and digits to about three times the normal diameter in young *Tadarida*, probably due to a decrease in circulation caused by the tightness of the bird bands. Many banders have noted scar tissue growing over bands; complete healing is seldom found. Some banders who exercised extreme care in banding, but still observed injuries, blamed the small size of bands provided and the sharp edges for many of the injuries.

With the initiation of large scale banding projects in studying the role of bats in spreading rabies (Eads *et al.*, 1957), Hitchcock (1957) noted that the effectiveness of banding "is lessened materially by the use of improperly designed bands." He cited a letter from Richard B. Davis reporting his examination of 190 *Tadarida* one month after banding: "Of these, 86 showed no irritation or swelling; 104 were injured. Of the latter group, 33 were so badly injured that Davis killed them." Hitchcock called for trials of a lipped band he had seen in use in Europe, which "will be welcomed on humanitarian grounds by all who are aware of the injuries to bats caused by the type of band now employed."

Since the European bands, with rounded corners and lips at the contact point along the wing membrane, rarely caused injury, a similar bat band was manufactured and distributed in this country by the banding office. A comparison of injuries caused by the two bands on *Tadarida* (Herreid *et al.*, 1960) showed a great reduction in rate and seriousness of injuries. When the bat bands were used, no embedded-in-the-bone injuries were ever noted, and while wing-tears were about the same shortly after banding, 50% of the tears caused by bat bands were well healed after 6 months whereas bird bands caused considerably more tearing. Hope was expressed for additional modification of the bands. This has occurred, but the perfect band has not yet been produced.

Bats as Carriers of Rabies

Absence of human disturbance does not guarantee survival according to recent investigations of declining *Tadarida* populations. The mystery of large "die-offs" in the Southwest and in Mexico has been at least partly dispelled by exhaustive investigations by Constantine (1967) of the U.S. Public Health Service and E. Lendell Cockrum and Russell Reidinger, Jr. of the University of Arizona. Rabies, pesticides, and the environmental stresses encountered in migration have all been identified as factors affecting survival of bats. Rabies represents the most serious threat to man.

Vampire bats were implicated in the death of horses of the earliest Spanish explorers in Latin America, but they were not recognized as carriers of rabies until the early 1900's in Brazil. Laboratory tests in Trinidad in 1931 first proved the transmission of bat rabies to man. Between 1929 and 1937, there were 89 human deaths there from rabies, while in Mexico 31 deaths were recorded during the decade 1951 to 1961.

Economic losses in Latin America have been staggering. Greenhall (1968) cites the 5th World Health Organization Report, 1966; "vampire bat rabies is the major cause of death in cattle in Latin America and has proved a major obstacle to the expansion of its agricultural economy".

Despite pleas for reasonable population control programs such as the ones which proved effective in Trinidad, eradication programs on the continent have been waged with relentless vigor. Poison gas, flame throwers, electrocution, poisoning, and bacterial warfare have been employed. In Venezuela, 2,700,000 bats of all types were killed between 1964 and 1966. In one Brazilian province, the Antirabies Service killed bats in 8240 caves in five years, generally by destroying the caves or all life within them (Constantine, 1970).

It is perhaps not surprising that overreaction by some health authorities in the U.S. followed the disclosure in 1953 that *insectivorous* bats could carry rabies virus and transmit it to man. The extent of bat eradication activities that followed has been poorly documented. The National Communicable Disease Center in Atlanta publishes quarterly and annual summaries on rabies identification and bites by wildlife (including bats) and domestic animals, but little has appeared in print regarding bat destruction.

Speleologists and other biologists undoubtedly have played a key role in encouraging a calm stance by public health officials, and they have assisted in many surveys and samplings of bat populations. Now that rabies virus has been isolated in bats in all 48 states south of Canada, it is increasingly important that spelunkers be well informed in all phases of rabies-related matters. In a recent article, Smith (1971) alerted thousands of NSS members regarding potentially dangerous bats. The majority of NSS grottoes already have made or are establishing contact with their local health officials. Most of them in areas where large bat roosts exist have agreed to reduce the risk of their own exposure by bite or airborne virus *by staying out of those caves*. Others have taken rabies prophylaxis or are planning to do so. The danger of infection with rabies virus doubtless is greatest in large maternity roosts. On the other hand, hibernating bats, if not handled, evidently involve little risk until they become active as spring approaches.

Causes of Decline in the Southwest

It is an established fact that a significant number of bats survive rabies. Constantine (1967), in his investigations of bat mortality in *Tadarida* colonies, at first suspected rabies as a major cause of death. While he did determine that certain carcasses showed evidence of death by rabies, he believes that most mortality can be traced to the physical stresses of migration. Banding and field observations reveal that waves of migrants, travelling hundreds of miles from caves in Oklahoma, were rather often caught by cold fronts and rain during the southward flight and carried far off course. Some missed the target caves; others arrived in an exhausted state, exhibited confusion and disorder, and failed to make foraging flights. Inability to congregate in dense masses in warmer portions of the caves constituted a real hazard. Wet bats finding shelter in marginally cool caves or exposed to excessive air circulation became moribund and died.

Constantine noted a relationship between maintenance of maximum populations in maternity roosts and success in raising young. In a marginally cool cave like Carlsbad Caverns, bats need to be tightly massed to create the high temperature level essential for the growth of young bats. Factors that reduced the numbers congregating in the caves—leaving the bats too diffusely scattered—resulted in increased mortality of young bats. Annual variations in weather and the availability or utilization of non-cave roosting places evidently are related to fluctuations in numbers using the cave and variations in breeding success. Real reductions in populations can apparently accelerate the decline if the temperature of a total roosting population fell below the minimum safe threshhold. Certain marginal caves might therefore become deathtraps and eventually cease to be bat

caves. This may account for bone deposits in certain caves, like New Cave in Carlsbad Caverns National Park and portions of Carlsbad itself, comprising bushels of skeletons, some of which have been dated at 17,800 BP (Baker, 1963). A number of other southwestern caves that once supported large colonies are now devoid of bats.

Influence of Pesticides

A new factor appeared after World War II—the widespread use of DDT for the control of agricultural insect pests. Evidence of DDT-related mortality among insectivorous birds led biologists to suspect that bats might be affected too. Luckens and Davis (1964) fed DDT to *Eptesicus* and found the LD_{50} to be 40 mg/kg—about 10 times as sensitive as other laboratory animals, such as mice, rats, and rabbits. But in further tests, Davis (1965) noted that "a dose 20 times that which is lethal in spring is not lethal in fall. The chlorinated hydrocarbon pesticides are fat soluble and apparently are quickly deposited in the fat when eaten in autumn." Two *Eptesicus* fed 240 mg/kg of DDT and then placed in hibernation survived throughout the winter but showed DDT poison symptoms and died several months after arousal from hibernation.

Biologists have been mystified by the occasional discovery of tremendous numbers of dead and dying bats. Generally, the encounters have been so unexpected that the observers had no provision for collecting and preserving specimens for later analysis. Villa (1956) found hundreds of thousands of dead *Mormoops* in a cave in Nuevo Leon, and several thousand more in a mine several miles away. Booth (1965), returning in December 1963 to a cave in Tamaulipas which he had visited many times, found "hundreds of thousands of dead and dying bats on the floor. Many were alive but only a few could fly."

A similar die-off at Carlsbad led to Constantine's investigations, already noted. Rabies, while identified in a few individuals, was considered a minor factor. Rabies was also ruled out in the studies at Eagle Creek cave, Arizona. Cockrum (1969b) reported that tests of dead bats discovered by ranchers and farmers around the cave in 1968 proved negative for rabies. Near Carbo, Sonora, Mexico in 1968, biologists from New Mexico Highlands University found the hillside outside the Cave of the Tiger "covered" with dead and dying bats, but the cause of the deaths could not be determined. Cockrum thought it highly probable that poisoning by chlorinated hydrocarbon insecticides was responsible.

Most people probably would not associate the Southwest with large scale agricultural operations, and it is true that most of the bat caves are not located in farmland. Banding studies by biologists (Cockrum 1969a, 1969b) at the University of Arizona between 1952 and the present have established a relationship between cave-dwelling *Tadarida* and the agricultural use of pesticides: (1) Their nightly foraging flights take them as much as 50 miles from the caves. Even the more remote *Tadarida* roosts are within range of extensive irrigated agricultural areas where they feed heavily on small moths, beetles, and flying ants (Ross, 1967). (2) Migratory flights ranging from 500 to 1000 miles take many of them over agriculturally developed areas of Sinaloa and Sonora, Mexico, where pesticides are used abundantly.

Records kept by University of Arizona biologists on 38 Arizona bat populations for 19 years provide a substantial basis for determining population trends. This has been the just completed doctoral research project of Russell F. Reidinger, Jr. (1972), in which he has isolated, evaluated, and verified the factors involved. Trends in over 20 populations were studied on the basis of the most recent past estimate in the same month at the same roost site. Thirteen showed definitive trends: nine "Down", one "Stable-Down", one "Stable", and two "Up". Eight of the nine populations with "Down" trends had no live members on the 1969 and 1970 visits. The ninth, Eagle Creek Cave, contained 1% of the *Tadarida* population estimated for the same month in 1964. In commercially developed Colossal Cave, in Pima County, Arizona, three populations—*Leptonycteris sanborni*, at 1000 in 1960; *Myotis velifer*, 94 in 1956; and *Plecotus townsendii*, at 40 in 1955—had disappeared completely. Colonies of *Tadarida* in nearly inaccessible portions of two bridges were "Up"—from 35 to 70 in one instance and from 1000 to 4000 at a second site. Unfortunately, newer bridges are mostly unsuitable for bat roosts (Davis and Cockrum, 1963), and a number of mine roosts have been destroyed as a result of a shift to strip or open-pit mining. One population of *Antrozous pallidus* had disappeared as a result of "over-sampling" by scientists.

Most of the persons who have expressed concern over declining bat populations have indicated that they believed the persistent chlorinated hydrocarbon insecticides somehow were poisoning bats, and laboratory tests had confirmed the fact that bats fed large diets of DDT could die from the poison, as already noted (Luckens and Davis, 1964).

Reidinger collected 58 bats of six species in caves, mines, buildings, and under bridges. The samples analyzed included pooled brains, livers, GI tracts plus contents, mammaries, embryos, and remaining whole bodies. Analysis was by gas chromatography at the Denver Wildlife Research Center. DDE, DDD, DDT, o p'-DDT, dieldrin, toxaphene, Aroclor 1254, and Aroclor 1260 were seen in one or more samples. Residues in insectivorous bats were far higher than among other Arizona mammals reported in the literature.

As might be expected, residues in bats varied with the site of collection:

Low usage areas—
2 individuals averaged 2.1 ppm
Low-medium—
33 individuals averaged 4.9 ppm
Medium-high—
10 individuals averaged 220.0 ppm

Since records of sales and application of insecticides in Arizona are treated as confidential, Reidinger arbitrarily classified collecting areas as of high, medium, or low insecticide usage according to their proximity to agriculture and/or cities where insecticide use is often quite heavy. The increased exposure of bats is accounted for by the diet, roost sites, and foraging behavior of the bats, and the time of maximum build-up of residues in the lipid tissue corresponds with the time of maximum spraying of insecticides in nearby agricultural areas. Reidinger found that the incidence of poisoning in non-cave bats increased in direct relationship to their occupancy of man-made structures where insecticide use was heaviest.

Nearly 20% of the bats contained sufficiently high residues to cause acute toxic effects during periods of rapid lipid utilization, such as during long migratory flights at the conclusion of the hibernating period. Five of 11 bats examined were found dead after an early migration from Mexico and an unusual cold wave. These averaged 320 ppm total chlorinated hydrocarbon insecticides. A high DDT/DDE ratio in three of the bats indicated recent exposure to DDT and diet as the source of contamination. Reidinger reports that DDE is the metabolic form of DDT which he found in highest concentration in most bat samples. He believes that this derivative is probably premetabolized from DDT by the insects before they are eaten by bats.

Residues in embryos proved low, but after birth young bats showed an increase while the lactating females showed a gradual decrease in insecticide residues—an indication of the transfer of the poison from mother to offspring through nursing. Heavy mortality among young bats is especially critical in view of the low reproductive rate (one young a year among most genera other than *Lasiurus*.)

The extreme longevity of bats (up to 20 years or more), as pointed out by Cockrum (1969b), provides time for the accumulation of high residue levels. Possible sublethal effects, indicated by Reidinger's field observations, include decreased tolerance by *Tadarida* and *Macrotus waterhousii* of the

excessive ammonia fumes characteristic of nursery roosts and loss of ability of young *Tadarida* to hang on to cave ceilings.

In contrast to the heavy exposure to pesticides resulting from the extended foraging and migratory flights of *Tadarida*, the very limited movements of *Pipistrellus hesperus* and its avoidance of man-made structures probably explains why colonies of this species have remained stable or even have increased in numbers (Jones, 1966; and Jones and Suttkus, in press).

The flower-feeding *Leptonycteris sanborni* comes into direct contact with DDT while gathering pollen and nectar. Reidinger believes that the insecticide causes liver damage in this non-insectivorous bat.

For most species, Reidinger concludes, the widespread use of organochlorine insecticides is "a significant factor in the reduction of Arizona bat population sizes." Unless use of these pesticides in large scale agricultural operations is markedly reduced, the peril to insectivorous bats may actually increase. This possibility is based on the knowledge that an increasing number of insects exhibit resistance to pesticides. Instead of representing dangerous targets for only a brief period before death ensues, poison-resistant insect "carriers" may constitute a sizeable portion of the nightly intake of foraging bats. A lethal level of poisoning might be reached more quickly than is the case now.

While insecticides as a cause of bat mortality have been suspect, most scientists apparently have been unaware of government documents on toxicity of pesticides in the environment such as those by Stickel (1968) and Tucker and Crabtree (1970) which were issued in small editions and went out of print quickly. Others, like Reidinger's research and Jones paper (1971), have not been published or, like Jeffries' report (1972) on bats in Southeast England, were in press at the time this paper was presented. The evidence that the survival of a number of species of bats is threatened by organochlorine pesticides is now so clear that organizations of scientists would seem to be obligated to support legal action against further use of these chemicals.

Growing Concern Expressed

Concern about the survival of many species of bats has become world-wide. Following the discussions of 60 bat experts from 20 countries immediately before the 2nd International Bat Research Conference in Amsterdam in 1968, Stebbings (1970) summarized the main causes in the decline of bat populations as loss of habitat through urbanization and deforestation, loss of roost sites through destruction of old buildings and appropriation of caves by mushroom growers, harmful effects of chemicals (both insecticides and fumigation), vandalism, disturbance during banding, killing for "scientific" studies, and the development of an international traffic in bats.

Gould (1970) reminds biologists of the wealth of ideas on bat conservation in the pages of *Bat Research News*, edited from 1960 to 1970 by Wayne H. Davis, and recalls the editor's plea for responsible people to handle the commercial sale of bats for research. Gould also makes the point that bat students have a twin responsibility: (1) to inform the public of the possible dangers of bat rabies and (2) to inform them of bats "inherent benefit to potential insect control and their intimate relevance to the ecosystem," noting that an average colony of 100 small insectivorous bats consumes at least 24 lb of insects between June and September.

Jones (1971), at the 1971 North American Symposium on Bat Research at Albuquerque in November, recalled special pleas for bat conservation by Davis (1967), Manville (1962), and Cockrum (1969a, 1970) and outlined some steps which might be taken by the banding office.

The current surveys of bat banders by Jones and of NSS grottoes by the author reveal that awareness and concern have been rising sharply among bat researchers and many organized spelunking groups. This results partly from the fact that many college and university grottoes include or have intimate contact with research workers. Perhaps the best analysis of the problem, "Disturbances and Bats," was written by Humphrey (1969) at the request of the Central Oklahoma Grotto of the NSS and published in its newsletter. It has already been cited here and some of its recommendations, along with others proposed in the two surveys, are incorporated in the list below.

Conservation Proposals

On the basis of a proven need for corrective measures to reduce the threats to survival of many species of bats in North America, we urge that the following proposals be initiated promptly and pursued vigorously:

1. Encourage the U.S. Banding Office to
   a. Further restrict banding, authorizing the use of bands only when absolutely essential to an approved research program.
   b. Recall inactive permits.
   c. Further modify the bands to eliminate or reduce irritation or injury to bats.
   d. Seek the placement of the following additional species on the list of Rare and Endangered Mammals: *(Myotis grisescens, Lasiurus cinereus, Plecotus townsendii ingens* and *P.t. virginianus, Tadarida brasiliensis mexicana,* and *Euderma maculatum).*
   e. Encourage investigation of the status of other species for whom information is lacking.
   f. Computerize data to make their use available to research scientists.
2. While encouraging needed investigations on the ecology of bats, urge all investigators to familiarize themselves with the manual "Bats and Bat Banding" (Greenhall and Paradiso, 1968) concerning health hazards to the investigators and ways of handling bats to minimize disturbance or injury. Other procedures which have been suggested are:
   a. Substitute mist nets, hand nets, and Constantine-type traps at nursery cave entrances for large-scale bat handling operations inside caves.
   b. Employ photography in estimation of population sizes (Humphrey, 1971b) and consider automatic photo surveillance of movements during hibernation and development of neonatal bats (Fenton, personal communication).
   c. Monitor bat activity with ultrasonic sound detection equipment (Hooper, 1964; Fenton, 1970b).
   d. Speed and refine data collection in on-site physiological studies of hibernating bats.
3. Intensify the current effort to enlist the cooperation of organized spelunkers through voluntary action based on education and conservation policies adopted by the National Speleological Society, leading to drastic reduction of trips to bat caves during critical life history periods. Replies indicate a readiness of the grottoes to avoid trips which might disturb bats. Support for suppression of publication of cave location data is also evident (Williams, *et al.*, 1971).
4. Encourage liaison between NSS grottoes and knowledgeable members of university and museum staffs. Improve communication through prompt reports on bat conservation matters to *Bat Research News* (quarterly). Create a "Bat Conservation Task Force" within the NSS Internal Organization structure, responsible for notices and reports in the monthly *NSS News* and the *North American Biospeleological Newsletter* (occasional) and for development of research and conservation programs.
5. Establish or strengthen liaison with health authorities and with exterminating firms to attempt to limit control or eradication efforts and to establish a procedure for salvaging specimens for scientific research if occasional bat elimination measures prove unavoidable.
6. Accelerate efforts to bring additional hibernation, transient, and nursery roost cave sites under the protection of private groups such as The Nature Conservancy, The Ozark Underground Laboratory, etc., and persuade federal and state agencies to declare and enforce a moratorium on

visits to bat caves during periods determined to be critical.

7. Investigate the feasibility of providing substitute roost or hibernation sites when bat-proofing operations are anticipated or access to mines, caves, or tunnels (Mohr, 1942) will be ended. Stebbings (1970) reports the provision of bat boxes in lieu of hollow trees in Britain, USSR, Czechoslovakia, Poland, West Germany, and East Germany. Conservation officers keep records of the content of the boxes.
8. Seek national legislation and international agreements (since many species migrate across one or more national boundaries) to protect all species of bats against collecting or destruction (unless authorized by scientific permit or appropriate public health license) and against exposure to organochlorine pesticides (by supporting legal and legislative efforts to ban their use).

Conclusions

Responses to the survey questionnaires indicate a readiness, even an impatience, to be underway with an *active* program of bat conservation. The forthcoming meetings of the National Speleological Society and the American Society of Mammalogists will provide the first forums for reaction to and implementation of the proposals listed here.

Positive steps taken recently by informed and alert persons have corrected certain situations, such as replacement of improperly designed cave closures, and have prevented the carrying out of potentially harmful plans such as:

1. Developing a self-guiding spelunkers' tour of Dixon Cave, Mammoth Cave National Park. Revelation of data on the year-round importance of the cave to bat populations brought a quick veto of the plan.
2. Scheduled aerial spraying of an insecticide in Mark Twain National Forest, Missouri, was cancelled when Aley (1969) pointed out the hazard it presented to a small colony of *Myotis sodalis*, an endangered species, in Tumbling Creek Cave, 15 miles away.
3. A seriously considered proposal to close Bracken Bat Cave because of the hazard to aircraft at Randolph AFB presented by flights of free-tailed bats was dropped because of arguments based on the value of bats in the ecosystem.

With the development of master plans for many public lands, proposals for wilderness status, including the concept of *underground* wilderness (Davidson and Bishop, 1971), and the designation and use of environmental study areas in cooperation with educators, a new era has dawned in which the knowledge and influence of biologists and speleologists should be welcomed by responsible officials and by the concerned public.

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Bats as Primary Producers in an Ecosystem

Roy Horst *

ABSTRACT

An ecological system has developed in an abandoned mine near Alamos, Sonora, Mexico. This "cavern" contains a permanent bat colony of *Glossophaga soricina, Natalus mexicana,* and, during part of the year, *Leptonycteris nivalis.* A population of troglophilic cockroaches (*Periplaneta americana*?) also resides in this cavern, subsisting entirely on bat guano and moribund bats. The cave crab *Pseudothelthusa sonoriensis* is also present, feeding on guano, decomposing bats, and cockroaches. The frog *Rana pipiens* also occurs in moderate numbers and feeds primarily on cockroaches. The tadpoles feed on the plant life in the guano-enriched pool within the cavern entrance. Movement of these secondary species between the cave and the outside is minimal. Finally, predators enter and remove animals from the system but make no meaningful contribution to the energy content of the system. The energy expenditure of the bats (resulting in guano deposition) appears to be the primary and only significant support of the entire system.

From time immemorial, caves have been used as ritual sites, burial grounds, and even art museums. They have also been utilized in more mundane fashion as dwellings, store houses, and fortifications. In recent times and in more civilized areas, the use of caves has been largely confined to recreational exploring and not until the mid-nineteenth century did serious scientific exploration and study of caves begin (Schmidt, 1832; Sturm, 1844; and Tellkampf, 1844a, 1844b). In 1875 the first recorded scientific list of cave dwelling animals was published (Bedel and Simon, 1875), and the new science of biospeleology was established. Since that date, a rather large body of information has been presented in the literature and has been summarized and reviewed by Barr (1966, 1968) Poulson (1964), and Poulson and White (1969)—to name but a few of the more outstanding bibliographers.

From the volume of literature on caves alone, it is obvious that such environments are of great interest. In addition, the increase of interest in such cavernicolous vertebrates as bats and a host of cave-dwelling invertebrate species has brought a large number of nonspeleologists into direct contact with cave environments. The recent dramatic surge in the study of caves and their biological contents is accordingly not at all surprising. It is a callous observer indeed who fails to be impressed by the complex relationships of animals which can prosper in such seemingly barren and totally dark recesses of the earth. Some cave communities are quite simple, perhaps but a single species living on detritus brought into the cave by occasional floods, and Poulson and White (1969) present a strong and convincing case that these simple communities are ideal study models. Other caves, however, possess ecosystems of great complexity, and an example of the latter type is the abandoned mine tunnel of this study.

This mine, or cavern, contains three

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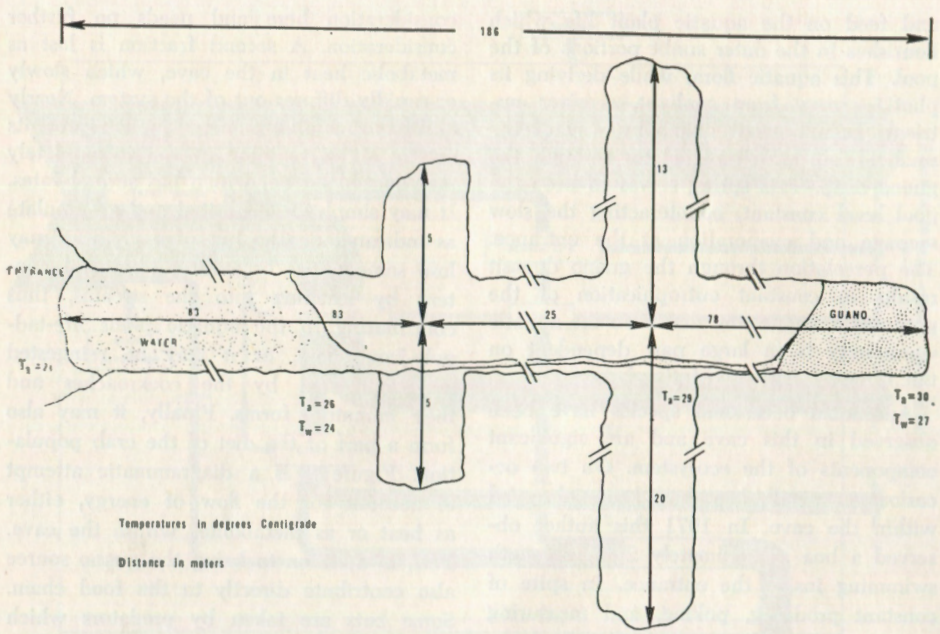
species of mammals as well as reptiles, amphibians, crabs, cockroaches, and other unidentified invertebrates, all living together in some sort of apparent harmony. The most interesting aspect (to this author at least) of this cave was the observation that the only significant source of energy available to this ecosystem was provided by the bat population. This report is a tentative and preliminary description of the food or energy chain in this cave.

Las Minas Cucaracha is located some 8 km west of Alamos, Sonora, Mexico, in mixed tropical deciduous and thorn forest at approximately 500 m elevation. This mine is an exploratory shaft excavated by Amos Yeager in search of silver in the late 19th century and abandoned when no ore was struck. The old tunnel has now taken on many of the characteristics of a small cave with the exception that it is manmade. Its physical aspects are as follows: The entrance leaves the surface at a slightly upward inclination from the horizontal, resulting in a slope of approximately 1%, allowing for drainage. The surface at the entrance falls away in a 20% incline increasing to 30% and ending in a shallow canyon some 100 m below the level of the cave. The entrance of the tunnel leads out onto a tailings heap, giving the false impression that the area immediately in front of the cave is relatively level. The entire area around the entrance is heavily covered with second-growth hardwood scrub. The entire cave has nearly uniform cross-sectional dimensions, varying in width from 2.5 to 4 m and in height from 2 to 3 m. At the inner end of the tunnel, a small permanent spring seeps from the rocks and trickles the length of the tunnel as a small stream. The main passage is 183 m in length and is straight enough so that the entrance is just visible from the inner end. The lateral arms vary in length from 5 m to 20 m. The overall floor plan, with dimensions, is given in Fig. 1. The terrain around the entrance has collapsed to the extent that it forms a low dam across the entrance, impounding the stream to a depth of approximately 50 cm. This body of water extends into the cave for 58 m, making it impossible for small animals to reach the dry part of the cave without flying over it or swimming through it. This pond serves as an effective barrier to any non-flying or non-swimming animals, but it is of course possible that insects may gain entrance to the cave by simply crawling along the rough walls. The temperature at the inner end is constant to within 2° of 30° C according to readings taken in March, June, August, and December, 1971. The temperature demonstrates an even, linear gradient toward the temperature at the entrance. The temperature of the water at various points tends to show the same gradient toward the outer end. The only marked water temperature deviation is at the very shallow edges of the small exterior portions of the pool. The entrance is depressed into the hillside and heavily overgrown so that air currents into the cave are held to a minimum.

The most obvious animals in the cave are cockroaches, *Periplaneta americana,* which are present on the walls of the cave and throughout its length but reach a density of over 100 per m² in the rear of the cave on the walls near the guano deposits. This horde of cockroaches, estimated in excess of 25,000 individuals, in fact gives this mine its present name. The cave contains a population (in 1971) of approximately 400 to 500 funnel-eared bats of the species *Natalus mexicana.* These are very small bats and the adults generally weigh less than 7g. Three color phases have been described for this species: gray, yellow, and reddish-chestnut (Walker, 1964; Hall and Kelson, 1959; and Villa, 1966); and all three color phases occur in this population. These bats are insectivorous, and they return to the cave soon after feeding to spend the resorptive phase of digestion in the cave, with the result that their droppings accumulate beneath their roost. This deposition of guano is the prime source of energy input into the ecosystem of this cave. The second bat species that is invariably present is the long-tongued bat, *Glossophaga soricina,* with approximately 200 individuals (in 1971) of this species



FLOOR PLAN OF "COCKROACH" MINE

Figure 1. This semi-diagrammatic floor plan of "Las Minas Cucaracha" shows the location of the guano deposit (far right). The bat colony is generally, but not always, found in this area. The symbols T_A and T_W are ambient air temperature and water temperature. All distances are in meters.

present on a year round basis. These are also rather small bats, the adults weighing less than 10 g. *Glossophaga* is primarily a nectar and pollen feeder but is known to take fruit and, on occasion, insects as well (Villa, 1966). The third bat species present is a population of approximately 100 to 150 *Leptonycteris sanborni,* which are present at this site on a seasonal basis. Their dietary habits are roughly parallel to those of *Glossophaga* (Howell, 1970), but the contribution of this species to the overall economy of the cave is minimal. The entire bat colony is crepuscular, leaving the cave at twilight and returning some hours later; so, according to Schiner's definition, these animals are not true troglobites but rather troglophiles, in that they inhabit a cavernicolous environment but leave it to forage.

This cavern is also populated by approximately 100 Mexican freshwater cave crabs, *Psuedothelthusa sonoriensis.* What role these animals play in the overall ecology of this system is difficult to determine with certainty. They have been observed feeding on dead bats, a decomposed frog carcass, and digging into the guano. It is assumed that they, like the cockroaches, are somewhat omnivorous and opportunistic in their dietary behavior.

As one enters the pool and wades into the cave, one is immediately impressed with the large number (undetermined) of frogs and tadpoles *(Rana pipiens)* in the pool. The tadpoles are of necessity confined to the water, but the frogs are found throughout the cave and travel to the guano region where they have been observed eating cockroaches. The tadpoles are vegetarians

and feed on the aquatic plant life which flourishes in the outer sunlit portions of the pool. This aquatic flora, while deriving its photic energy from sunlight, receives nutrients from the bat guano by way of the small stream which percolates through the guano heap. This spring serves to keep the pool level constant, counteracting the slow seepage and evaporation at the entrance. The percolation through the guano deposit results in constant eutrophication of the pool water, suggesting that even the aquatic community is in large part dependent on the foraging activity of the bats.

Additional occasional species have been observed in this cave and are significant components of the ecosystem. On two occasions a small boa has been observed within the cave. In 1971 this author observed a boa approximately 2 m in length swimming inside the entrance. In spite of constant prodding, poking, and measuring attempts, the snake was reluctant to leave the cave and in fact remained in the entrance pool during my entire 3-hour stay. Baker (1971) also reported seeing a smaller boa a few years previous to this, and this may be the same individual, the difference in size representing 2 year's growth. In 1970, I also observed tracks of one or more raccoons *(Procyon lotor)* in the mud at the inner edge of the pool. Turtles *(Kinosternum mexicana)* have been observed and reported by Keasy (1971), and I have observed as many as six individuals in one group. These animals are generally quiescent and lie in the shallow parts of the pool in water 5 to 10 cm deep.

The energy flow in this system is essentially as follows: The source of energy in this system is almost exclusively dependent on the foraging efforts of the bat population. Digestion in both groups of bats (insectivores and nectar-fruit feeders) occurs after the bats return to the cave, and their subsequent defecation results in the deposition of guano. Of the total energy intake of the bats, a large portion is spent in foraging outside of the ecosystem under consideration here and needs no further consideration. A second fraction is lost as metabolic heat in the cave, which slowly or rapidly diffuses out of the system. Nearly all of the remaining energy input represents energy still remaining in the incompletely metabolized guano, which has several fates. It may simply be deposited and accumulate as indicated on the left of Fig. 2. It may lose some of its organic and mineral content by leaching into the streams, thus contributing to the aquatic plant life-tadpole-frog chain, or it may be reingested and redigested by the cockroaches and their immature forms. Finally, it may also form a part of the diet of the crab population. Figure 2 is a diagrammatic attempt to account for the flow of energy, either as heat or as metabolites within the cave. Bats, in addition to being the guano source also contribute directly to the food chain. Some bats are taken by predators which enter from the outside of the cave, such as the boa or raccoon mentioned earlier. In this particular cave a significant predator is the investigator himself. Moribund bats are consumed by both crabs and cockroaches. These forms in turn fall victim to each other and to outside predators or simply die, decay, and become part of the guano deposition.

The question has arisen as to whether this ecosystem is in balance or not. The present animal community may possibly be consuming the guano at a greater rate than it is being replenished by the bats. In this event, the flow diagram (Fig. 2) would need to be altered as follows: the sum of predation and heat loss would be greater than energy input and the arrow leading to guano deposition would be reversed and labeled guano depletion. This could in fact be the case at present, as bat populations are decreasing in a great many areas (Mohr, 1972; Jones, 1971). Increased molestation of the fauna in this cave both by this author and by his equally sincere fellow biologists poses a real and constant threat to this ecosystem. The mere act of

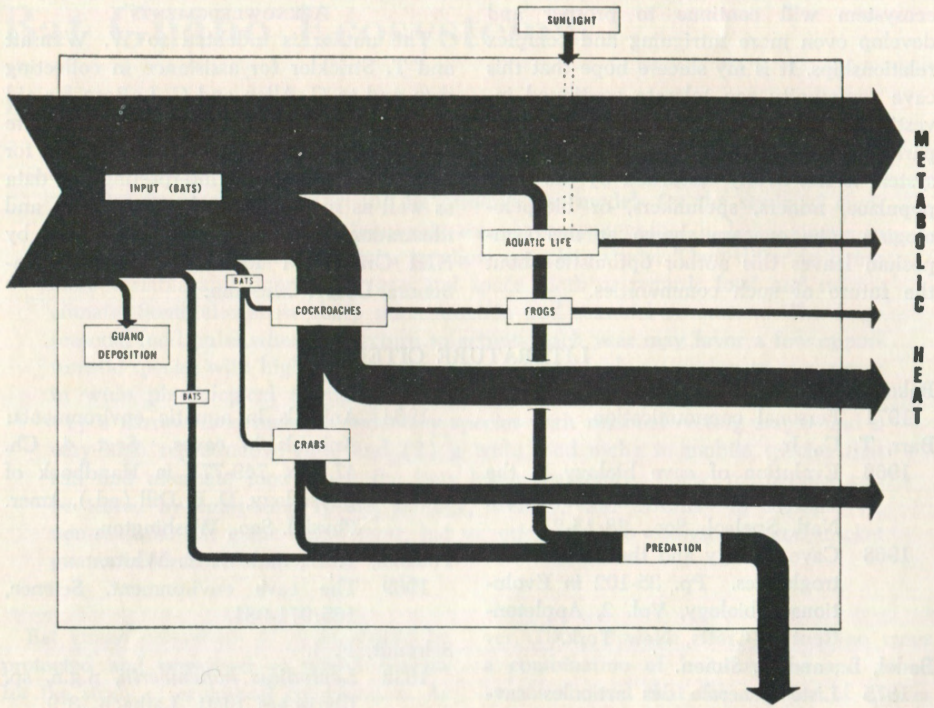


Figure 2. This diagram represents the theoretical flow of energy through this cave ecosystem. The area inside the rectangle represents the inside of the cave. Input is the total energy (in all forms) brought into the cave. The arrows leaving the "cave" on the right represent energy lost, primarily as metabolic heat. The arrow leaving below represents the loss to predators (and collectors). The relative width of the lines and arrows correspond to an estimate of the actual amounts of energy involved, but may actually be too wide or too narrow. Energy leaving should equal energy entering plus energy stored (guano deposition) if the system is in balance. Note that (lower left of diagram) some bats (probably moribund) are lost to both cockroaches and crabs as well as to predators.

investigating the complex nature of this system may in fact destroy it, and this rather sobering fact accounts at least in part for my reluctance to make a massive and exhaustive data gathering assault on this community.

To conclude on a more encouraging note, it is possible that this colony is relatively recent. Observations are not recorded for more than 15 or 20 years, and in any event the cavern is only approximately 100 years old. If the bat population was established fairly recently and was never much larger than at present, then the deposition of several tons of guano by only a few pounds of bats is a rather remarkable achievement. The secondary animals, i.e., cockroaches, crabs, frogs, etc., have in all probability arrived in significant numbers since the bats and may, in fact, be consuming the energy resources at a greater rate than they are presently being replenished. If this is the case, the negative balance will perforce eventually reach equilibrium and then in all probability show only minor fluctuations. In that event this remarkable little

ecosystem will continue to prosper and develop even more intriguing and complex relationships. It is my sincere hope that this cave community can tolerate continued investigation of its energy budget. It is of paramount importance then that this ecosystem is not overly disturbed by the local populace, miners, spelunkers, or biospeleologists. The concern shown at this symposium leaves this author optimistic about the future of such communities.

ACKNOWLEDGMENTS

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Bat Guano Ecosystems

Thomas L. Poulson *

ABSTRACT

Bat guano ecosystems should be preserved as models for the study of communities. They are like other temperate zone cave communities in being simple in structure with few enough species to allow complete study. They differ in being more variable and rigorous in time and space, both as regards food and microclimate. Some also show sharp microzonation and seasonal succession. The large seasonal food pulse when bats return to activity each year may favor a few opportunistic species with high reproductive rates. The variable microclimate may result in wide physiological tolerance. There should be two strategies for feeding: (1) a narrow food niche in sedentary species with seasonal resting stages and a very high reproductive rate; and (2) a wide food niche in mobile species that can find alternate food when the bats leave seasonally. These predictions can be tested by comparing species biology, ecology, and diversity in seasonal vs. non-seasonal bat guano ecosystems, bat vs. cricket guano ecosystems, and cricket guano vs. detrital ecosystems.

Bat guano ecosystems in caves should be protected and preserved as model systems for the study of ecological communities. As a subset of cave communities, they share the advantages of simplicity in trophic structure and in number of species (Poulson and White, 1969; Poulson, 1971). This makes it possible to study the physiology, life history, behavior, and ecology of each species in enough detail to see how each species fits into the community.

It is my hypothesis that a species' biology is determined through natural selection by such characteristics of food supply and microclimate as rigor (extremes), variability (variance/mean), and predictability (autocorrelation) and that the species' biology in turn determines community structure and function. Guano ecosystems in caves will provide field tests of this hypothesis. Until recently my field studies have concerned cave entrances (Culver and Poulson, 1970) and areas in the deep cave that differ primarily in microclimate and substrate heterogeneity (Poulson and Culver, 1969; Poulson, 1971). In these cases a combination of bait-trapping and visual census showed that the number of species and their evenness of abundance were inversely correlated with rigor of flooding and desiccation and directly correlated with substrate cover diversity and perhaps with food supply. The latter two correlations may be reflections of other important factors, microclimate in the case of cover and the general scarcity in the case of food in caves. To sort this out, it would be nice to have a wider range of conditions accessible to the same cave organisms that live in the deep cave and/or near entrances. For this reason, guano communities are of interest.

Bat guano ecosystems differ from other cave communities in being more variable and rigorous in time and space, both for microclimate and food. Harris (1970) has described the seasonal cycle associated with the predictable spring-summer occupation of a cave by a maternity colony of bent-winged bats in Australia. As the bats arrive, there are fast changes in food, temperature, moisture relations, and pH. Food quantity, rate of daily input, and freshness all increase. The guano temperature rises 10°C

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within a week. The fresh guano along with bat respiration and urination combine to increase the relative humidity from 60 to 95%, and the substrate becomes visibly moist. The urine-ammonia aerosols and fecal material modify the substrate pH and other chemical characteristics. Henshaw (1960) and Herreid (1963) also describe the effect of immense maternity colonies of free-tailed bats in Texas on cave microclimate. The movement of bats around the cave within a season, presumably to avoid the highest temperatures and ammonia concentrations, add to seasonal differences in variability. In addition, many of these same parameters vary within one guano pile with depth in the guano and distance from the center.

Spatial variation in guano piles leads to sharp microzonation. Other than at cave entrances, zonation is not seen in other cave ecosystems because microclimate and food vary so little and change so gradually. The zonation on a guano pile is most striking in simple communities, as in the case of *Myotis griscescens* (grey bat) caves that I have visited in Missouri and Arkansas. The fresh guano at the apex of the pile is swarming with mites (1-2 thousand/dm^2) with a few rhaphidophorine crickets (1-2/dm^2). As the guano becomes drier in time or in space down from the apex of the pile, there is a sharp change to molds with white hyphae (aspergillus-like species with green mats of fruiting bodies and a more spottily distributed penicillium-like species dotted with yellow fruiting bodies). With further drying, visible life disappears. In the case of a year-round colony of only about a hundred *M. sodalis* (social bat) in Kentucky, the phorid flies are common and mold of a white-tufted variety is scattered over the guano pile. The more complex guano communities of the Nullarbor Plain (Richards, 1971) or Queensland (Harris, 1970) caves of Australia and of the free-tailed bat caves of Texas and New Mexico (Barr and Reddell, 1967; Mitchell, 1970) may also be sharply zoned; the authors do not address this point, but zonation seems likely since there are at least two different sets of microclimate and food preferences for the fauna. The freshest and wettest guano has an abundance of mites, mite predators (including other mites and pseudoscorpions), rhaphidophorine crickets, and bat ectoparasites, especially fleas. The older and drier guano, with presumably lower food content, has large numbers of tenebrionid or dermestid beetles, a ptinid scavenger beetle, a tineid clothes moth, and a web-building spider; some flies, such as phorids and heliomyzids, are sporadically common, and there are many species such as carabids, millipedes, and a psocid that are more like troglobitic species in being regular, but uncommon. If this zonation is normal, then the species diversity in each zone is no higher than in the more complex deep cave communities with much lower numbers of individuals. Each zone is characterized by a high number of one or two species with other species being rare or absent. Even the guano community as a whole has relatively few abundant species and thus a low species diversity.

In addition to zonation, guano communities can be differentiated from deep cave communities by a seasonal decrease in diversity. Seasonal migration of bats in temperate zones leads to seasonal succession in one guano community (Harris, 1970), and incidental data of my own and others from different seasons (Barr and Reddell, 1967; Mitchell, 1970) suggest that seasonal succession is widespread. Harris suggests that some species show an analogue of hibernation when the bats are not present. If these resting stages are eggs, spores, or very small life history stages, then it will appear as if there are no animals in the inactive season. This succession is probably a function of microclimate and not just food supply (Harris, 1970). The change from a mite- to a collembola-dominated porcupine guano community with increasing decomposition (Calder and Bleakney, 1965) suggests the sort of changes to be expected seasonally when the relative humidity and temperature are relatively constant. The poorly decomposed guano with a pH of 5.1 and 43% organic matter had 5.7 collembola and 165.6 mites per 100 ml, whereas the well decomposed guano with a pH of 7.2 and less than 30% organic matter had 127.1 collembola and 7.2 mites per 100 ml. As in bat guano communities, two or three species made up over 85% of the total number of animals.

Although guano communities are more variable and rigorous in food and microclimate than other cave communities, they are potentially just as predictable. The bats come back every year at the same time and have probably been doing so, judging from guano accumulations, for many thousands of years. This means that any species living only in guano—let me call them guanobites—could be highly keyed to seasonal cycles and could be active in or select only particular food qualities and microclimates. If so, this would help account for the observed microzonation as well as the seasonal succession. Such guanobites, unlike other troglophilic cave animals that might rely on guano only part of the time, would not have to be very mobile. I do not know if there actually are any guanobites as most guano-associated animals seem to be mobile troglophiles with wide food and habitat niches (e.g., phorid flies and rhaphidophorine crickets), but the saprophagous mite–predatory mite–pseudoscorpion community common to many guano ecosystems show adaptations that I would expect for guanobites. I would differentiate guanobites from the occasional troglobites associated with guano in the inactive season by the high reproductive rate of guanobites necessary to take advantage of the food pulse at the beginning of the active period as the bats arrive from their wintering grounds or hibernation caves.

The most striking, and I think most important, difference between guano and other cave communities is the large and fast increase of food input that starts again each year when bats return to a maternity cave. I believe that this food pulse favors a high reproductive rate, whether by sedentary specialized guanobites with a combination of innate seasonal rhythm and timing by proximate clues or by mobile generalist troglophiles that are reproductive opportunists. In either case, a high intrinsic rate of natural increase allows quick monopolization of the food resource. Unfortunately we do not even have life history data or reproductive rate and generation length for many of the more obvious large troglophiles. What we do know is their niche breadths. However, their wide food and habitat niche breadths may be dictated by temporal and spatial variation in food and microclimate irrespective of reproductive strategy. In the Nullarbor caves of Australia, Richards (1971) finds that the four troglophiles that make up more than half of the biomass are the widest distributed species, which have by far the widest food and habitat niches. The animals involved—a tenebrionid beetle, a ptinid beetle, a rhaphidophorine cricket, and a clothes moth—are also important components of guano communities in the United States.

The preponderance of troglophiles and trogloxenes in temperate zone bat guano ecosystems (Barr and Reddell, 1967; Mitchell, 1970; Richards, 1971) suggests to me that large food pulses, and not average food supply per se, preclude troglobitic adaptation. Thus a large and variable food supply and associated microclimatic variation would result in selection for the high reproductive rate and wide food and habitat niche that separates troglophiles from their troglobitic relatives with low reproductive rate and relatively narrow niche. If this is correct, then there should be a systematic ordering of trogloxene–troglophile–troglobite species composition in different guano communities. Specifically, I predict an increasing proportion of long-lived slow-reproducing, narrow-niched species along a sequence of guano communities starting with the most seasonal bat caves with the biggest bat population—and so the greatest temporal and spatial variation in food and microclimate—and ending with a deep cave community with minimal food input and little variation in food or microclimate. This se-

quence of guano communities should be as follows: (1) Free-tailed bats, *Tadarida mexicana,* (Barr and Reddell, 1967; Mitchell, 1970); (2) Grey bats, *Myotis griscescens,* in the U.S. (personal observation and communication with J. E. Cooper) or little chocolate bats, *Chalinolobus morio,* (Richards, 1971) and bent-winged bats, *Miniopterus schreibersii,* (Harris, 1970) in Australia; (3) social bats, *Myotis sodalis,* (personal observation) in Kentucky; (4) cave rat, *Neotoma magister,* (personal observation), porcupine, *Erethizon dorsalis,* (Calder and Bleakney, 1965), rhaphidophorine crickets, e.g., *Hadenoecus subterraneus,* (Barr and Kuehne, 1971; personal observation); (5) isolated fecal specimens or carcasses; (6) rotting wood and other vegetable debris; and (7) mud with a high organic content. Though data still are required from one single cave or at least one cave region in order to make valid comparisons of these categories, the fragmentary data are not at odds with the hypothesis. In the most extreme bat guano situation, there is a high proportion of omnivores, herbivores, and saprophages; a few species with high density and biomass and a moderate number of much rarer species; and a high proportion of trogloxenes and troglophiles which have wide food and habitat niches. All in all, this is a simple community that may vary little from year to year but varies considerably from site to site and season to season. In contrast, in the mud community there is a high proportion of predators; a moderate number of species with low density and biomass with no one dominant in number or biomass; and a high proportion of troglobites with both wide and narrow food and habitat niches. All in all, this is a complex community that varies little from year to year, season to season, or site to site.

I have tried to show how guano communities fit into my earlier studies of the relation of food and microclimate to species diversity in extending the range of conditions examined in caves to higher and more variable food supply and more variable and rigorous microclimate. I have made qualitative correlations among guano communities which are consistent with the quantitative correlations done previously (Poulson and Culver, 1969; Culver and Poulson, 1970) on a narrower range of food and microclimate variation. What remains to be done is: (1) to examine the species biology in situations 1-7 (especially to test my prediction of high reproductive rate, wide food and habitat niches, and wide physiological tolerance for the species in guano communities) and, more importantly, (2) to test, by perturbation experiments in nature, my hypothesis that rate of change in food supply is as important or more important than the amount of food in influencing a species' biology through natural selection. Under this hypothesis, community structure and function is an inevitable outcome of the biology of the species present.

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Niche Specificity and Adaptability in Cave Bats

Robert E. Henshaw *

ABSTRACT

Bats originated in the tropics. Their morphology is essentially unchanged today from the earliest Eocene fossil. Their behaviors also evolved in the tropics and are retained mostly unchanged in bats inhabiting temperate and subarctic regions. Niches may be best defined in terms of microclimate, principally temperature, evaporation of water, and light. Actual isolating mechanisms related to sound, olfaction, and social behavior have differentiated but are yet undescribed. Karyotypes of bats are very similar. Bats, then, appear to be an implastic order that is poorly capable of responding to large rapid changes in their environment such as are produced by man today.

Permutations of the environment by man must be examined with respect to the degree of lethality on each organism affected, the percentage of all organisms affected, and the rate of change of the environment with respect to the possible rate of evolution (compensation) by the organisms. Likewise, the distribution and habits of organisms can ameliorate or potentiate negative effects of environmental change. These points are most dramatically supported when examining the interaction of man and bats. In Fig. 1 is schematized the possible degree of negative effect on bats caused by environmental insult. We must consider the effect on the entire interbreeding population of a species, i.e., the "gene pool". Even lethal accidents to individuals have little effect on the gene pool if there are many individuals, i.e., the species is common over its range. Even lethal accidents to many individuals in a local area have little effect on the gene pool if the species is widely distributed, assuming that there are few genetic differences in populations from different parts of the species' range. Likewise, rarity within the organism's geographic range and small geographic range make accidents of greater importance to the total gene pool.

Social habits affect exposure to environmental insult. Concentration seasonally in hibernating caves, or year around in clusters, causes a greater percentage of the gene pool to be affected by locally applied insults, and the spread of disease and parasites is facilitated. The gene pool of solitary tree bats might be little affected by very local permutations. Two interesting effects should be noted: air pollution or insecticide residues in food insects may affect solitary and colonial bats alike because these environmental insults affect food rather than habitat, and hibernation in cold caves might provide a measure of protection from some air pollutants, e.g., smoke particles, and from background radiation and its mutagenic effects (note Fig. 1, ubiquitous, lethal, colonial).

Social habits also affect the ability of the species to adjust to environmental change. Wright (1970) has shown that in many situations a species subdivided into semi-isolated breeding units has a faster rate of genetic change than does a large, undivided population. This would suggest that social bats, and bats such as the little brown bat that copulate after congregating

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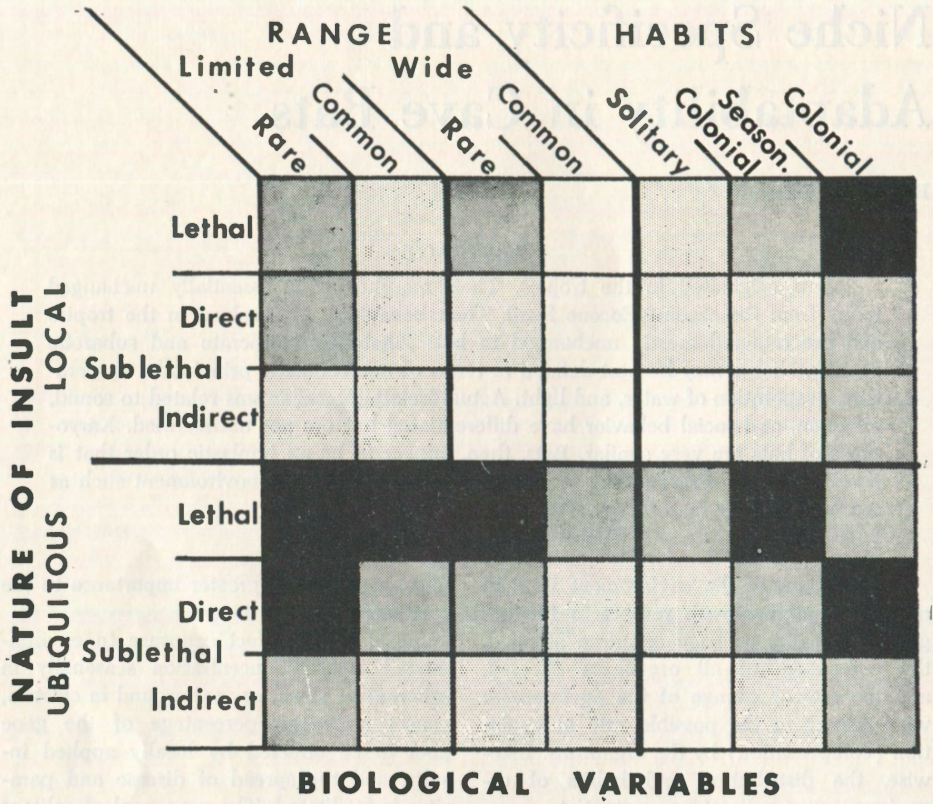

Figure 1. Potential for environmental permutations to affect bats. The darker the shading, the greater would be the likely negative effect on bat species. Environmental shifts will be of importance to a species in relation to the portion of the entire gene pool which is adversely affected. Geographic range, density within that range, and social habits which concentrate and thus expose larger portions of the gene pool, therefore interact with area and intensity of insult. Each species must be examined independently from a population point of view. All potentially interbreeding individuals throughout that species' geographic range contribute to a common gene pool. Environmental damage to the gene pool, by removal of individuals, jeopardizes the species.

in winter hibernacula, will be less able to change genetically than will solitary bats.

Two generalizations may be made:

1. As an insult becomes widespread or "ubiquitous," that is, as it approaches the entire gene pool in number of individuals affected, it has greater damaging effect on the species.

2. Concentration of bats increases potential for an insult to affect a larger percentage of the gene pool and hence to have greater damaging effect.

In the following discussion I will draw together facts related to the past evolutionary history of bats, their morphology, physiology, behavior, ecology, and chromosomal patterns. Taken together, these facts strongly suggest that bats are a conservative group evolutionarily and that their potential for either short-term physiological

Figure 2. Northern limits of North American (Nearctic) families of bats. Homeothermic tropical/subtropical Phyllostomatids (leafnose bats) reach tropical and desert regions of the U.S.; migratory and possibly hibernating Molossids (freetail bats) extend from Mexico into western cold temperate regions where caves abound; migratory and/or hibernating Vespertilionids (plainnose bats) have fully invaded cold temperate and subarctic regions.

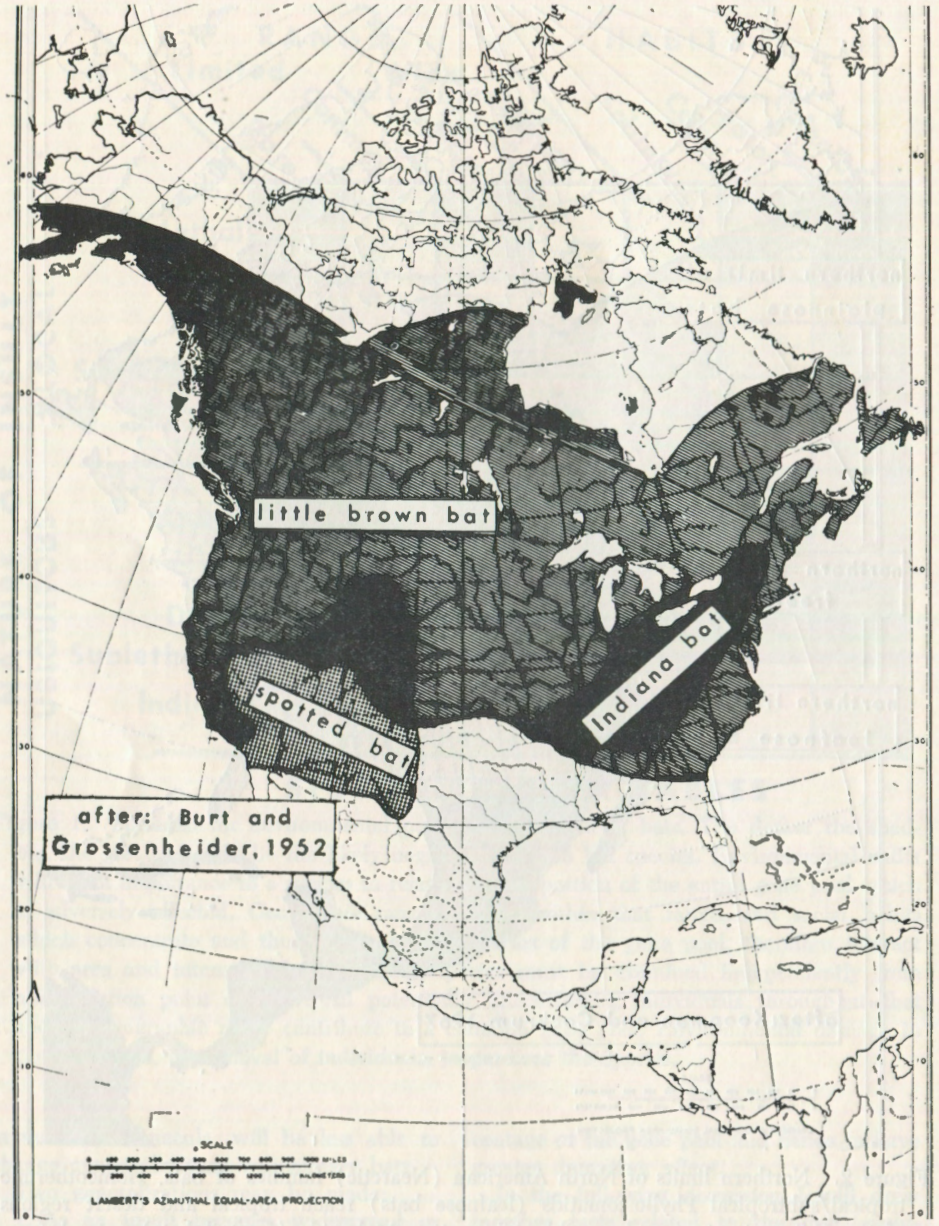

Figure 3. Geographic ranges of three species of Vespertilionid bat. The little brown bat *(Myotis lucifugus)* is widely distributed and common *(presently)* throughout its range. The Indiana bat *(Myotis sodalis)* has a limited range and is common when in winter hibernacula. This species is on the Department of Interior Endangered Species List because of rapid decimation of populations in recent years. The spotted bat *(Euderma maculata)* has a limited range, is rare throughout, and has been nominated for inclusion on the Endangered Species List.

change or long-term genetic change is much less than that of many other groups of organisms.

Bats originated in the tropics (Jones and Genoways, 1970; Koopman, 1970), and few have evolved the capability of survival in cold temperate climates. Of the 16 extant families of bat, all are represented in the Old or New World tropics. Only two of these, the Vespertilionidae ("plainnose bats") and the Molossidae ("freetail bats") have significantly invaded the North American temperate region (Fig. 2). Only the Vespertilionidae and the Rhinolophidae ("horseshoe bats") have extended to northern Eurasia. A few species of Vespertilionids reach the subarctic (Koopman, 1970). Although all species tolerate hypothermia, only those capable of natural seasonal hibernation have successfully settled into northern latitudes.

Hibernation probably evolved in the tropics, prior to extension of ranges into temperate latitudes, associated with low homeothermic metabolic rates during diurnal inactivity and nocturnal feeding (Henshaw, 1970; McNab, 1969). Likewise, such behaviors as selection of overwintering hibernacula and migration may be indicative of ancestral tropical origin. In North America, only three species of Phyllostomatids cross into hot regions of southwestern United States; all are mostly homeothermic. Six species of Molossids enter the U.S., but only the Mexican freetails and big freetails, which are seasonally migratory (Jones and Genoways, 1970) and probably hibernate (Herreid, 1963), reach cold temperate areas. In contrast, of the 28 species of Vespertilionids in the U.S. and Canada, only seven are restricted to warm southern regions. All hibernate seasonally and in some cases daily throughout the summer also. In the northern reaches of their distributions, most species migrate at least to central latitudes. No hibernating bat can overwinter where winter cave temperatures are continuously below 0°C. In summary, basic life styles of bats are very similar and differ largely in tolerance of one or more environmental variables, e.g., summer night air temperature, or in social habits.

Niche overlap may be great in small bats, although it has not been quantified for any two species. Many species of bats are sympatric, feeding on the same flying insects and inhabiting the same colonies and hibernacula (e.g., in Fig. 3). Comparative feeding studies have not been designed to yield this sort of information, yet it appears that most or all of the similar-sized sympatric species of bat feed on the same size range of insects. McNab (1971) has shown that the bat fauna on small Caribbean islands is structured to partition resources, but he found two high-flying insectivorous species always present, and these presumably take the same prey. It is likely that North American bats forage in different microhabitats even while consuming the same insect species.

Although the feeding niches, as defined by microclimatic variables, are usually somewhat different, there is no character displacement or competitive intensification (Ford, 1964) apparent to the observer. As an illustration, in one cave hibernaculum where four species of Vespertilionids regularly overwintered, each species selected roosting sites with differing climatic variable sets (Fig. 4). Microclimates selected for hibernation by animals in different genera were more different than those selected by congeners: *Eptesicus fuscus*, the big brown bat: very cold and variable; *Pipistrellus subflavus*, the eastern pipistrel: warm and stable; *Myotis lucifugus*, the little brown bat: cool and somewhat variable; *Myotis sodalis*, the Indiana bat: cooler and variable. Similar microclimatic analyses with similar results have been made by Twente (1955), Davis (1959), and Davis and Reite (1967). In all species so far studied, the microclimatic limits of each niche are very similar but very precisely set. That is to say, each species of bat seems to be very inflexible in its adjustment to its environment (Henshaw and Folk, 1966).

Social behavior appears to be related not

TABLE 2. Diversity of Orders and Certain Families of Mammals: Abundance of Taxa *

Taxa** Order	Family	Families per order	No. of genera	No. of species	Species per genus
Very Common					
Rodentia		..	35	1687	4.8
Common					
Chiroptera		..	175	875	4.4 (Average excluding below)
	Rhinolophidae	..	11	131	12.0
	Phyllostomatidae	..	50	129	2.6
	Vespertilionidae	..	35	287	8.3
	Molossidae	..	11	88	8.0
Less Common					
Primates, Artiodactyla, Marsupialia, Insectivora, Odontoceti, and Carnivora		7–10	409	1312	2.2–5.3
Carnivora		..	96	253	2.2 (Average excluding Felidae)
	Felidae	..	4	37	9.2
Uncommon					
Mysticeti, Edentata, Perissodactyla, Pinnipedia, Monotremata, Sirenia, Tubulidentata, Proboscidea, Dermoptera, Hyracoidea, and Pholidota		1–3	68	186	1.0–3.2 (excluding Lagomorpha)
Lagomorpha		..	9	63	7.0
Pholidota		..	1	8	8.0
		Total	1004	4060	3.5 Average of all Orders

* Compiled from Anderson and Jones (1967). Taxonomic categories are a human contrivance and may not reflect real biological diversity; however a high proportion of species with respect to genera may be indicative of small evolutionary changes, i.e., "microevolution". Note the unusually high ratios in the selected families in contrast to average ratios for all orders.

** Arranged in order of number of families per order.

forms. Of importance to this discussion is that these three families are the only families of the order Chiroptera that have extensively invaded the cold temperate regions where man, during recent times, has made large environmental perturbations with air pollution, insecticides, and attacks on colonies. Their genome apparently confers fitness in regions with low temperature and seasonal food abundance, but extension of range has been a quantitative shift of already evolved characters. We must ask whether these formerly successful families of bats are not now in especially great danger, due to an inability to evolve compensatory mechanisms at a rate fast enough to keep pace with environmental change.

The basic body plan of bats clearly has provided a very successful way of life. Chiroptera are second only to the rodents in numbers of families and total number of species. Given the permissive environment of the tropics (except for use of DDT, etc.), tropical bats could be considered safe from man's negative effects. However, we must question how precarious is the niche of the Vespertilionids, the Molossids, and possibly the Rhinolophids, with their probable evolutionary conservatism in technologically dominated north temperate regions. When compared to the rapidly evolving Rodentia, Chiroptera may be found to possess a body plan which limits it to more narrowly defined ecological niches.

It seems entirely likely that bats as a whole are quite implastic, incapable of macroevolution today, and responding to selective pressures largely by microevolution. Early bats may have evolved rapidly in jumps, i.e., were highly adaptable (early large-step evolution conveyed a high degree of fitness in a permissive environment), but extant species may now have low adaptability and be incapable of survival if habitats are markedly changed. Of course, discussions about adaptability and future evolution are conjectural at best. However, if we take available information and if chiropteran chromosomes are found to have little heterochromatin, I for one would propose that the bat's niche is unusually precarious in a world dominated and modified by the caprice of modern man, and that the bat would suffer unduly if man increases his environmental insults on the bat and its ecosystem. Radical conservation measures would seem fully justified.

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Discussion

After the formal presentations of the symposium, an open discussion was held. The following is from a tape recording of that discussion and has been edited and condensed.

ROBERT HENSHAW (Pennsylvania State University): O.K., let's talk. The papers you have just heard very nicely set the stage for the most important portion of this meeting: a chance for us all to do a bit of brain-storming on the demise of bat populations. I have here in my hand a letter from a professional collecting agency who would like to collect and supply "limited numbers" of bats for research purposes. They claim "our collecting interferes with no research work of any kind and collecting is conducted in a manner to insure continuation of any colonies." I also am holding a letter from a scientist in a prominent eastern medical college who states that he needs bats for his research. He does not specify the number of animals he needs nor the nature or importance of his research. His letter was answered by John Holsinger, Chairman of the Research Advisory Committee of the NSS, stating that he should contact experts in the area of bat biology and that he should consider in his requests that many bat species appear to be declining in numbers from their previously large populations. Finally I have here a letter from Robert R. Stitt, a Conservation Chair-One for the NSS. He has sent an urgent request that biologists and concerned persons in this country form a Conservation Task Force to deal with the problems of the declining bat numbers.

Let's come to grips with the overall question of conservation of bats.

ROY HORST (University of Vermont): In 1970, scientists actively doing research on bats from all over the country gathered in Tucson, Arizona. Attention rapidly focused on the declining numbers of all species of bats, and we resolved to discuss this at our 1971 meeting. Last month [November, 1971] we met again at Albuquerque, New Mexico, where a number of us reported on the declining numbers and possible causes. A number of resolutions were passed regarding the use and misuse of bats for science. Anyone who is interested in receiving the summary of that meeting should write to me and I will be happy to send them a copy free of charge. [Address follows Horst's paper in symposium.]

HENSHAW: Would you characterize your attitude there as similar to Charles Mohr's?

HORST: The only difference is that I feel Charles Mohr did not get mad enough.

DODY COVALT-DUNNING (University of West Virginia): We need much more information on the rates of human predation on bat populations in different areas. I am aware of some data in the tropics that attempts at extermination of vampires were all but ineffective.

HORST: Vampires are moving within large circular home ranges. They would collect all the bats in one cave on one night, and when they went back the next day, they would find an equal number of animals again. So bats are moving among many caves in their home range. But the killed animals were not so rapidly replaced in the population as they seemed to be in the colony. The population may be more vulnerable, but as several here can testify individual vampires are tough little . . . [remark did not register on tape recorder].

THOMAS POULSON (Notre Dame University): Bats are long lived. But they also have very low reproduction rate, one young per year in most species, and it therefore takes a very long time for the population to bounce back.

DENNIS TURNER (Johns Hopkins University): Very recently, Griffin has estimated

that even though bats may live up to 25 years in the temperate region, the average life expectancy in the tropics is 8 months!

HENSHAW: Rarity to the collector may not be the best estimate of population fitness. We need to consider what is a breeding unit. That is, what is the minimum number of individuals in the population that can maintain that population indefinitely. We have no such data on any species of bats. We do not know how rare a rare species is and how they find mates. We do not even know how rare is the seemingly common little brown bat from the standpoint of the little brown bat.

I trust it is clear that bat populations are declining rapidly and are possibly dangerously low. What can we as scientists and cavers do?

BRO NICHOLAS (LaSalle College): I think Charles Mohr was entirely too polite in two areas: the first is our reluctance in the past to discuss the problems of bat conservation with commercial cave operators. We should approach The National Cave Association. We should ask them to give in their interpretative programs a better image of bats to the public. Where commercial caves have large hibernating colonies, they should be encouraged to stay away completely. They don't have to show that area of the cave or the bat to the public.

Secondly, I think we must become much more critical of the work done in the name of science by groups such as physiologists, biochemists, and natural historians. I don't mean to single out these groups as especially guilty, but I know people in three different universities here in the city of Philadelphia who conduct nearly weekly trips to collect bats around the city. Others from the New York City area have notified me that they have cleaned out the New York area, and they now need more bat locations to continue their research. Every year I get many letters from researchers around the country requesting information about where they can capture bats for their research. Frequently they give no indication of the number of animals they need or the specific nature of their research. In most of these cases, I have chosen not to answer the letters at all. Clearly these people need to be communicated with; they are surely naive about the status of bats.

CHARLES MOHR (Delaware Department of Natural Resources): I was restrained earlier because I can't get in writing from you scientists specifics of the events which you have referred to many times, including here today. My statement therefore is based largely on general information of which I am aware. The recognition by bat researchers is very recent. Many people were sincere in their dedication to science, but decisions must now be made regarding the relative worth of the study, taking other factors such as bat conservation into account. The man who decides who gets bat bands and which bat banding programs should be supported is in the audience today [indicated Dr. Clyde Jones]. He needs our support in his choosing who gets and who doesn't get bat bands. He needs more information than just the researchers' credentials and whether the study is wisely conceived.

We need to get into literature other than scientific journals—magazines and journals with a large circulation such as the Audubon Magazine, National Wildlife Magazine, and Natural History Magazine. There is a vast reading audience out there which simply has not been made aware of the problem, but would be sympathetic and cooperative if well informed.

We also could keep better informed ourselves by subscribing to the several bat-related informal scientific publications. I mentioned earlier the Bat Research News. It appears quarterly for an annual subscription rate of only $1.00 (!) by writing to Dr. Robert L. Martin [Department of Biology, Treble Hall, University of Maine, Farmington, Maine 04938].

RICHARD E. GRAHAM (Upsala College): Within the NSS, we put out several times a year the North American Biospeleology Newsletter also for only $1.00. You can get it by writing to me, the Secretary, care of the Department of Biology, Upsala College, East Orange, New Jersey 07019. In it, all of the cave biologists keep in touch; it is related not just to bat conservation but to conservation of all cave species.

HORST: The 1970 and 71 bat research conferences to which I referred before will likely be annual events where bat researchers come together to talk. I just want to remind you that we would be happy to have any of you on the mailing list to receive the abstracts and minutes and invitations of the future meetings. And ours at the moment are free (!); so please write to me.

HENSHAW: What about formation of a Task Force and what would be its function?

CLYDE JONES (Department of Interior): The formation of a Task Force would be very useful if it could serve in an advisory capacity to the wildlife biologists in the Department of Interior. However, it is my feeling that a Task Force should be as small as possible in order to maximize its ability to respond and its effectiveness in presenting its point of view when called upon. Certainly the Task Force could serve as liaison to our office, but what we really need is input from all of you scientists who care and who have data already put on paper. We need to get all of the information possible from you collated in our office.

HENSHAW: What office and what are your activities in bat conservation?

JONES: The Department of Interior through its Bureau of Sports, Fish, and Wildlife is charged with the responsibility of study and management of all wild animal species. As many of you here know, we are vitally concerned about bats no less than we are concerned about game animals. My office in the National Museum of Natural History has the responsibility of collating all of the information scientists can get to us regarding bats. We will then write a status report and be able to recommend species of bats for the official Department of Interior Endangered Species List. That is the first step which serves to gain public attention. As a second step corrective measures can be recommended in federal and state programs. A good example was the placing of a gate across the entrance of the Carter Cave in Kentucky to protect *Myotis sodalis*. Ultimately our agency, better than any other, can push for legislation in Congress to have bats treated the same as migratory birds. Inclusion under the migratory bird act would make killing of all bats illegal. It would permit us to limit bat-banding permits and would require permits for collection of animals for research and other purposes. All scientific grant proposals submitted to any agency are now scanned for the researchers' intent to use any endangered species. With bats included in the migratory bird act, all proposals would be scanned for the use of any species of bats. It is my feeling that such legislation would solve 60% of our bat problems. You can see then why I have suggested that what we want is a maximum amount of scientific and natural history input from all scientists involved with bats. We need also maximum input in the form of letters of support for bat conservation and their suggested inclusion under the migratory bird act. This places a very heavy responsibility on all of your shoulders I am aware, but as you can see, the Department of Interior would serve as a stopgap and liaison on the way to congressional action.

MOHR: Rane Curl, President of the NSS, wrote me recently and asked that we form a Task Force for bats. So the NSS is ready and willing for this effort. Also the American Society of Mammalogists have asked that we draw up a resolution to present at their annual meeting next spring.

Recommendations of the Symposium

Further discussions as to constructive steps which could be taken to aid bat conservation were held throughout the day. As a result of the decisions reached, the following recommendations are offered:

1. A Task Force on Bat Conservation should be formed immediately.
   a. with the independence to speak for scientists and concerned citizens;
   b. possibly within the NSS;
   c. with one or two individuals acting as principal spokesmen;
   d. with all scientists, cavers, cave managers, and citizens encouraged to join and thus to add weight to opinions expressed by the principal spokesmen.

2. It was recommended that Charles E. Mohr be the leader of the U. S. Task Force on Bat Conservation.
   a. He is well qualified as a biologist;
   b. He is renowned for years of speaking for conservation.

3. The minimal operating expenses of the Task Force, e.g., postage, should be provided by the NSS.

4. The Task Force should carry out the following:
   a. immediately contact and enlist support of all concerned;
   b. prepare a position paper on bat conservation for presentation at the American Society of Mammalogists meeting;
   c. prepare a position paper for use by the Fish and Wildlife Service, Department of Interior;
   d. prepare and collect resource data on bat populations for use in public statements and use by Dept. of Interior;
   e. enlist services of competent writers to prepare articles for biological journals and wide-circulation biological magazines;
   f. contact and enlist support from cave managers in the National Cave Association;
   g. organize a scientific advisory board to be available to any public agencies needing expert opinion;
   h. develop channels of communication with public health officials whose interests include epidemiology of rabies;
   i. encourage and support faster, much more basic, ecological and natural history, mostly non-lethal, studies of bats;
   j. encourage scientists to discuss and discourage lethal experiments conducted by their colleagues and themselves, even at the risk of some ill will in return;
   k. follow insecticide and other pollutant uses, to alert appropriate agencies to crises;
   l. encourage scientists to communicate findings informally to the Task Force or to the Dept. of Interior. Discourage them from always waiting to release a formal journal article;
   m. mobilize on other efforts as appropriate.

[Editors' comment: In view of the evidence presented in this symposium which strongly implicates DDT as a serious factor in the decline of bat populations, it is somewhat surprising that the recommendations above avoid the politically controversial issue of pesticide prohibitions. We feel that the evidence is sufficiently clear regarding the magnitude of the crisis and the part played by DDT. While absolutely conclusive scientific evidence may not yet be available, the dangers in postponing a decision are

far greater than the dangers in making a premature decision to impose a pesticide ban. The benefits of DDT are declining as insects acquire a resistance to it. At the same time the insects' natural predators, the bats and the birds, are being pushed perilously close to extinction by the effects of pesticide residues. Should we ever reach the point where the insects are immune to pesticides while their natural enemies have been eliminated, mankind will be in real trouble. The present benefits of DDT do not justify the future dangers. Furthermore, the effects of other organochlorine pesticides are sufficiently similar to DDT that we must not fall into the trap of abandoning DDT for an alternative which is equally disastrous.

We feel that the National Speleological Society, bat researchers, and all individuals concerned about the conservation of bats should oppose the continued use of DDT and other organochlorine pesticides. We feel that this opposition should include active participation in current political and legal efforts to ban the use of such pesticides in the U. S.]