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Source: *The Journal of Wildlife Management*, Vol. 43, No. 1 (Jan., 1979), pp. 1-17
Published by: Wiley on behalf of the Wildlife Society
Stable URL: http://www.jstor.org/stable/3800631

STATUS, CAUSES OF DECLINE, AND MANAGEMENT OF ENDANGERED GRAY BATS

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Abstract: Twenty-two summer colonies of the endangered gray bat, *Myotis grisescens*, were censused in 1968–70 and 1976. A conservative estimate revealed a 54% decline in that time period and a 76% decline from known past maximum population levels. A strong association between decline and disturbance by people in caves was observed. Some major colonies disappeared entirely within the 6-year period. Gray bats are restricted to caves year-round and, due to specific temperature and foraging habitat requirements, they aggregate in large colonies in fewer than 5% of available caves. Management requires that the 9 known hibernation caves receive immediate protection, followed by protection of the most important summer caves used by bats from each protected winter cave. Adequate protection may prove impossible unless accompanied by public education. Environmental disturbances such as pesticide contamination, water pollution and siltation, and deforestation may pose serious threats and require further investigation.

J. WILDL. MANAGE. 43(1):1–17

Populations of some North American insectivorous bats are known to have declined markedly in many areas over the past 20 years or more (Mohr 1952, 1953, 1972, 1975, Cockrum 1970) (C. Jones 1971 and J. S. Findley 1973, in unpublished reports). The causes and rates or extent of decline rarely are well documented. Quantification of decline is hampered by the difficulty of accurately censusing large populations (Davis et al. 1962) and by the variation among techniques used by different investigators (Humphrey 1971), even for the same populations. The problem of determining causes is complicated by the fact that population trends and causes of declines may vary greatly among species, even within a single locality (Cockrum 1970, Mohr 1972). But the primary impediment to understanding cause and effect relationships is that local movement patterns, locations of alternate roosting sites, and seasonal behavior generally are poorly known.

In this paper, I present my observations on the decline of gray bats, discuss some of the problems encountered in evaluating the status of bat populations, point out immediate management needs, and suggest areas of concern that require additional investigation. Although gray bat populations have declined alarmingly in parts of their range (Barbour and Davis 1969), most reports of colony locations provide little more than vague estimates of numbers (Hall and Wilson 1966) and are of minimal value in estimating population trends. In the present analysis I restricted myself to a representative sample of my most intensively studied localities in Alabama and Tennessee. Local movement patterns, locations of alternate roosts, and seasonal behavior are unusually well documented at these localities (Tuttle 1975, 1976*a,b*, Tuttle and Stevenson 1977), and censusing techniques have been consistent throughout.

I am indebted to Diane E. Stevenson for help in the field and for her editorial assistance. P. B. Robertson was of invaluable assistance in the field in 1968. M. B. Fenton, T. H. Kunz, and R. K. LaVal kindly reviewed an early version of the manuscript. Many cave owners and members of the National Speleological Society, especially W. W. Torode, contributed information, and R. Jordan, R. Morgan, and J. Thurman of the Division of Forestry, Fisheries, and Wildlife Development, Tennessee Valley Authority, were of invaluable logistical and personal assistance.

Fieldwork from 1968 to 1971 was supported by grants from the Watkins Museum of Natural History Grants and Biomedical Sciences Support, administered through the University of Kansas, the Theodore Roosevelt Memorial Fund of the American Museum of Natural History, and the Ralph W. Stone Graduate Research Award of the National Speleological Society. Censusing and analysis of foraging habitat requirements in 1976 were supported by the Division of Forestry, Fisheries, and Wildlife Development, Tennessee Valley Authority.

METHODS

Bat Population Estimates

Estimates of past and present populations of gray bats were made in more than 100 caves in late July and early August from 1968 through 1970. During 3 weeks from 28 July to 17 August 1976, I resurveyed 22 of the summer colonies that in 1968–70 had shown the least decline from their prior peak population sizes.

Population estimates were based on the area of stained cave ceiling, area covered by the existing colony, and area covered by old versus new guano deposits. Length and width of each part of irregular shaped roosts or diameters of round roosts (or guano deposits) were measured with a 50-ft steel tape, and these measurements were used for calculation of the number of square meters covered by roosting bats. Only well-defined, clearly reddened areas of staining were included in measurements of roosts, and guano was measured only to the edge of accumulations that clearly were dropped by roosting bats. I carefully avoided measuring areas around old guano piles that appeared to be the result of outward spread of steeply conical-shaped deposits.

In all calculations of colony size I assumed the mean clustering density to be 1,828/m^2 (Tuttle 1975), multiplied this density estimate times the number of square meters estimated to have been covered by roosting bats, and rounded to the nearest hundred. Although density of roosting bats varied among colonies, due to differences in roost texture and configuration, it appeared to vary only slightly within individual colonies, regardless of changes in colony size. Consequently, variation in clustering density is assumed to have had minimal effect in biasing estimates of population trends within colonies over time.

The largest past colony size achieved in a given cave was calculated from the area of staining on the roost surface or, in a few instances, from the area covered by old guano deposits. Roost staining on cave ceilings apparently requires many years and may not occur at all in a few caves. In such caves I was forced to rely on measurement of old guano deposits. Because guano falls directly to the floor beneath clustered bats this measurement provided a good alternate estimate. For the same reason, the area covered by new guano provided a good indication of the size of extant colonies in 1968–70 and again in 1976. Visual observations of clustered bats were often used to verify my conclusions regarding roosting configuration and density, but only twice were they used as the basis for final estimates of population size.

The classification of guano as new or old was made as follows. Guano deposited during the current season is recognizable by a combination of factors such as kind and stage of growth of associated fungi, general moisture content, appearance and odor of the guano, kinds and life stages of invertebrates present, stage of decay of dead young bats, and amounts of guano removed by streams known to undergo seasonal fluctuation.

Disturbances by Humans

Frequency of human disturbance was estimated for each roosting area based on a combination of landowner and local caver observations, and on my own verification through evidence seen near the roosts. I lumped numeric disturbance estimates into categories of rare (1 disturbance or less/2-month period), infrequent (1/month), moderate (2–4/month), and frequent (more than 5/month), and these were compared with calculated rates of decline in the period 1970–76.

The direct impact of disturbance is difficult to evaluate. Rare and frequent disturbance categories were easily assigned, but the moderate and infrequent categories were, at best, only approximations. Furthermore, even absolute knowledge of disturbance frequency is not necessarily an adequate indication of disturbance intensity. Important determinants of intensity include (1) seasonal and daily timing of disturbance, (2) height of roosts above cave floor or water, (3) nearness of roosts to the most heavily explored passages, (4) presence of alternate, less accessible roosts within the cave, (5) length of disturbance, and (6) kind of disturbance, i.e., accidental versus vandalistic.

I assumed that most disturbance occurred in the daytime when it would be most damaging. Since all caves censused were used by bats almost exclusively from April through October, human visitation in other months was considered to be of little or no consequence. Bat colonies that roosted high above cave floors or beyond deep water or muddy or dangerous passages were least disturbed by individual human visits. The average length of time of disturbances could not be determined, but evidence of vandalism in the form of sticks, rocks, fireworks fragments, spent shotgun and rifle cartridges on guano piles, smoke stains on ceilings, and dead bats often provided clues to the kinds of disturbance. My estimates of disturbance frequency represent disturbance at or near roosts rather than including every human visit to any part of a cave. Even so, I could not quantify the effect of vandalism or height above floor.

RESULTS

The estimated maximum past population for the 22 localities censused was 1,199,000. By 1970 numbers had diminished to 635,700, a 47% reduction, and just 6 years thereafter the combined population had fallen to 293,600, an additional 54% reduction (Table 1).

In 1970 7 colonies were still as large as their all-time past maximums; however, by 1976 this number was reduced to 4. The largest maternity colony in the stable category in 1970 (population of 111,400 in cave 19) had declined by at least 95% by 1976. Whereas this cave housed the largest gray bat maternity colony known anywhere within the entire species range in 1970, and was used continuously from early April through October, in 1976 not more than 6,000 gray bats visited the cave at any time, and none used the cave for more than a few days in succession.

From 1970 to 1976 evidence of human disturbance, and especially vandalism, increased markedly. When estimates of disturbance are compared with those of percentage declines by locality (Table 1), it is clear that mean rates of disturbance and decline are related. Nevertheless,

Table 1. Census data from 22 summer gray bat colonies subject to different degrees of disturbance by humans during April through August.

Cave numbers by disturbance category	Number of gray bats			% population decrease		
	Maximum pre–1968	1968–70	1976	From max. to 1968–70	1968–70 to 1976	Total max.—1976
<1 per month						
1[a]	20,400	10,200	10,200	50	0	50
2[c]	7,800	6,100	6,200	22	0	21
3[c]	4,000	3,900	4,000	2	0	0
4[c]	12,200	12,200	12,200	0	0	0
5[a]	29,800	19,000	18,700	36	2	37
6[c]	17,700	10,000	8,000	44	20	55
7[a]	12,200	12,200	9,700	0	21	21
1 per month						
8[a]	25,500	10,200	6,500	60	36	74
9[a]	36,700	15,600	9,200	57	41	75
10[a]	46,200	46,200	18,900	0	59	59
2–4 per month						
11[c]	219,400	174,700	127,500	20	27	42
12[b]	121,200	32,500	18,500	73	43	85
13[c]	23,800	12,200	6,100	49	50	74
14[a]	19,100	19,100	8,700	0	55	55
15[b]	126,400	26,200	9,100	79	65	93
16[a]	31,100	31,100	9,000	0	71	71
17[c]	12,800	9,400	0	27	100	100
≧5 per month						
18[c]	127,500	28,600	4,100	78	86	97
19[b]	111,400	111,400	5,100	0	95	95
20[b]	15,600	13,600	1,900	13	86	88
Gated—1968						
21[a]	132,600	10,900	0	92	100	100
22[a]	45,600	20,400	0	55	100	100
Totals	1,199,000	635,000	293,600	47	54	76

[a] Maternity site.
[b] Maternity site in 1968, bachelor site in 1976.
[c] Bachelor site.

the unexpectedly small decline in cave 11 and the considerable reductions that occurred in caves 6, 7, 10, and 17, for example, may indicate the existence of factors in addition to disturbance.

Colonies in caves 20 to 22 were exceptional because their marked declines may have been caused primarily by single events. Cave 20, according to the owner, had been visited by a group of teenage boys who shot large numbers of bats at their roosts and during evening emergence. Many spent cartridges in the cave verified the report. Caves 21 and 22 had been gated for protection of bats, but their colonies refused to return due to inadequate gate designs (Tuttle 1977) and are feared lost.

Reduction in the number of individuals in a colony can have an effect which brings about further decline in numbers. Thermoregulatory requirements may result in a baseline population size, varying among caves of different temperatures or ceiling configurations, below which a maternity colony cannot successfully rear young (Constantine 1967, Tuttle 1975). Colonies in 5 caves (Table 1) changed from maternity to bachelor status from 1970 to 1976. Four of those had under-gone major population decline (43–95%) during those years. This problem is aggravated by the colder nature of the secondary roosts to which the bats retreated to escape disturbance. The implications of these effects are of great concern. Due to the long lifespan of adults, colonies may appear to be relatively stable for several years, even after young are no longer successfully reared. Extinction of such seemingly stable colonies could then occur rapidly when the adults reached the end of their life span.

DISCUSSION

Censusing Problems

Although a variety of different censusing techniques has been used by other investigators (Humphrey 1971), none is suitable for large-scale censusing of gray bats. Emergence counts, including those incorporating photography, are not feasible due to factors such as dense surrounding vegetation at some sites and multiple cave entrances at others, and are of no value in determining past population sizes. Techniques requiring direct observation of bats at their roosts must be restricted to daytime during the maternity period in order to find maximum or even constant numbers of bats in a single cave, thereby causing major disturbance and mortality of flightless young. A method whereby only the young were observed after the adults emerged to feed at night, combined with entrance trapping, was used by Tuttle (1975) and resulted in minimal disturbance. However, that method is time consuming, useful only during June, provides no means of comparing past versus present population sizes, and still causes more disturbance than the techniques used in the present study.

Timing of censuses is important. Most summer colonies of gray bats use several different caves in a home range area which may be as much as 50 km long, and they may occupy a succession of several caves through 1 season. This normal movement among caves makes censusing difficult and requires a prior familiarity with each colony's normal preferences and timing and patterns of movement. These movements had been documented in prior (Tuttle 1976*a*) and continuing studies of 40,182 banded gray bats from these and adjacent colonies.

Maximum concentration of a gray bat colony takes place during June when young are reared. A gradual breakup of colonies and movement among alternate caves often occurs by late July or early August (Tuttle 1975, 1976*a*). Censuses conducted in April or May usually include only a fraction of a given colony and might cause abandonment of preferred roosts. Those made in June or early July entail some level of disturbance of maternity groups. Although colony breakup often already had occurred or was in progress by late July and early August, sampling was done then to avoid needless disturbance during critical periods, while still sampling the peak population for the year. Use of areas of stained ceiling and of old versus new guano deposits minimized the problems posed by disturbance or colony breakup, because in most caves it was unnecessary to see the bats. Censusing later than mid-August is inadvisable due to potential loss of evidence such as new guano (through flooding) or fungal growth.

Because entire colonies of gray bats, including reproductive females and bachelor groups (adult males and nonreproductive females), often aggregate in a single cluster in maternity caves just before parturition or following fledging of young, my censuses of maternity caves often represent entire colonies. On the other hand, censuses in bachelor caves frequently do not. Nevertheless, caves chosen for this analysis all appeared to be essential focal points of activity for their colonies, and fluctuations of numbers in these caves should indicate changes over time for their respective colonies.

An additional census variable is that colonies often move among several alternate roosts within a single cave at 10- to 14-day intervals within a season, except when flightless young are present. For this reason it is not accurate to measure and combine all areas of recent guano within even 1 cave. Instead, in a maternity cave I located and measured the maternity roost only, ignoring the smaller nonmaternity roosts. Maternity roosts were recognizable, almost without exception, by the presence of at least a few dead young and unusually large numbers of mites that result from long, continuous use of a single roost. In caves used only by bachelor segments of colonies, I simply measured either the largest stained area or guano deposit, or used the average of several that were of similar size but of varied shape.

Simultaneous use of 2 or more roosts in a single cave was uncommon but most likely to occur where colonies were large or where suitable roosting surface was limited in any 1 place. Such behavior was easily detectable through observation of guano decomposition and associated fungal and invertebrate faunal indications, and in these cases the different areas were combined. This problem had negligible effect on the estimates of 1970 or 1976 populations. For estimates of past populations it was impossible to detect simultaneous use of multiple roosts in a single cave. Bias of this kind undoubtedly led to underestimation of past population maxima.

Another source for underestimation of past population figures lies in the ease with which even sizeable guano piles are made unrecognizable. Two examples of the possible extent of past population underestimation due to this bias were observed.

Paul B. Robertson and I measured areas covered by old and new guano in cave 18 on 10 July 1968 and found a single deposit 12.2 m long by 10.7 m wide and 2.4 m deep, giving an estimate of maximum past colony size of 238,600. However, due to the possibility that 2 adjacent roosts were used alternately to produce the large area of guano observed in 1968, I later averaged our 1968 measurements for 3 different roosts in this cave, arriving at a figure of 127,500. By July 1976 this deposit was virtually unrecognizable due to heavy traffic by spelunkers. The guano had been scattered, compacted, and covered with clay carried over the surface by muddy feet. For unknown reasons, ceilings where bats roosted were never stained clearly, so if I had not visited this cave in 1968 and earlier I would have suspected a past colony size there of no more than 30,000. Nevertheless, careful recent observations at cave 19 indicate that even the figure of 238,600 for past size could be a considerable underestimate.

In cave 19, from 1969 to 1970 measurement of recent guano and direct observation of the bats indicated that, during periods of maximum use, the cave housed 111,400 or more gray bats. Yet by 1976 this cave was used infrequently by small, transient bachelor groups, and much evidence of past use had been obliterated by flooding reservoir water and by the muddy feet of spelunkers. Additionally, in this cave there were 5 distinct roosting areas, and during its period of maximum use all 5 roosts, and much area between them, were being used simultaneously. Without prior knowledge, only 1 roost would have been counted, leading to an underestimate of roughly 80%.

A third source of past population underestimation results from the slowness of the roost staining process. In 5 other caves where colonies were stable or growing and roost staining was distinct enough to permit reliable comparisons between area of staining and area covered by bats or by new guano, the 1970 colony sizes averaged 11% (range 7 to 17%) larger than the maximum area of roost staining would have indicated.

In summary, the varied, unavoidable biases discussed above all tended to obscure rather than accentuate detection of decline over time. Other potential problems, such as inaccuracies involving estimation of areas covered by irregularly shaped roosts or of mean clustering density, could have biased my estimates equally in either direction in any given cave. Since these problems appeared to remain constant in most caves, I believe that they have caused negligible error in my conclusions.

Causes of Decline

The gray bat is, perhaps, the most narrowly restricted to cave habitats of any U.S. mammal (Hall and Wilson 1966, Barbour and Davis 1969, Tuttle 1976*a*). With rare exception (Hays and Bingham 1964, Gunier and Elder 1971) it lives in caves year-round. In summer, gray bats select only a few caves, which must be located near (rarely more than 2 km and usually less than 1 km from) rivers or reservoirs (Tuttle 1976*b*) and provide certain temperature or roost conditions (Tuttle 1975). They hibernate in deep, vertical caves of exceptionally low (6–11 C) temperature (Tuttle and Stevenson 1978), and often travel hundreds of kilometers in order to reach these scarce sites (Tuttle 1976*a*). As a consequence of their combined thermoregulatory and other habitat requirements, gray bats congregate in larger numbers and in fewer hibernating caves than any other North American vespertilionid. "This concentration of such a large proportion of the known population into so few caves constitutes the real threat to their survival" (Mohr 1972).

In the present analysis I completely ignored caves where the greatest reductions already had occurred or were clearly in progress in 1970, concentrating only on those colonies which appeared stable enough in 1968 to 1970 to warrant further attention. Consequently, it is important to note that this report is on the status of gray bats only in the "healthiest" summer colonies of gray bats that were known to me in 1970, in the area of gray bat distribution south of Kentucky and east of the Mississippi River. It is probably, therefore, a gross underestimate of true population losses.

Disturbance and Vandalism.—In a brief plea for bat conservation, Manville (1962) noted the extreme vulnerability of the gray bat to human disturbance and vandalism, and Barbour and Davis (1969) pointed out that "in the last few years human disturbance has threatened the very existence of the species." They concluded that ". . . *M. grisescens* is destined to continue a rapid decline in numbers and probably faces extinction." In the course of my field studies of this species from 1960 to 1970, I noted numerous examples of local gray bat extirpation throughout the southeast both as a result of apparently innocent disturbance and of direct, intentional vandalism.

In 2 summer caves in Tennessee, for example, I estimated that approximately half a million gray bats already had been lost prior to 1960. In 1 case the owner of a commercialized cave personally described to me how he and his assistants had killed bats with torches. In the other cave, ceilings were too high to permit much direct destruction, but the bats apparently were driven out simply by the high frequency of human visitation. Already, in 1968, gray bats were gone from many and possibly most of their previously occupied caves in Tennessee. The largest remaining summer colony in the state (cave 10) numbered only about 46,000 and was down to roughly 19,000 by 1976.

During the 1960's old-timers frequently enjoyed telling me that when they were children, bats emerged from local caves in great clouds and that they killed the emerging bats with switches, just for fun. Bats frequently were caught at roosts in caves, to be used in local pranks. Also, due to premature, erroneous claims from local health authorities (Fredrickson and Thomas 1965), some cave owners tried to exterminate entire colonies on their properties. An elderly man who had owned cave number 1 for many years told me that rabies researchers informed him that his bats were rabid and would transmit the disease to his cattle if he did not get rid of them. Consequently, he poured fuel oil into the cave where the bats roosted and lit it. Most of the colony apparently escaped, and since my first contact with this landowner in 1968, these bats have received strict protection and have remained stable in numbers.

As these accounts demonstrate, it was apparent prior to my 1976 investigations that human disturbance was often a primary cause of gray bat decline. Nevertheless, no one had attempted to quantify a cause and effect relationship, and other sources of stress were unknown. The relationship between frequency of disturbance and mean rates of decline found in this investigation is obvious. The 2 most heavily disturbed caves lost over 90% of their bats while 5 colonies in rarely disturbed caves remained stable or nearly stable. Nevertheless, considerable variation existed within some classes of disturbance.

The most extreme variation (caves 11 and 17) appears explainable based on cave size and contours and location of the roosts. In cave 11, bats roosted approximately 15 m above the floor over an area of large guano-covered boulders that appeared to keep most spelunkers from getting close to the bats. Approaching cavers did not startle the bats and usually kept at least 50 m away from them. The disturbances, while of moderate frequency, were not intense.

Cave 17 illustrates the opposite extreme, where nearly every disturbance was intense. The bats roosted only 100 m inside that cave, and 2 m above the floor where anyone exploring the cave passed by closely. Bats could not detect intruders until the intruders rounded a nearby corner. The roost was located over water deep enough to drown fallen young and possibly some adults, but not enough to deter cavers. Furthermore, such a roost was especially vulnerable to intentional vandalism.

Much of the remaining variation within disturbance categories (Table 1) could have resulted from failure to quantify intensity of disturbance. Single acts of destruction could greatly alter average trends. Also, I probably erred occasionally, especially in the 2 intermediate categories, in estimating frequency of disturbances.

Emigration to Other Caves.—Cavers and others often have speculated that when bats abandon one cave, they move to another previously unoccupied cave. However, this rarely occurs. Gray bat colonies are extremely loyal to single caves or groups of caves (Tuttle 1976*a*) and usually have environmentally limited ability to move to alternate caves for the rearing of young, even within their own home range. They require caves of specific roost and temperature conditions, and maternity colonies are found only in caves that are near a river or reservoir.

Any cave that is used only as an alternate, transitory roosting place undoubtedly receives such limited use for a good reason. Some essential condition is not continuously met, or the cave is too heavily disturbed. Consequently, only a small proportion of the caves in any area are or can be used regularly. In Alabama, for example, although 1,635 caves had been mapped by 1975 (Varnedoe 1973, 1975), only 39 (2.4%) were known to have sheltered even small summer colonies of gray bats. Two more (0.1%) were used for winter hibernation. These figures are the result of my own surveys combined with assistance from members of the Huntsville and other Alabama grottos of the National Speleological Society. Even if these figures were doubled, 95% of Alabama's caves would not have been used by gray bats.

This species probably occupied all suitable caves within its range long before the arrival of modern man. In support of this belief, I have not observed the establishment of a single new colony in a previously unused cave in 17 years of work in more than 200 southeastern caves. Gray bats readily colonize newly available sites such as storm sewers and abandoned mines when these sites provide required conditions (Hays and Bingham 1964, Tuttle, unpublished data). Any cave not already used by gray bats, however, should be assumed to be unsuitable for future use. Such caves probably do not provide essential temperature or roosting conditions, are too distant from acceptable foraging or hibernating sites, or are too vulnerable to predation or flooding. Others that have been used but that are now abandoned may be recolonizable. Prior to any reuse, however, these caves would have to receive strict protection from human disturbance or other environmental perturbations which caused their abandonment.

Although approximately 23,000 banded gray bats have been recaptured during my studies, I have found no evidence of successful emigration by members of declining colonies to previously unoccupied caves or to caves outside the colony's originally occupied home range (Tuttle 1976*a*). Near cave 19, where some 111,000 gray bats disappeared in only 6 years, I censused 3 other caves that were used by gray bats within a 30-km radius and found declines in all 3. Cave 11, located only 20 km away, is known to serve as the primary roosting place for the bachelor segment of this colony, yet even there numbers fell by 27%. There is no evidence that any nearby cave sheltered an increased number of bats following human vandalism and disturbance in cave 19.

Further studies of long-term changes in relative recapture rates among colony cohorts at winter hibernating sites have shed additional light on this subject. Over the past 9 years the cave 19 cohort ($N = 1{,}274$) has shown a greater decline ($P < 0.01$) than the cohort ($N = 5{,}713$) in the stable cave 4 colony (Stevenson and Tuttle, in prep.). Based on this and additional winter band recovery data from the other localities, I believe that few declines noted in this study can be attributed to simple emigration.

Environmental Disturbances.—I hoped

not only to quantify the relationship between disturbance and decline, but also to detect additional factors. The very large proportion of gray bat decline that appears to be directly attributable to human disturbance renders detection of other potential problems extremely difficult. The fact that 5 of 7 rarely disturbed colonies remained essentially stable over the past 6 years certainly is encouraging when one considers the potential for recovery if human disturbance can be controlled. Unexplained declines of roughly 20% in caves 6 and 7 and the relatively high loss in cave 10, however, may indicate stressful influence from other sources as well.

The possible influence of pesticides in causing decline of North American populations of insectivorous bats has been reported (Mohr 1972, Reidinger 1972, 1976, Clark and Prouty 1976, Geluso et al. 1976), and a recent study has documented mortality and probable population decline in gray bats resulting from routine insecticide usage (Clark et al. 1978). Clearly, further investigation is needed. Donald Clark has received and is currently analyzing samples of guano from each of the 22 caves censused in this study. His initial results (pers. comm.) suggest considerable variation among localities, with levels of PCB, DDD, DDE, heptachlor epoxide, or lead at possibly dangerous levels in the guano from several caves.

A further possible cause of decline may involve other chemical pollution or siltation of waterways over which gray bats forage. Although studies of specific prey preferences are not yet complete, gray bats are known to forage primarily over rivers, streams, and reservoirs (Tuttle 1976*a*,*b*, LaVal et al. 1977) where, among other insects, they consume large numbers of mayflies (Tuttle 1976*b*, Tuttle, Stevenson, and Rabinowitz, in prep.). Mayflies are thought to be quite sensitive to aquatic pollution. Through broad areas of their former habitat, they have been virtually eliminated, and they are now rare in other areas of former abundance (Fremling 1968). Clearly, such declines could prove disastrous for predators that depend upon them as a major food source.

I have found few observations on the potential effects of siltation. Carlander et al. (1967) seemed to believe that at least some siltation benefited nymphs of the 2 species of mayflies that they studied, but other species apparently are unable to survive where the substrate consists of mud or silt (Lyman 1943, Minshall 1967). At least in areas surrounding the Cumberland Plateau in Kentucky and Tennessee, recent increases in strip mining have produced levels of siltation which could have extreme and far-reaching effects on aquatic biota and consequently on the future survival of any gray bats living along affected waterways. None of the 5 colonies that remained relatively stable between 1970 and 1976 foraged over heavily silted waterways. One that did (from cave 20) declined markedly, but vandalism was so intense there that it alone may have accounted for the 86% loss. Problems involving the effects of both chemical and silt pollution on the aquatic insects upon which gray bats depend need more investigation.

Additionally, deforestation of areas near cave entrances and between caves and rivers or reservoirs where gray bats feed may have affected them detrimentally. In brief, perhaps critical, periods during exceptionally cold spring weather I have observed that gray bats sometimes appear to limit much of their foraging activities to forested areas near their caves. Also, during evening emergence gray bats usually fly in the protection of forest canopy en route to rivers or reservoirs where they feed (Tuttle 1976*b*). I repeatedly have observed gray bats traveling considerably out of their way in order to take advantage of even scattered trees along a fence row. I also have seen screech owls capturing emerging gray bats and have observed that these owls have much greater difficulty when the bats are able to take cover in the forest canopy.

Female gray bats produce their 1st young when they are 2 years old (Tuttle 1976*a*) and thereafter produce only 1 per year. Clearly, with such low reproductive rates, even slight increases in predation could prove significant. Young gray bats are slow and clumsy fliers during their 1st week of flight, and at caves surrounded by forest, they often spend several nights foraging in the forest before venturing farther away. The trees provide convenient resting places for weak fliers and protection from predators and wind. Factors such as deforestation may account for the fact that at least 2 colonies (caves 1 and 5) have markedly declined in the past but stabilized at reduced sizes recently. Deforestation, however, cannot have caused losses since 1970 in the 22 caves studied because no major cutting of timber occurred near any of them in that period.

Natural Calamities.—Cave flooding is by far the most important natural calamity faced by gray bats, and it is becoming increasingly important as they retreat farther back into inaccessible places to avoid human disturbance. Summer colonies often retreat to roosts over deep water in order to avoid disturbance by humans. In some caves this is a successful avoidance strategy, but in others such roosts become death traps during flooding.

An additional problem involves cave entrance closure. On rare occasions cave-ins or gradual fill-in of sinkhole entrances render a cave entrance or an important passage too small for a large colony to pass through without greatly increased danger of predation. One Florida cave was abandoned by a large maternity colony following the collapse of the largest of its 3 entrances. No other cause for the abandonment could be found.

Impoundment of Waterways.—Gray bat preference for caves near rivers has made their roosts particularly vulnerable to inundation by man-made impoundments. The initial effect of long-established impoundments, such as the Tennessee Valley Authority reservoir system, is difficult to evaluate due to a lack of pre-impoundment data. The little information available indicates that many important caves, and probably their bat populations, were extirpated. An account by M'Murtrie (1874) describes a cave in Alabama, since flooded by a reservoir, which was "inhabited by countless thousands of bats" and had guano piles 4.5 m deep. Longtime residents have told me of many other such caves now submerged. Timing of the initial flooding may be a critical factor in whether the flooded populations are destroyed immediately. The bats' strong philopatry and narrow ecological requirements, however, make survival of displaced populations questionable even if they escape initial destruction.

On the other hand, it was initially suspected that reservoirs might increase the amount and quality of foraging habitat for colonies that survived (Tuttle 1976*b*). Recent studies of gray bat foraging habitat and prey preference requirements support an opposite conclusion, however (Tuttle, Stevenson, and Rabinowitz, in prep.). Furthermore, recreational activity associated with reservoirs has greatly increased the number of people visiting gray bat habitat, and many caves formerly long distances from population centers and roads are now within easy access by boat.

Management Recommendations

Priorities for Site Protection.—Clearly, the immediate objective must be to reduce human disturbance in occupied caves. First, the locations of gray bat caves must be made known to appropriate federal, state, and private agencies along with recommendations of options for protection. Locations of most gray bat wintering caves are known to bat researchers, and many summer caves also are known. Even those not yet known to researchers are usually known locally to spelunkers. Access to such location lists, however, should be severely restricted prior to protection of the sites.

Because resources are limited, there must be some systematic method of determining priorities for protection. I propose that as gray bat caves become known, they should be designated according to the following categories: (1) primary hibernating caves (those occupied now or in the past by more than 50,000 gray bats); (2) secondary hibernating caves (those used by less than 50,000); (3) primary maternity caves (those occupied now or in the past by 50,000 or more gray bats; (4) secondary maternity caves (those presently occupied by smaller colonies); (5) primary bachelor caves (those used now or in the past by more than 50,000 male and nonreproductive female gray bats); (6) secondary bachelor caves (those continuing to be used by smaller groups); (7) gray bat caves not included in the previous categories, such as caves which receive only brief seasonal use by small numbers of gray bats, and abandoned caves which in the past housed only small colonies. Bachelor caves often shelter pregnant and postlactating females as well as juveniles either before or after the maternity period in June and may sometimes receive as little as 60 days of major use annually. Their transient use pattern does not reduce the importance of these caves to their colonies.

All caves in categories 1, 3, and 5 should receive immediate protection, with those in categories 4 and 6 next in line. Categories 2 and 7 should receive consideration when possible, especially in marginal areas of the species' range where large colonies do not exist. Few caves will be included in categories 1, 3, and 5, and over sizeable geographic areas outside of Alabama and Tennessee such large colonies may not occur at all. In such areas colony sizes accorded priority status probably should be lowered to as few as 25,000 gray bats for category 1 and 10,000 for categories 3 and 5. Occupied caves within a category should take priority over unoccupied caves, and some caves used only briefly by spring and fall migrants may also be critical. Individual summer colonies usually use, and may often require, several different caves throughout a single active season. This permits adjustment for seasonally changing temperature requirements as well as for more efficient exploitation of patchy food resources. The above recommendations are provided only as guidelines and are flexible.

There are only 9 caves known which fall in the first category (50,000 minimum population), and they are believed to contain roughly 95% of the known species population for half of each year. If gray bats are to survive it is imperative that these caves be acquired and protected by federal, state, or private agencies. Without such action all other measures may prove meaningless.

As each primary hibernation population is protected, a special effort should be made to identify and protect the most important summer colonies, especially in categories 3 and 5, of which that population is composed. Only such a systematic approach, which provides year-round protection, can guarantee long-term survival of the species. As a result of extensive banding studies in Missouri (Myers 1964, Elder and Gunier 1978), Kentucky (Hall and Wilson 1966), and Alabama, Florida, Tennessee, and Virginia (Tuttle 1976*a*), most geographic patterns of movement are relatively well known, making this approach feasible.

For example, the most important hibernation population known, with its complex of associated summer colonies, is located in northeastern Alabama. Three caves of this group all require immediate protection (caves 44, 45, and 50 in Tuttle 1976*a*; the 2 important summer caves—45 and 50—are numbered 11 and 19 in this paper). The hibernaculum contains between half and two-thirds of the entire known species population each winter, is privately owned, and is threatened increasingly by disturbance. Cave 19 recently has lost nearly all of its formerly large colony, and in January of 1977 the owner of cave 11, the largest summer colony known anywhere, applied for federal and state permission for construction of a major resort, train ride, and trout hatchery in that cave. Following state approval of the impact statement, personnel in the Division of Forestry, Fisheries, and Wildlife Development of the Tennessee Valley Authority, using information on file from Tuttle, recognized the potential disaster and notified proper authorities. Consequently, construction in the cave was halted and the U.S. Fish and Wildlife Service started purchase negotiations that will be completed in 1978.

The loss of at least 106,000 gray bats from cave 19 and the near loss of 127,000 in cave 11 within 6 years illustrate the need for *immediate* acquisition and protection of critical gray bat caves. Equally clear is the need for increased communication among members of the National Speleological Society, bat researchers, and federal, state, and private agencies. Many potential problems can be detected and avoided only through the kind of information exchange and cooperation that saved cave 11.

Public Education.—Government officials at all levels should be educated regarding the ecological role of bats. Many officials, through exaggerated fear of bats as disease vectors, feel that the only good bat is a dead bat. Disease problems should be put in perspective and officials should be informed, for example, that the gray bats from cave 11 alone consume more than 900 pounds of insects nightly and 80 tons annually.

Major efforts should be made to educate and gain the cooperation of land-owners. Many would cooperate if contacted by local wildlife officials or conservation groups. Cave owners should be provided with an official written statement outlining the basic problem, the potential value of having the bats, and federal and state laws and penalties for disturbing them. Additionally, federal and state agencies should offer to post privately owned gray bat caves, as well as posting their own, with signs briefly outlining reasons for protection and specific times during which entry is prohibited. At summer caves, this period should be 15 March through October, and at winter caves it should be 15 August through April. Some caves are important to gray bats only during migration, and others, including some maternity caves, are used for 2 months or less annually. These caves may not require such long periods of protection, but when in doubt the best approach is to grant March to October protection. A few caves must be closed year-round.

Such procedures impress the landowner that protecting bats is important enough to warrant his participation and lets him "off the hook" with neighbors and others who might otherwise think of him as unfriendly. Also, informative signs often elicit cooperation even from would-be vandals, especially if a definite time period is stipulated.

Methods of Protection.—Some gates that were built to protect gray bats have done more harm than good (Tuttle 1977), and this continues to be a major problem. It is difficult to construct vandal-resistant gates without restricting the free movement of bats or air. Gates should be used only where other protective measures are inadequate to prevent disturbance. Unfortunately, many caves cannot be adequately protected without fences or gates.

For advice on where and how to construct gates versus fences for protection of gray bat caves see Tuttle (1977). More investigation of this problem is needed, and in the meantime no gates should be built without careful planning. Follow-up studies to evaluate success or failure and to permit changes, where required, before critical populations are destroyed also are vital.

Progress Thus Far.—Although improperly constructed gates have resulted in the loss of several entire colonies, some correctly constructed gates have proven successful in protecting gray bat summer colonies in caves in Missouri and Oklahoma (R. K. LaVal, pers. comm.). Aside from 3 locations in Missouri, most gray bat wintering sites have not yet received adequate protection, and several have lost all or most of their once large populations. One hibernaculum in Arkansas has been gated for 3 years, but has received no follow-up study to evaluate the gate's effect (M. J. Harvey, pers. comm.). Such carelessness is potentially disastrous.

Since the gray bat was listed as endangered (Federal Register, 28 April 1976), encouraging progress has been made. The U.S. Fish and Wildlife Service is purchasing the major gray bat hibernating cave reported by Hall and Wilson (1966) in Kentucky as well as the most important known summer cave (no. 11 in this paper), and is considering other important acquisitions (H. W. Benson, pers. comm.). It also has fenced and posted cave 15 of this study on the Wheeler National Wildlife Refuge. During more than 10 years of precipitous decline, the formerly large maternity colony in cave 15 had been destroyed, and only a transient bachelor remnant of approximately 9,000 bats remained. Following only 2 years of strict protection from human disturbance, this colony has now returned to maternity status and has increased to more than 19,000 bats.

The Division of Forestry, Fisheries, and Wildlife Development, Tennessee Valley Authority, is supporting major investigations of habitat requirements and status of gray bats in areas under its jurisdiction, has fenced and posted 1 summer cave, and is initiating efforts to post and otherwise protect several other important caves, including cave 19 of this study. The Army Corps of Engineers has gated 1 summer cave and has fenced another in Missouri, and has funded research on habitat requirements in that area. The Missouri Department of Conservation in early 1977 hired Richard and Margaret LaVal to conduct further investigations of the status and management needs of gray and Indiana bats (*Myotis sodalis*) in Missouri and has acquired 5 gray bat caves, with further purchases anticipated.

Studies Needed.—Gray bat seasonal habitat requirements (Tuttle 1975, 1976*a,b*, LaVal et al. 1977) and movement patterns (Myers 1964, Hall and Wilson 1966, Tuttle 1976*a*, Elder and Gunier 1978) are relatively well understood, and available information is adequate to permit management initiatives. Nevertheless, several areas require further investigation. Especially in Arkansas, Kentucky, Missouri, and Oklahoma, more information on critical cave locations, status, and recent and total declines is needed.

Throughout the range of gray bats, investigations of the effects of human environmental distrubance are essential. The most important areas of concern involve the potential effects of water pollution and siltation on aquatic insect life upon which gray bats depend, as well as those of pesticide contamination and local deforestation. Foraging habitat and prey preferences are necessary baseline data.

Guidelines for Researchers.—Plans for further studies raise the question of potential research-related disturbance. Gray bats are especially vulnerable to any disturbance during winter hibernation and immediately before and during their maternity period. Because roughly 95% of all known gray bats are believed to aggregate into only 9 caves in winter, it is important that these caves not be disturbed unnecessarily. Major banding of gray bats during winter hibernation should not be tolerated under any circumstances, and the frequency of all unnatural arousal must be kept to a minimum. As a general rule, disturbance of hibernating populations should be limited to once per winter and totally avoided except when essential for research purposes.

Whenever possible, entry into maternity caves should be avoided from April through at least mid-July. Research which demands visitation of maternity roosts during that period must be restricted to the 1st hour following the evening departure of adults to feed. Gray bats are far more tolerant of disturbance during late July and August than at any other time during the active season, and whenever possible censusing and any other activities which might necessitate sampling or visual observation at summer roosts should be restricted to that period.

Preferably, major summer sampling of live bats should be limited to trapping or mist netting at cave entrances or foraging areas. As long as whole cave entrances are not blocked, and only a small proportion of any given colony is sampled, such disturbance is negligible, assuming that traps or nets are never left unattended and that this disturbance is not repeated nightly. At all times, the use of dim electric lights and avoidance of unnecessary noise greatly reduce disturbance. Lights that are adjustable for intensity are ideal. Also, captured bats should not be crowded, left in potentially stressful temperatures, or restrained longer than necessary.

When the above recommendations are combined with common sense and sensitivity, the negative effects of research can be negligible. Even banding, when restricted to summer caves and careful use of number 2 lipped bands or size XCL celluloid split rings, is not known to cause more than slight initial wing irritation in most cases; detrimental long-term effects appear to be rare. When harm does occur it is usually the result of careless banding procedure or improper handling.

CONCLUSIONS

Although recent decline of gray bats has been precipitous there is no reason to believe that this trend cannot be reversed if adequate measures are taken to prevent human disturbance and vandalism. The rate of loss of major colonies and the rate of decline in general, however, demand that action be immediate. Once lost, some colonies may be difficult or even impossible to reestablish. Efforts by cave owners, state and federal agencies, private environmental groups, National Speleological Society members and researchers, and education of unorganized cavers as well as the general public, will be vital to the future of the species.

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Received 9 December 1977.
Accepted 7 August 1978.