CHAPTER 14

LONG-TERM MONITORING PROTOCOL FOR BATS: LESSONS FROM THE LUQUILLO EXPERIMENTAL FOREST OF PEURTO RICO

Michael R. Gannon and Michael R. Willig

INTRODUCTION

Population studies are necessary to understand community- and ecosystem-level interactions. The fundamental theories of population, community, and ecosystem ecology involve growth and composition of populations, the ways in which these affect other populations, and how they are in turn affected by them. As conservation of biodiversity becomes of increasing world-wide concern, management schemes designed to conserve populations and ensure ecosystem stability need to consider the consequences of temporal variation of populations, whether it be cyclic, directional, episodic, or catastrophic. Only long-term monitoring of populations can examine such variation.

In many tropical ecosystems, bats are keystone species by virtue of their roles as pollinators and as seed dispersal agents (Charles-Dominique, 1986; Fleming, 1988). In the Luquillo Experimental Forest of Puerto Rico, bats are critical in dispersing seeds for a number of plant species (Devoe, 1990; Gannon and Willig, 1994, Willig and Gannon, 1996), thus helping maintain seed banks that are a source of colonists in recently disturbed areas (Uhl *et al.*, 1981, Swaine and Hall, 1983; de Foresta *et al.*, 1984). Bats also play an important role as pollinators of flowers in tropical systems (Howell, 1974; 1978; Stuart and Marshall, 1976; Gould, 1978; Ng, 1978; Sazima and Sazima, 1978). As a result of these roles, both frugivorous and nectarivorous bats likely have a large impact on plant populations by affecting their spatial distribution and genetic structure.

Monitoring of bat populations presents its own unique and inherently difficult problems. Taxa such as birds often can be counted visually or by their vocalizations. This is not true of most species of bats, which are nocturnal, highly mobile creatures that exhibit variable behaviors. In most cases, researchers must employ special equipment to operate within the nocturnal domain of bats, including bat detectors to detect the ultrasonic calls bats emit while navigating, radio telemetry or night vision scopes to locate bats in the dark, and mist nets or harp traps to capture the bats. These apparatuses are costly. As a consequence of cost and logistics, most studies that have examined bat populations in the neotropics have been short term – one or two years at most – in duration (e.g. Thomas and Fenton 1978; Bonaccorso, 1979; Willig, 1983; Willig and Moulton,

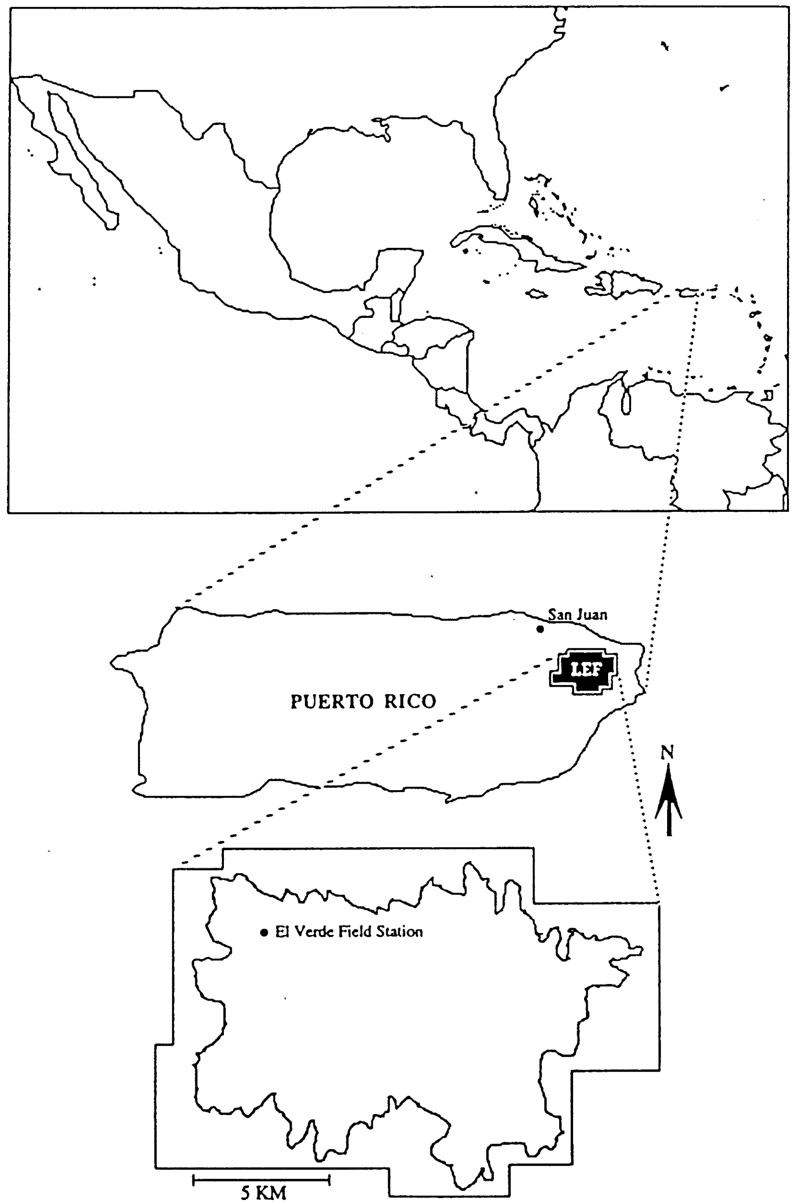


Figure 14.1 Puerto Rico shown in relation to other Caribbean Islands (top), the location of the Luquillo Experimental Forest (LEF) on the island (middle), and El Verde Field Station (bottom)

which struck the LEF in 1989, on bat populations at the site were recently examined by Gannon and Willig (1994). Results of that work found that bat species at this locality were affected differently by the hurricane and subsequently recovered in differing ways.

The goal of this paper is to discuss a methodology used in an on-going, multi-year study at the LEF and provide insights that could be applicable to long-term monitoring programs at other sites. This study provided the necessary data and understanding to assess the response of the LEF bat community to Hurricane Hugo and to evaluate the condition of bat populations with respect to future management and conservation decisions.

METHODS

Bats were captured using mist nets (10 × 2 m, 50 denier, two-ply, 1.5-inch mesh; Avinet, Inc., Dryden, New York) at sites chosen within the tabonuco rain forest of the LEF. Our primary netting site was located along an unimproved road at the entrance to El Verde Field Station (18°19'18"N, 65°49'12"W). This site was selected based on two criteria: previous netting success and accessibility. Previous netting experience and visual observation had shown us that bat activity, as well as capture success, in the Luquillo Experimental Forest is highest along trails, roads, and streams. Bats use these areas regularly as flyways through the otherwise dense forest canopy, and very few bats were taken at other locations throughout the forest.

As to accessibility, the road's close proximity to the field station allowed us to conduct frequent monitoring throughout the night, thus cutting down on personnel requirements. Although numerous sites were netted periodically over the course of the study, this was the only site that was regularly sampled over the long term. All nets were set in sequence along the roadside at ground height, using aluminum poles. Between 10 and 12 nets were used to cover approximately 100 m of the roadside. Nets were placed in this same location during each mist-net survey, beginning in 1987. Since 1988, this site has been surveyed bi-annually – once during the rainy season (June or July) and once during the dry season (January or March). Canopy nets, placed in trees approximately 20 to 25 m in height with slingshots and rope, were used several times at nearby sites. They captured few, if any bats. Because netting success was so much higher with roadside nets and because the canopy nets were difficult and time consuming to place and monitor, results from their use were not included in our survey.

Our survey protocol called for nets to be open five nights during each sample period, from 1900 h to 0300 h. However, actual netting hours varied depending on weather conditions. For each captured animal, species, sex, weight, and age (adult, sub-adult, or juvenile, based on ossification of the metacarpal-phalangeal joint, following Anthony, 1988) were recorded. Reproductive condition for females was assessed as pregnant, lactating, or pregnant and lactating. Pregnancy was determined by abdominal palpation (Gannon and Willig, 1992). We also permanently marked bats with small necklaces, each carrying a uniquely numbered aluminum band. During the first 3 years of the study, ball chain necklaces (Barclay and Bell, 1988) were used. However, proper attachment of these necklaces required excessive handling of each bat. In addition, smaller individuals could not be tagged because of the ball chain was too heavy. In 1990, we began using a new, lightweight necklace (Gannon, 1994) that alleviated many of these problems. Collars are constructed from adjustable, self-locking plastic cable ties or seals that can be obtained through a variety of sources. A cable tie is threaded through medical grade tubing, which minimizes movement of the collar and irritation to the bat. The length of tubing used is determined by the circumference of the neck and will differ depending on the species of bat. Silicon spray facilitates threading the tie through the tubing. Finally, a numbered aluminum band is fitted to the collar. When the finished collar is closed into a loop, it can easily be dropped over the head of the bat and adjusted for proper fit from the rear within several seconds. The excess plastic is then clipped from the collar, and the bat is ready for release.

This lightweight collar has been successfully tested in the field on bats that weigh as little as 9 g. Banded *M. redmani* on Puerto Rico, recaptured several months after being collared, appeared in good health and showed no problems stemming from the collars. The total weight of the collar with aluminum band used for these individuals was 0.18 g. Other bats collared using this method include *A. jamaicensis*, *S. rufum*, *Brachyphylla cavernarum*, and *Erophylla sezekorni*. To date, no adverse effects have been noted for any recaptured individual.

Population analyses

In an attempt to evaluate population trends of bats in the LEF, we utilized several different techniques. The number of bats captured/net hour during each sampling period was determined and compared over time. In addition, relative importance for each bat species (compared to other bats in the community) was assessed from netting records in two ways. First, numerical dominance (ND) for each species was measured as n_i/N, where n_i is the number of captured individuals of species i and $N = \sum n_i$ is the total number of captured animals regardless of taxonomic identity (Gannon and Willig, 1994; Willig and Gannon, 1996). This index of the proportion of each species of bat present in our sample gives equal weight to all individuals regardless of size differences. Second, biomass dominance (BD) was calculated by

$$n_i Y_i / \sum_{i=1}^{S} n_i Y_i$$

where Y_i is the mean biomass of species i, and S is the number of species in the community (Gannon and Willig, 1994; Willig and Gannon, 1996). This is an index of the ecological impact of each species based on energetic considerations.

These techniques do not yield estimates and cannot be used for direct evaluation of species density. They reflect the importance of a population within a community based on the proportion of all individuals represented by a particular species. Nonetheless, they provide estimates of population trends (increasing, decreasing, remaining stable) over time.

RESULTS AND DISCUSSION

Seven species of bats were captured at El Verde between, 1987 and, 1994. Of these, only three species were considered common – *S. rufum*, *A. jamaicensis*, and *M. redmani*. Other species rarely captured at El Verde during this period include *B. cavernarum*, *E. sezekorni*, *Eptesicus fuscus*, and *Lasiurus borealis*. Population trends were examined individually for each of these three dominant species and for all bats regardless of species.

The majority of bats in the tabonuco forest at El Verde, in relation to numbers captured/net hour and importance values, comprise the two dominant species, *A. jamaicensis* and S. rufum, and, thus, they drive the overall trend when examining all species (Figure 14.2A). Although these two species are frugivorous and consume a variety of fruit, their diets, roosting requirements, and foraging habits are distinctly different (Gannon and Willig, 1994; Willig and Gannon, 1996). Still, both exhibited similar trends in numbers during the monitoring period 1987 to 1989, before Hurricane Hugo.

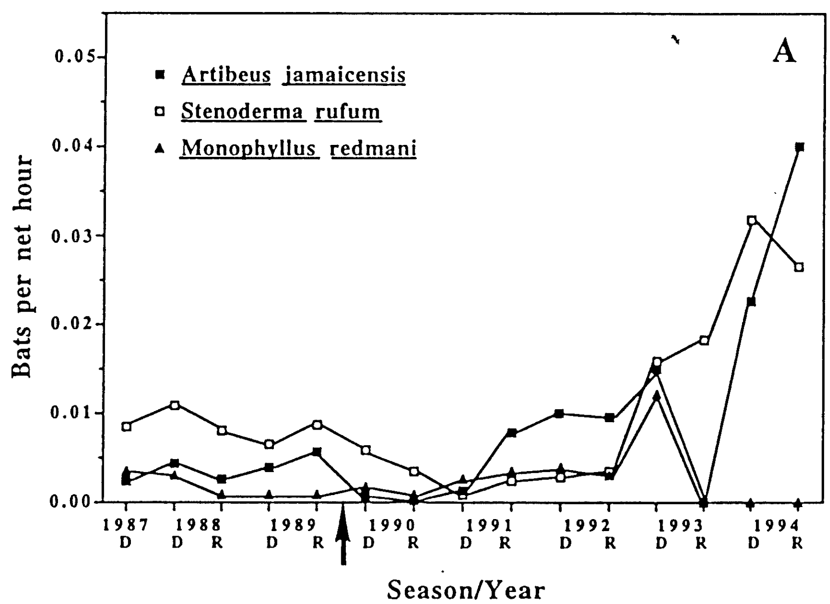
The effects of disturbance on bat populations

Observations on populations – using bats captured per net hour, numerical dominance, and biomass dominance – showed similar trends (Figure 14.2). In general, the number of bats regardless of species captured at El Verde during the first three years of the study was low (Figure 14.2a). Slight fluctuations in numbers were observed during this period, occurring in a similar fashion in populations of the frugivorous bats *A. jamaicensis* and *S. rufum* (Figures 14.2b and 14.2c).

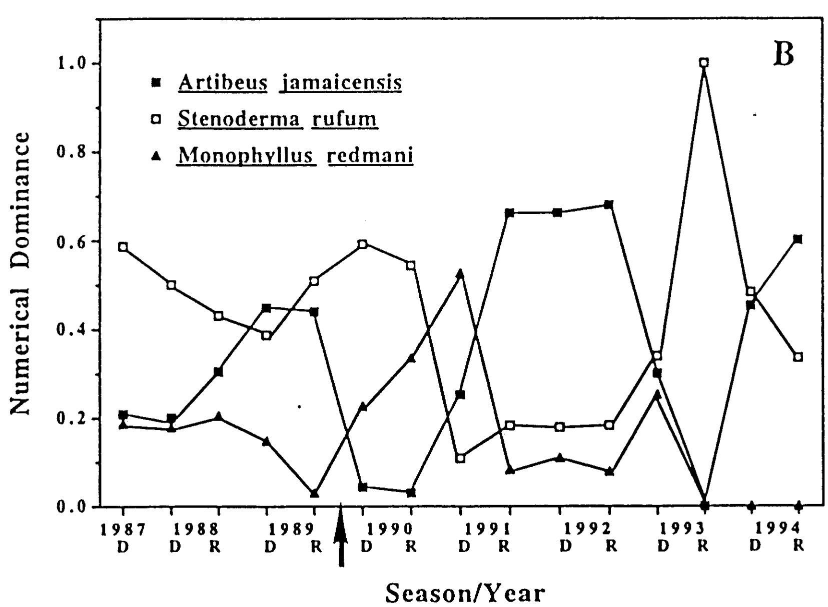
Hurricane Hugo altered the forest in September of 1989, during a time when our survey indicated that numbers of both *A. jamaicensis* and *S. rufum* were on the increase. Fruit-eating bats and the nectar-feeding *M. redmani* exhibited different responses to Hugo. After the hurricane, the density of each species decreased, but the form of the decrease was species specific (Figure 14.2).

Effects on A. jamaicensis

A. jamaicensis declined quickly and immediately after Hurricane Hugo in both numbers and relative importance (Figure 14.2b). The population remained depressed for approximately 18 months. This species was the first to return to



A
Artibeus jamaicensis
Stenoderma rufum
Monophyllus redmani
Bats per net hour
0.05
0.04
0.03
0.02
0.01
0.00
1987 D
1988 D R
1989 D R
1990 D R
1991 D R
1992 D R
1993 D R
1994 D R
Season/Year



B
Artibeus jamaicensis
Stenoderma rufum
Monophyllus redmani
Numerical Dominance
1.0
0.8
0.6
0.4
0.2
0.0
1987 D
1988 D R
1989 D R
1990 D R
1991 D R
1992 D R
1993 D R
1994 D R
Season/Year

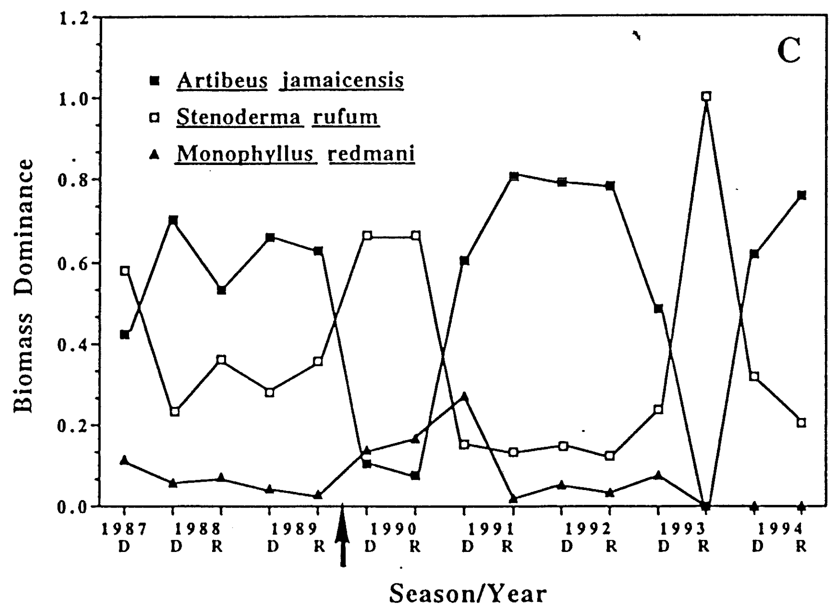


Figure 14.2 Long-term population trends based on bats captured/net hour (A), numerical dominance (B), and biomass dominance (C) for the three most common phyllostomids in the tabonuco rain forest at El Verde. D and R indicate the dry (D) and rainy (R) seasons for each year

and exceed the capture and dominance levels (proportional representation of the fauna and captures/net hour) of the pre-Hugo monitoring period.

Prior to Hurricane Hugo, juveniles composed a modest proportion (between 15% and 30%) of the local population of *A. jamaicensis* (Figure 14.2a). Large fluctuations in the proportion of juveniles (0% to 100%) characterized periods following the disturbance. Some of this variation is attributable to the low number of captures for this species during the first 2 years after the hurricane. Data from 1994 indicate that the proportion of juveniles may be stabilizing at pre-hurricane levels.

Reproductive patterns of *A. jamaicensis* are characterized by geographic variation throughout its range (Tamsitt and Valdivieso, 1963, 1964; Bonaccorso, 1979; Gannon and Willig, 1992). Long-term data for Puerto Rico suggest that this variation has a temporal component as well (Figure 14.4a). Reproductively active females occurred in all samples for which females were present except one, but varied greatly in the percentage they represented in the sample. (The dry season of 1990, our first sampling period after Hurricane Hugo, yielded few *A. jamaicensis*, and only one was female.) Pre-disturbance percentages of reproducing females (ranging from 40% to 100%) do not differ statistically (95% confidence intervals overlap) from post-hurricane percentages (ranging from 30% to 75%). This indicates that the hurricane had little or no effect on reproduction of this species.

A. jamaicensis is a strong flier, capable of moving long distances (Morrison, 1978a, 1978b; Handley *et al.*, 1991b). Our radio telemetry observations indicate that A. jamaicensis does not usually roost in the tabonuco forest, but commutes from surrounding areas. Radio-tagged individuals were never located within the forest during the day. We suspect that suitable roost sites for this species within the LEF are rare, as there are no caves and rocky outcroppings within its bounds. In this case, the changes we observed in population numbers of *A. jamaicensis* may reflect not direct hurricane-induced mortality, but rather a change in foraging patterns of individuals toward areas of the island that were less affected by the hurricane and where food was more easily available. This proposition is supported by the high variation we observed in juvenile numbers between sampling periods along with the lack of significant change in reproduction between pre- and post-hurricane samples shown by our data.

Effects on S. rufum

S. rufum was negatively affected by the hurricane (Figure 14.2c), although initially to a lesser degree than was *A. jamaicensis*. Its decline was more gradual, reaching the lowest level during the dry season of 1991. Other periodic surveys at various locations throughout other life zones in the LEF indicated that *S. rufum* was restricted to tabonuco rain forest both before and after the hurricane. Telemetric observations showed that this species is solitary and roosts in the forest canopy in close proximity to its food source. It is a weaker flier than *A. jamaicensis* and maintains a small home range of about 2.5 km^2 (Gannon, 1991; Gannon and Willig, 1994; Willig and Gannon, 1996). The probable cause of this species decline is its inability to disperse from the tabonuco rain forest, as suggested by its limited foraging and home ranges, combined with increased exposure to the elements (temperature, precipitation, wind) at canopy roost sites as a consequence of severe hurricane-induced defoliation (Gannon and Willig, 1994).

We were able to assess the impact of Hurricane Hugo on the reproductive status of *S. rufum*. On average, the proportion of juveniles decreased from 40% before to 17% immediately after Hurricane Hugo (Figure 14.3b); none were present in samples for two years between 1991 and 1993. In addition, few post-hurricane females have been reproductively active (pregnant or lactating; Figure 14.4b). On average, the proportion of reproductive females decreased from 93% before to about 29% after the hurricane. Not until 5 years after the hurricane did we begin to detect a reversal in both of these trends. Juveniles are beginning to reappear in the population, although still at levels well below those before the hurricane. Captures of reproductive females are increasing. As well, numbers of *S. rufum* in recent samples exceed all previously measured levels, and importance levels of this species are almost equal to those of the pre-hurricane levels.

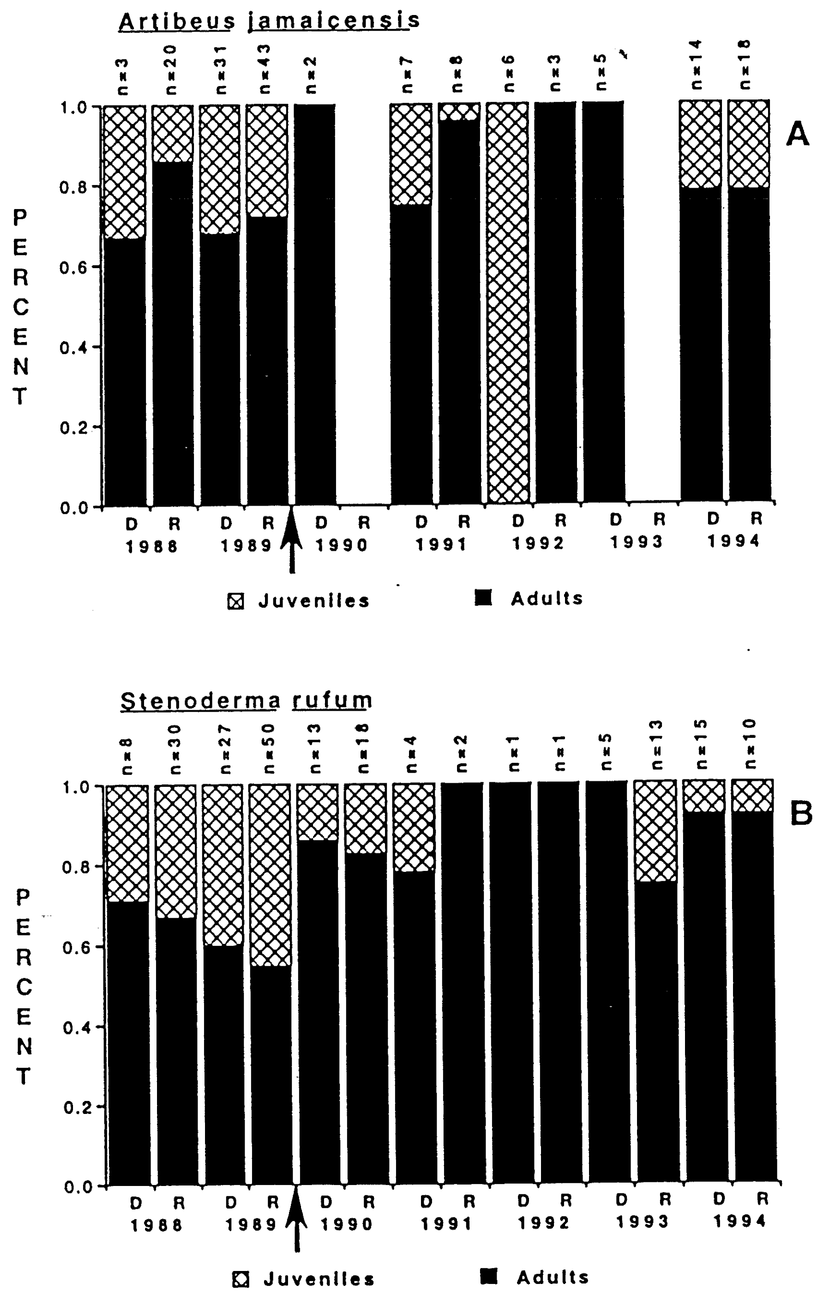


Figure 14.3 Histograms representing the demographic structure of two bat populations, *Artibeus jamanicensis* (A) and *Stenoderma rufum* (B) from the netting site at El Verde Field Station. The arrow represents the occurrence of Hurricane Hugo. Sample sizes are shown at the top of each column

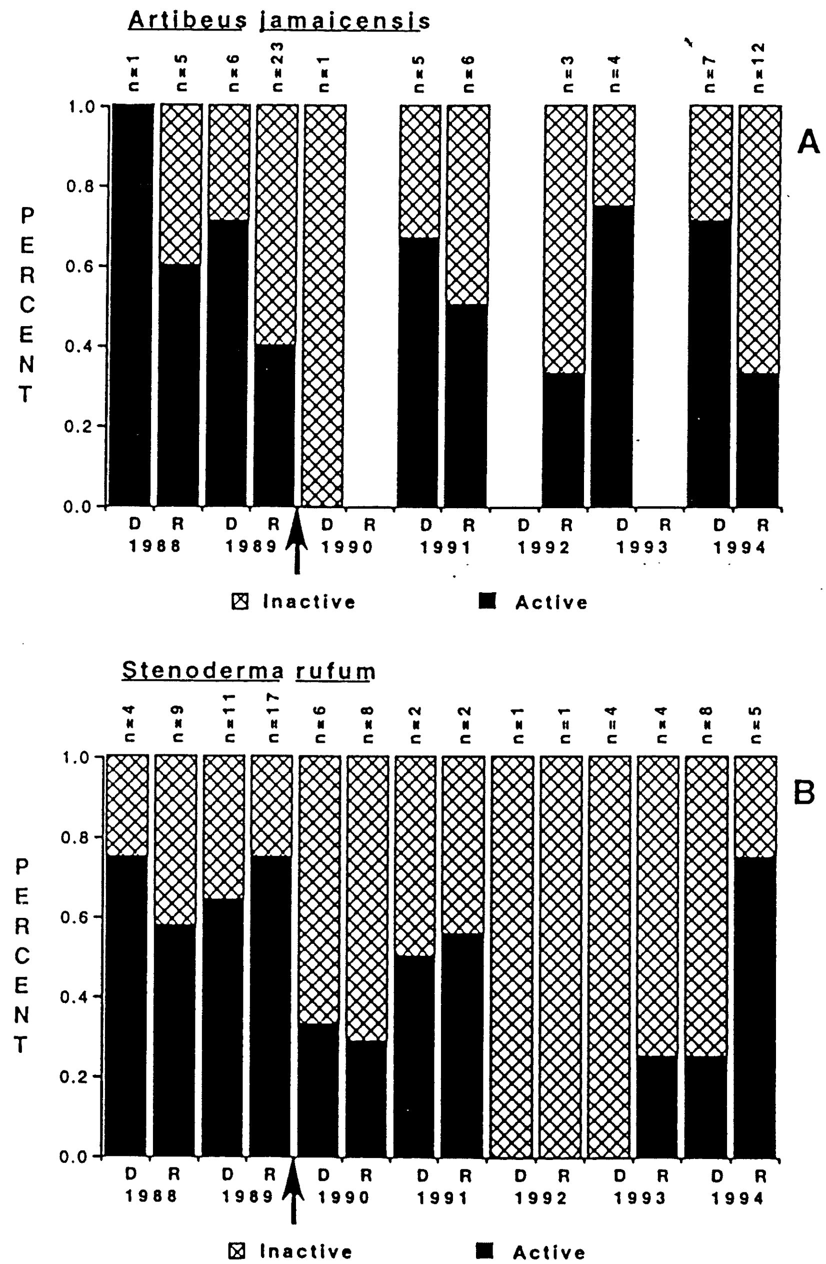


Figure 14.4 Histograms representing the proportion of breeding females in our sample of two bat populations, *Artibeus jamanicensis* (A) and *Stenoderma rufum* (B) from the netting site at El Verde Field Station. The arrow represents the occurrence of Hurricane Hugo. Sample sizes are shown at the top of each column

Effects on M. redmani

M. redmani has always been present in lower numbers than the two frugivores. Initially, this species appeared to be positively affected by the hurricane, with an increase in both biomass dominance and numerical dominance compared to pre-hurricane levels. However, captured numbers only slightly increased, and the resulting increase in importance can be attributed partly to the decrease of the previously dominant species *A. jamaicensis* and *S. rufum*. Moreover, the rapid increase in flowering plants in the forest understory after Hurricane Hugo may have had an effect on *M. redmani*, providing a newly available and increasing supply of food. Since 1993, no individual of this species has been captured at El Verde, an occurrence that may be either a delayed or indirect consequence of the hurricane. As the forest canopy continues to recover and close, we have witnessed large changes in the composition of plant species. Many early successional flowering plants have begun to decline in number. This may have caused a reduction of resources on which *M. redmani* could feed and accounted for the bat's decline.

Many of the population changes that took place between 1990 and 1994 are attributed directly or indirectly to the impact of Hurricane Hugo. It was a major disturbance and may have disrupted or masked any seasonal, annual, or cyclic patterns that otherwise might have occurred during this period. Hurricanes are not uncommon in the Caribbean. Puerto Rico is subject to storms of hurricane magnitude at intervals of approximately 60 years on average (Doyle, 1981, 1982). We recognize that the alteration of the forest as a result of the hurricane potentially could have altered our net-capture success. Prior to Hugo, the LEF had a thick canopy, approximately 30 m in height, with a relatively open understory. However, because the hurricane resulted in almost complete removal of the forest canopy, the only remaining food sources for frugivorous bats were early successional shrubs on the forest floor. In this case, with our nets located in close proximity to the only available fruit sources, the netting bias would likely be to enhance capture success. Since our data reveal trends in the opposite direction, we feel we have taken a conservative approach in our interpretation.

Presumably, bats have evolved at these locations over a sufficiently long time to acquire adaptations to the periodic, large-scale alterations wrought by hurricanes. The time needed for recolonization of vertebrates after a disturbance such as a hurricane can differ considerably and depends on many factors, including disturbance intensity and reproductive rate of affected taxa (Karr and Freemark, 1985). Lag time between the disturbance and changes in population numbers differed for each of the bat species in the LEF. In relation to recovery, most of the changes occurred within 3 years of Hurricane Hugo's impact. *S. rufum* took longer to exhibit attributes of recovery than did *A. jamaicensis*, but both frugivorous bat populations have now exceeded pre-hurricane numbers. It is likely that both species will stabilize in the near future with no long-term deleterious effects on their demography.

Conservation and management protocols for populations in general, and keystone species in particular, need to consider the consequences of seasonal and annual fluctuations in the environment. Conservation plans should manage for minimum numbers likely to occur over scores of years and insure that the lowest likely densities (resulting from an environmental catastrophic event, whether it be natural or anthropogenic) remain above estimated minimum viable population levels. The case of *S. rufum* illustrates this well. The consequences of Hurricane Hugo resulted in massive declines of adults, and adversely affected reproduction to the point of concern for its continued viability. Other known populations of this species are few in number and occur as isolated pockets separated by many miles of urbanization (M. Willig *et al.* unpublished data). This, along with the fact that *S. rufum* is not a strong flier, suggests that immigration to rescue declining populations is unlikely. Only after considerable time has this population begun to return to pre-disturbance levels. Hurricane Hugo struck at a time when numbers of *S. rufum* were on the increase. Had it occurred during a point when numbers were lower, or had another major disturbance followed Hugo (e.g. a second hurricane or severe tropical storm), this population may very well have declined to a level from which it could not recover. The consequences of an event such as removal of a keystone disperser to an ecosystem can be far reaching. Bats are major dispersers of several important species of tree in the tabonuco rain forest (Devoe, 1990). For at least one tree species, *Manilkara bidentata*, they appear to be the only agent of seed dispersal (You, 1991) because within the tabonuco rain forest, only *S. rufum* is known to consume the fruit of *M. bidentata* in any significant amount (the tree's fruit comprises 23% of the bat's diet; Willig and Gannon, 1996). The absence of *S. rufum* undoubtedly would affect distribution and reproductive success of this and other plant populations that it disperses and easily could have consequences on the structure of the forest as it recovers from the hurricane.

RECOMMENDATIONS FOR LONG-TERM MONITORING

Measuring populations

The size or density of a population often is considered to be a sign of its health, as well as a guide for directing future conservation efforts. An ubiquitous problem concerns identification of a reliable and cost-effective method to estimate population size for the taxon in question. Ecologists recognize that populations can be measured in two ways: absolute density, or the enumeration of organisms/ unit area, and relative density, or the density of one population relative to another (Krebs, 1989).

Some have tried to provide absolute estimates of population density for bats based on classic mark-recapture techniques (Keen, 1988, Thomas and LaVal, 1988; Leigh and Handley, 1991). These techniques require certain assumptions, including a closed population, no mortality during the sampling period, and equal 'catchability' of all individuals. These assumptions often are unrealistic when examining most bat populations. Bats are highly mobile, capable of traveling large distances in relatively short periods. In addition, individuals are not equally catchable because of their ability to echolocate and avoid nets as a result of prior experiences. Over the 8 years and thousands of net-hours of our study, few recaptures of any bat species have occurred (less than 1%). These techniques can inflate population estimates if marked individuals have a lower likelihood of recapture that do unmarked individuals. At best, mark-recapture methods are useful only for intensive, short-term sampling of bats, and estimates based on results of such sampling should be interpreted cautiously. Attempts to assess populations in large hibernacula, or in large maternity colonies, by direct visual count have been used also (Gaisler *et al.*, 1979). This approach has the advantage of locating large numbers of bats relatively easily. It can be performed quickly, with minimal manpower, but has the additional inherent problem of large numbers (hundreds or thousands) that are difficult to count accurately. Many individual bats may be missed altogether or counted more than once. Moreover, closely related species that share roosts and are similar in appearance may be misidentified, further compounding error. Solitary bats or those that roost in small numbers within trees, cervices, or foliage are difficult to locate. Few population estimates have been attempted for these species (Constantine, 1966).

Accurately estimating absolute densities of bat populations using mark–recapture techniques or direct counts may not be possible in many instances. However, it is not difficult to examine relative densities of populations with the indices we suggest (numerical dominance, biomass dominance, individuals captured per net hour) using data from field netting. These indices provide an alternative to some of the methodological problems mentioned above by estimating the importance as well as numbers of each species in the forest. These values have the advantage of being comparable over time, and they do not require many of the assumptions of other estimates. Thus, they are useful in making long-term observations by indicating changes that take place within populations. They are especially helpful in situations such as those in Puerto Rico where recapture success is low. Moreover, the same data collected in a mark–recapture study can be converted easily for use in calculating importance values.

In addition, our approach provides information on changes in demographic patterns, particularly for reproductive females and juveniles. These individuals are most likely to make the greatest contribution to reproductive output of a population. Examining the proportion of these individuals in a sample gives an index of reproductive success and the potential for the population to increase in the near future. Nonetheless, our approach does not address many important demographic characteristics such as survivorship, roosting ecology, or growth and development. These parameters may be no less significant when considering the overall biology of an organism and designing its management and conservation scheme.

We should again be clear to point out that this methodology is a survey, not a census. Although it does seek to collect information on the size and characteristics of the population, it cannot provide any measure of absolute density or complete enumeration of a population. The information it provides via periodic surveys concerns how the population changes over time relative to previous surveys. It is useful in examining long-term trends of a population, not its absolute numbers. Given the difficulties and assumptions previously mentioned with providing accurate numerical counts and censuses of bat populations, this methodology seems to reduce some potential biases, while still indicating several important population parameters.

Developing a protocol

In constructing a long-term protocol for monitoring bats, it is important that questions and goals be defined clearly at the start because they directly affect the design of the protocol. Key points that should be considered include the choice of the number of sites, the placement of nets relative to bat activity (near vegetation, on trails, over streams, etc.), the specific location of nets (canopy versus ground nets), and the timeframe in which surveys are conducted. Many of these points will differ among localities, and the monitoring design should differ accordingly. For example, our netting protocol for an island forest where bat density is low would not be sufficient for tropical mainland forests where the bat density is many times higher.

Available, experienced human power is most often the limiting factor in determining the number and frequency of sites to be monitored and, thus, may limit long-term goals and overall design. Although we were successful in assessing some demographic parameters of bat populations, establishing a network of sites to be sampled simultaneously would reduce the effects of any site-specific sampling and temporal sampling error that can occur. Furthermore, we can presently say little about long-term trends in life zones other than tabonuco rain forest. If goals include comprehensive tracking of populations in forests with a variety of habitats, additional netting sites would be necessary in those areas. For example, for adequate sampling of a forest the size of the LEF for bats, we should at a minimum establish five or more netting sites in each of the four life zones.

The timing (annual, seasonal, multi-year) of each sampling period depends on the scale of the questions to be answered. We recommend that, at the least, surveys should be performed during distinct phenological seasons (e.g. wet season and dry season) to examine patterns in bat demographics. In some areas where climate and local conditions are more variable, quarterly sampling would be advisable. Demographic patterns could occur as changes in density of a population or in reproductive and breeding success. More frequent sampling performed on a monthly regime would provide finer resolution of annual patterns (e.g. reproductive patterns), but would substantially increase time and effort.

Reduced capture success on successive nights of netting has been demonstrated by several authors as a consequence of the ability of some species of bats to avoid nets based on previous encounter (LaVal, 1970; Kunz, 1973; LaVal and Fitch, 1977). We found this to be true with the phyllostomids in the LEF. Few tagged individuals are ever recaptured. Therefore, our goal became not to recapture tagged individuals, but assess the number of each species of bat utilizing an area within a given time.

In addition, bat activity can be affected by weather conditions. These should be held as constant as possible for each sample period. Extending the number of nights in which each site is sampled may reduce variation caused by such factors. We chose to sample for 5 nights each period for these reasons. Although average monthly rainfall in the tabonuco rain forest varies from a maximum in May of 460 mm to a minimum of 290 mm in January, seasonal differences in precipitation are not pronounced (McDowell and Estrada-Pinto, 1988). Rainfall typically occurs in short bouts differing in intensity and frequency throughout the day and night, rather than as one continuous rainfall. Under usual conditions in the tabonuco forest at El Verde, 5 sampling nights would minimize variation caused by sporadic weather changes, especially because our indices are relative measures and would be biased only if inclement weather reduced activity in a species-specific fashion. We also noted that netting success did not vary on successive nights in the LEF. Night 4 or 5 was just as likely to yield as many, or more, bats as night 1 or 2. This may be due to the low density of bats present in the forest. Depending on the question being investigated, the locality being sampled, and the way the data are to be used and interpreted, it might be advisable under other circumstances to reposition and reconfigure nets on successive netting nights.

Under certain situations, the use of ultrasonic bat detectors may have application in the monitoring of bat populations. These electronic devices convert ultrasonic calls produced by bats into audible sounds and visual sonograms. They can be recorded in the field and analyzed at a later date. This approach was tested for a short period during our study, but proved less than satisfactory and was abandoned for several reasons. First, the units are costly (in 1996, they ranged in price from US$200 to US$2000, depending on features and sensitivity). Moreover, they require computer hardware and software to produce sonograms for analysis. Some bats, particularly individuals of closely related species, cannot be distinguished accurately otherwise. Resultant data are sensitive to bat activity, especially vocalization rate, and may not represent reliable estimations of density. For example, there is no correspondence among the number of times a bat passes over the detector and the number of individuals present in an area (Thomas and LaVal, 1988). It is not possible to distinguish one bat making many passes through an area or many bats making a single pass. Finally, not all types of bats can be detected easily with these devices. Most bats at our site, as in many areas of the neotropics, belong to the family Phyllostomidae (New World leaf-nosed bats). They emit a complex series of echolocation calls that include short pulses of low intensity. As a result, they are sometimes referred to as whispering bats.

Because of the low-intensity calls, the bat detectors we tested were unsuccessful at identifying most phyllostomids at distances of more than several meters. Bat detectors may therefore have a reduced application in areas where phyllostomids are dominate.

Another capture technique that may have application in bat surveys is the harp trap (see Kunz and Kurtra, 1988). These are typically single or double frames of aluminum (1 to 3 m^2 in size) strung vertically with fine wire at intervals of about 2.5 cm. The wires are not easily detected by echolocating bats, and the series of wires are sufficient to stop many bats, which then fall into a large bag attached beneath the trap. Initially, these devices were difficult to use – they were large, bulky, and laborious to transport. Recent modifications (Tideman and Woodside, 1978; Palmeirim and Rodrigues, 1993) have transformed existing designs into highly portable units that are easy to assemble. These devices have proven especially useful in capturing bats at caves or other roost-site entrances where individuals are concentrated in numbers. In our case, where we sampled in open forest, their application was clearly limited. First, their smaller size relative to a 10 × 2-m mist net and the low density of bats in the LEF made the likelihood of individuals encountering such a device unacceptably low. Second, small nectarivorous bats such as *M. redmani*, which typically hover when feeding on flowers, could easily escape.

CONCLUSION

This research demonstrates the utility of long-term studies and how a relatively efficient and cost-effective field procedure provides important indicators of population status and community composition of bat species. Accurate and precise monitoring of many species in a tropical forest would be economically unfeasible. Cost-effective and simple protocols such as ours could be followed in many forest biomes, thereby providing critical data for the management and conservation of biodiversity that would otherwise be extremely difficult.

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