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The Effects of Hurricane Hugo on Bats of the Luquillo Experimental Forest of Puerto Rico[1]

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ABSTRACT

Natural disturbances can have large effects on ecosystem structure and function depending on their scale, intensity, and frequency. On 18 September 1989 Hurricane Hugo struck Puerto Rico, with the eye of the hurricane passing within 10 km of the Luquillo Experimental Forest. This provided a rare opportunity to evaluate the effects of an infrequent but large scale and high intensity disturbance on tropical bat species. Data on demographic parameters of three common phyllostomid bats (*Artibeus jamaicensis, Stenoderma rufum,* and *Monophyllus redmani*) were examined for three years prior and three years after the hurricane. Population levels as estimated by captures per net hour of all three species were affected by Hurricane Hugo. Populations of *A. jamaicensis* and *M. redmani* returned to predisturbance levels within two years. In contrast, population levels of *S. rufum* declined to about 30 percent of prehurricane levels and have not recovered after three years. Moreover, telemetry data indicate that foraging and home range size expanded to encompass an area approximately five times larger than its prehurricane size. The cost of foraging, in terms of time and energy, may be considerably elevated over prehurricane scenarios. In fact, a significant change in the age structure of the population (juvenile individuals have been absent from the population since Hurricane Hugo) as well as significant decline in the percent of reproductively active females indicate a failure to reproduce in the posthurricane environment.

RESUMEN

El impacto de disturbios naturales en la estructura y funcinamiento de ecosístemas depende de la escala, intensidad, y frequencia de estos. El 18 de septiembre de 1989 el ojo del huracán Hugo pasó a menos de diez kilometros de el Bosque Experimental de Luquillo. Este evento proveyó la rara oportunidad de estudiar los efectos de un disturbio de alta intensidad y gran escala, pero baja frequencia, en las especies de murcielagos del bosque. Datos demográficos de tres especies comunes de murcielagos filostómidos (*Artibeus jamaicensis, Stenoderma rufum* y *Monophyllus redmani*) fueron colectados por tres años previos y tres años seguidos al huracán. Los niveles poblacionales de estas tres especies, estimados en capturas por red-hora, fueron afectados por el paso del huracán. Las poblaciones de *A. jamaicensis* y *M. redmani* retornaron a niveles prehuracán en dos años. Los niveles poblacionales de *S. rufum* depreciaron a cerca del 30 por ciento de los niveles prehuracán, y tres años despues del disturbio aún no se han recobrado. Más aún, datos de telemetría indican que el tamaño de las áreas de forageo y ámbito nativo de *S. rufum* fueron expandidas cerca de cinco veces lo que eran antes del huracán. El costo de foragéo, en terminos de tiempo y energía, puede que sea considerablemente más alto en escenarios posthuracán. De hecho, un cambio significativo en la estructura de edad de la población ha ocurrido (no hemos encontrado juveniles desde el paso del huracán). Esta reestructuración ha estado acompañada por una reducción significativa en el porciento de la actividad reproductiva de las hembras, lo que indica que esta especie no ha podido reproducirse exitosamente despues del huracán.

Key words: Chiroptera; disturbance; Hurricane Hugo; Puerto Rico; radio-telemetry; rain forest.

Hurricanes are large scale, high intensity disturbances that regularly occur throughout the Caribbean (Weaver 1989); their impact on the structure and function of tropical ecosystems is often great (Brokaw & Walker 1992, Walker *et al.* 1992). Although the importance of disturbance regimes is a contemporary concept in ecological theory (Pickett & White 1985), few empirical studies document their effects on animal populations, with the notable exceptions of Covich *et al.* 1992, Reagan 1992, Waide 1992, Willig and Camilo 1992, and Woolbright 1992. Although bats are keystone agents of pollination and seed dispersal in the tropics, little is known about their response to and recovery from hurricanes.

Effects of a disturbance can be immediate or long-term. Immediate effects are directly attribut-

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able to the hurricane (high winds, heavy rains) and affect individual mortality and spatial distributions. Indirect effects result in differential survivorship and reproductive success, with populations responding either positively or negatively to alterations that have occurred in the composition or structure of relevant habitats.

Frugivorous bats make a critical contribution to tropical forest succession by widely dispersing the seeds of early successional plants (*e.g.*, de Foresta *et al.* 1984, Charles-Dominique 1986). Indeed, the seeds of small, fleshy-fruited plants are often dispersed by bats and dominate seed banks of tropical soils. Moreover, such seeds are a source of colonists in recently disturbed areas (Uhl *et al.* 1981, Swaine & Hall 1983, de Foresta *et al.* 1984). Bats also have been implicated in having an important role in flower pollination in tropical systems (Howell 1974, 1978; Stuart & Marshall 1976; Gould 1978; Ng 1978; Sazima & Sazima 1978). As such, frugivorous and nectarivorous bats can have a large impact on the distribution and genetic structure of plant species.

Compared to mainland areas of similar size and habitat diversity, Puerto Rico harbors few mammal species, and population numbers are generally low. Bats compose the major portion of the Puerto Rican mammal fauna in terms of species richness and density (Willig & Bauman 1984, Willig & Gannon 1994). Within the Luquillo Experimental Forest (LEF), four species of bats dominate, although some are common in certain habitats and rare or absent in others. Three of these species, *Stenoderma rufum, Artibeus jamaicensis,* and *Brachyphylla cavernarum* are principally frugivorous. The fourth, *Monophyllus redmani,* feeds on flower nectar.

Stenoderma rufum, the red fig-eating bat, has been found only at two localities on Puerto Rico, and on the nearby islands of St. John and St. Thomas (Genoways & Baker 1972). Until recent times, it was thought to be extinct and was known only from fossil records. As a result, it is a poorly known species and is in rare scientific collections. Only the population in the LEF has been sampled and studied to any extent during the past 25 years. It is currently designated as a "sensitive" species by the U.S. Forest Service. The status of other populations on Puerto Rico or the Virgin Islands is unknown. Studies conducted prior to Hurricane Hugo have examined various aspects of its population biology and ecology, including foraging and home range (Gannon 1991, Willig & Gannon 1994), reproduction (Gannon & Willig 1992), and diet (Willig & Bauman 1984, Willig & Gannon 1994). These works indicate that *S. rufum* consumes a variety of fruits, exhibits asynchronous bimodal polyestry, roosts in canopy foliage, and has a relatively small home range (mean = 2.1 ha) to which it exhibits high site fidelity for at least several months during the rainy season.

Artibeus jamaicensis, the Jamaican fruit bat, has a wide geographic distribution in tropical and subtropical America. It is a much-studied species and is known to consume a variety of fruits, as well as some flowers and insects. Although extensive work has examined aspects of the ecology of several mainland populations (Handley *et al.* 1991; Morrison 1975, 1978a, b, 1979), little has been done with island populations in general, or with Puerto Rican populations specifically (see Kunz *et al.* 1983). Previous research from the Luquillo Experimental Forest indicates it comprises at least 60 percent of the bat fauna (Willig & Bauman, 1984) and exhibits aseasonal polyestry (Willig & Bauman 1984; Willig & Gannon 1994).

Monophyllus redmani, the Greater Antillean Long-tongued bat, feeds primarily on flower nectar. It has a distributional range restricted to the Greater Antilles and several islands in the Bahamas (Homan & Jones 1975). Little is known of its ecology other than anecdotal observations. It is common on Puerto Rico, where it comprises a substantial portion of the LEF bat fauna (Willig & Bauman 1984, Willig & Gannon 1994).

STUDY SITE

Puerto Rico, the smallest and easternmost of the Greater Antilles, is subject to storms of great magnitude at intervals of approximately 60 years (Doyle 1981, 1982). The Luquillo Experimental Forest (18°10′N, 65°30′W), also known as the Caribbean National Forest, is located in the northeast corner of the island, within the Luquillo Mountains. Increasing elevation in the Luquillo Mountains is accompanied by changes in climate, soil, and vegetation structure and composition. As a result, three distinct life zones occur within the bounds of the LEF (Ewel & Whitmore 1973, Brown *et al.* 1983). The tabonuco rain forest, the largest life zone, is located on lower mountain slopes of the LEF below 650 meters. Rainfall is substantial and varies between 2000 and 4000 mm annually. The palo colorado forest is found in valleys and on mountain slopes above cloud condensation level at 600 meters elevation; average rainfall is 4700 mm. The dwarf forest occupies the highest mountain summits and ridge lines above 850 meters. It comprises dense stands of short trees and shrubs. This area is continuously exposed to winds and clouds and receives rain nearly 350 days per year.

The LEF is a disturbance mediated forest (Crow 1980, Doyle 1981). Natural disturbances vary in frequency and intensity and include tree fall gaps, landslides, and hurricanes. The greatest disturbance in recent years has been Hurricane Hugo, which had a dramatic effect on the forest (Brokaw & Walker 1992, Scatena & Larsen 1992, Walker *et al.* 1992). On 18 September 1989, the eye of Hurricane Hugo, a category 4 storm with winds in excess of 220 km per hour, passed within 10 km of the forest. It was the first storm of this magnitude to pass directly over the LEF since 1932, and resulted in large scale disturbances, including thousands of snapped and tipped-up trees, hundreds of landslides of various sizes, and defoliation of virtually all hardwoods, effecting almost complete loss of the forest canopy.

METHODS

Bats were captured with mist nets at sites established within the tabonuco, palo colorado, and dwarf forest. Sites were chosen based on accessibility and our previous netting success. Age, sex, weight, and reproductive condition were determined for each captured animal. We also marked each bat by attaching small ball chain necklaces, each carrying a uniquely numbered aluminum band (Gey Band and Tag Co., Norristown, Pennsylvania, U.S.A.).

Individuals within bat populations are not equally catchable because of their ability to echolocate, and avoid nets after encounters with such devices. This is true of the bats in the LEF, where recaptures of bats are extremely low. Assumptions of most common population estimation techniques are violated severely when estimating bat density based upon netting. In an attempt to evaluate population trends of bats in the LEF, we utilized several techniques. We determined the number of bats captured per net hour during each sampling period, and compared those numbers 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. 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

$$N = \left(\sum_{i=1}^{s} n_i Y_i \right)$$

is the total number of captured animals regardless of taxonomic identity (Willig & Gannon 1994). Biomass dominance (BD) for each species is given by

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

where Y_i is the mean biomass of species i and s is the number of species in the community (Willig & Gannon 1994).

To evaluate foraging behavior and home range, *S. rufum* were selected and fitted with radiotransmitters using a previously described protocol (Gannon 1991). Radio-tracking was conducted in the same areas of the tabonuco rain forest during the rainy season (June, July, and August) for two years prior and two years after the occurrence of Hurricane Hugo. Transmitters weighing 1.2 g (Holohil Systems, Ltd., Ontario, Canada, model BD-2) were attached to the dorsal pelage of bats using "Skin Bond" surgical glue (Pfizer Hospital Products Group, Inc., Largo, Florida). Subsequent to release, tagged individuals were tracked from the ground by two observers using hand-held telemetry receivers and antennas (Wildlife Materials, Inc., Carbondale, Illinois, model TRX-1000S). Eighteen adult *S. rufum* (8 ♂♂ and 10 ♀♀) were tagged and tracked during 1988 and 1989 (prehurricane); whereas, eight *S. rufum* (4 ♂♂ and 4 ♀♀) were tagged and tracked during 1990 (1 year posthurricane). Similarly, eight (4 ♂♂ and 4 ♀♀) were tagged and tracked during 1991 (2 years posthurricane). All radio-tagged individuals were adults and nonreproductive at the time of tagging. Each bat's location was triangulated once during the day, and between 1 and 3 times during the night. Tracking continued for a minimum of 15 days. Day location points, indicating day roosts, and night location points, indicating night roosts, were recorded as coordinates on a gridded map. Previous work with bats in the LEF indicated this protocol resulted in stabilized areas and should therefore reflect an accurate estimate of space utilization (Gannon 1991). Telemetry accuracy using this protocol in the LEF was extremely high (Gannon 1991, Lindsey & Arendt 1991).

Home range is commonly considered to be the area traversed by an animal while it conducts essential activities (Burt 1943). Most home range studies of small mammals have relied on capture-mark-recapture methodologies. Telemetry studies have been conducted on some large (especially game) mammals; but until recent years, few such studies existed for bats. We calculated home range size

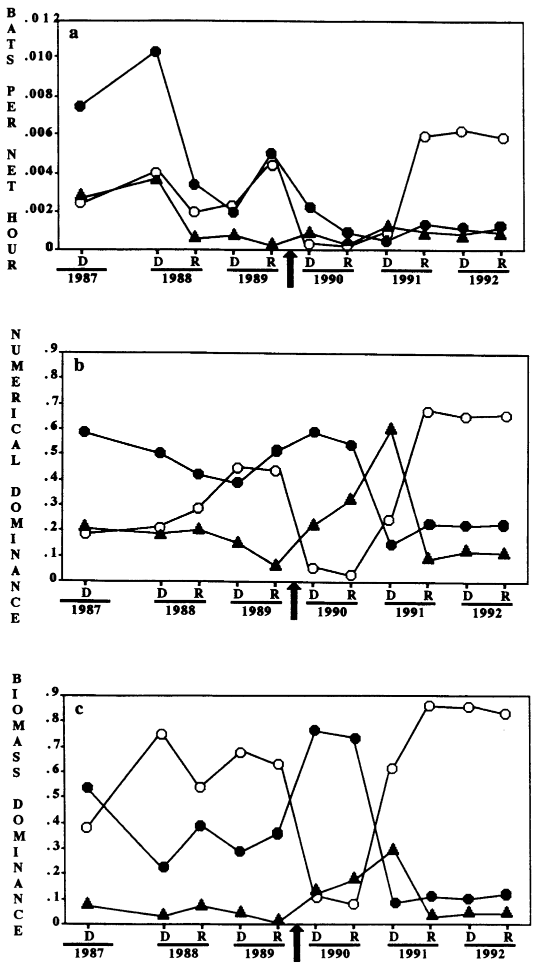

FIGURE 1. Long-term population trends of three common phyllostomid bats, from a single netting locality within the Luquillo Experimental Forest, (a) based on number of specimens captured per net hour of sampling effort, (b) numerical dominance, and (c) biomass dominance. An arrow indicates the occurrence of Hurricane Hugo. The open circles represent *Artibeus jamaicensis*, the closed circles represent *Stenoderma rufum*, and the triangles represent *Monophyllus redmani*.

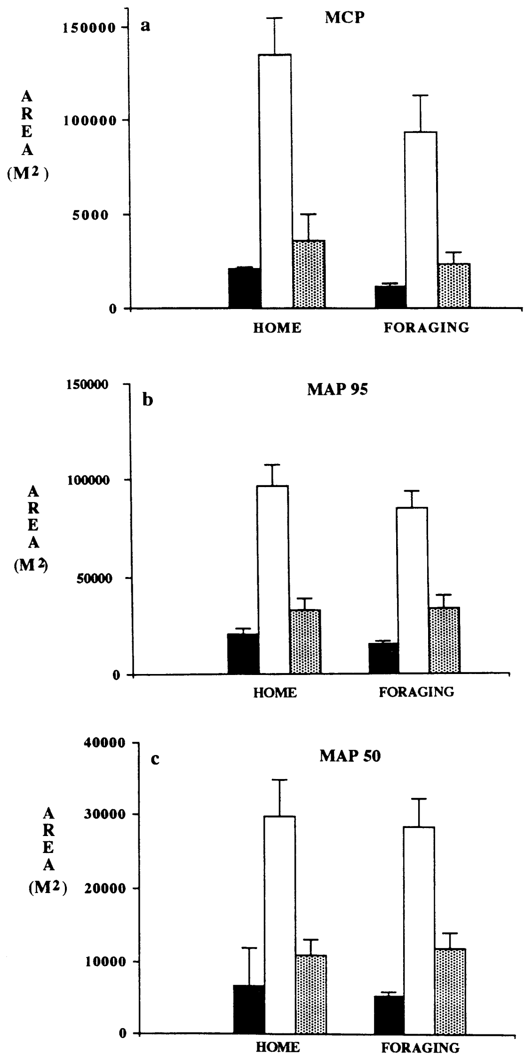

FIGURE 2. A comparison of mean home range (left) and foraging range (right) of *Stenoderma rufum* before (solid shading) and after Hurricane Hugo (1 year post-Hugo, unshaded; 2 years post-Hugo, stippled) based on (a) Minimum Convex Polygon, (b) 95 percent Minimum Area Probability, and (c) 50 percent Minimum Area Probability estimation methods.

based on telemetrically obtained location data using two methods: minimum convex polygon (Odum & Kuenzler 1955) and minimum area probability (Anderson 1982).

The minimum convex polygon (MCP) method is chosen frequently because of its simplicity. It assesses home range by drawing the smallest possible convex polygon around the outermost capture points. Although this method may be sensitive to sample size, and over- or underestimate home range size (Jennrich & Turner 1969, Dunn & Gibson 1977, Kenwood 1987, White & Garrott 1990), it was used as a first approximation in the field, and facilitated comparison with studies of other mammals.

Spatial patterns of an animal's activity should be dynamic and may reflect variation in resource utilization. Current methods of choice reflect this: Fourier Transformation (Anderson 1982); Minimum Area Versus Probability Method (Ford &

TABLE 1. *Sample size of three dominant bat species captured during the dry (D) and rainy (R) season from 1987 to 1991 at a single netting site in the Luquillo Experimental Forest near El Verde Field Station.*

	1987	1988		1989		1990		1991		1992	
Species	D	D	R	D	R	D	R	D	R	D	R
A. jamaicensis	6	3	20	31	43	2	1	7	8	6	3
S. rufum	17	8	30	27	50	13	18	4	2	1	1
M. redmani	6	3	10	11	3	5	6	10	2	1	1

Krumme 1979); and, Bivariate Normal Method (Jennrich & Turner 1969). Probabilistic models of home range represent space-use as a bivariate probability distribution, in which the z-axis is the probability of encountering an animal at a particular point in space. The nonparametric method uses actual patterns of movement rather than an assumed movement distribution (as in parametric methods) to generate spatial utilization distributions (UDs). Estimates of home range size are calculated as an area defined by a probability level (*e.g.,* 0.50, 0.95, and 1.00) that specifies the proportion of time that an individual was observed inside that area. These estimates are referred to as "minimum area versus probability" home ranges (MAP [0.50], MAP [0.95], and MAP [1.00] corresponding to each of the previously defined probability levels, respectively). This is a probabilistic, nonparametric model; it weights portions of an individual's range by the amount of use. MAP estimates are calculated as the smallest area that accounts for a fixed percentage of utilized space. The MAP method eliminates areas of low or no use that are included in home range estimates derived from the minimum convex polygon method. By selecting different percent utilizations, we can selectively eliminate the effects of outlier points and effectively compare more stable areas of frequent use.

Home range estimates for *S. rufum* were calculated in different ways. The MCP was plotted using program HomeRange (R. Huber & M. Willig, pers. obs.) for home range and foraging range. Foraging range can be distinguished from home range by excluding the location of day roosts from the estimation of range size. Thus the foraging range includes only locations obtained while bats are actively foraging. Home range also includes localities where bats are found roosting during the day. Any roost used during both periods was included in both analyses. We also calculated both MAP 95 and MAP 50 home range using a second option in program HomeRange (R. Huber & M. Willig, pers. obs.) that is a modification of program MacAnders (Anderson 1982, Wilkinson & Bradbury 1988). These MAP values are suggested analytical standards (Anderson 1982, Wilkinson & Bradbury 1988). MAP 95 is used because it closely corresponds to the standard definition of home range suggested by Burt (1943). However, when using large MAP estimates, occasional outlier points lead to large errors (Anderson 1982). Because smaller percent MAPs are less sensitive to outlier generated error, we also conducted analyses using MAP 50 home range estimates. MAP 50 values are as useful as MAP 95 values for comparative purposes, but have the advantage of representing smaller core areas

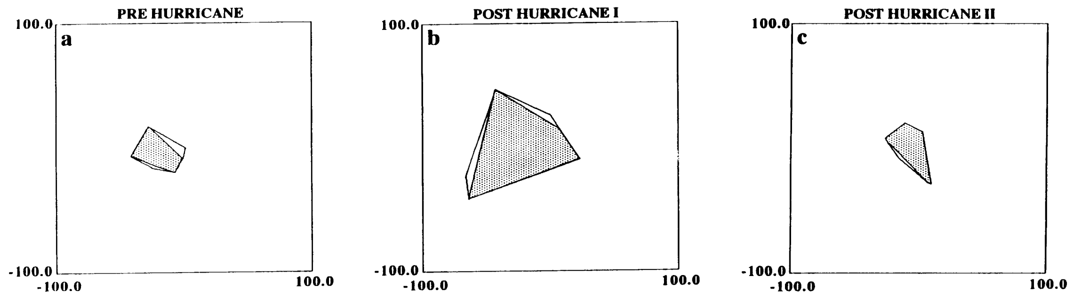

FIGURE 3. Schematic representation of home range and foraging range (stippled area) of *Stenoderma rufum* based on the Minimum Convex Polygon method (a) before, (b) 1 year after, and (c) 2 years after Hurricane Hugo. Three different individuals were used to construct Minimum Convex Polygons; comparisons are illustrative and do not represent a change of space use by a single individual.

TABLE 2. *Effects of sex and hurricane on home range and foraging range of* S. rufum *based upon a pure model I two-way analysis of variance. MCP = Minimum Convex Polygon, MAP (0.50) = 50% Minimum Area Probability, MAP (0.95) = 95% Minimum Area Probability, S × H = sex by hurricane interaction; home range is based upon both day roost and night roost captures, whereas foraging range is defined by night roost captures only.*

		MCP		MAP (0.95)		MAP (0.50)	
Source	df	Home range	Foraging range	Home range	Foraging range	Home range	Foraging range
Sex	1	0.43	1.23	0.07	1.49	1.06	0.05
Hurricane	2	34.89***	26.60***	52.75***	53.62***	41.94***	36.18***
S × H	2	0.56	3.09	0.43	1.73	1.60	0.28

*** = $P < 0.001$.

that reduce the effects of occasional outlier points on the resulting estimate of area.

The effects of hurricane (pre- versus post-Hugo) and sex (male versus female) on home range and foraging range size were evaluated via two-way analysis of variance (ANOVA), followed by orthogonal *a priori* contrasts (Sokal & Rohlf 1981). Separate analyses were conducted on home range and foraging range based upon MCP and MAP estimates.

RESULTS

POPULATION LEVELS.—Our primary netting site, near El Verde Field Station, in the tabonuco rain forest has been sampled for bats for the longest period, and thus should be the most useful in examining population trends within this life zone. This site was netted during dry and rainy seasons each year for six years beginning in 1987 (only the dry season was sampled in 1987). Population trends over this period were examined for each of the three dominant bat species at this locality, using numerical dominance, biomass dominance, and number of individuals captured per net hour (Fig. 1, Table 1).

Both *A. jamaicensis* and *S. rufum* exhibited relatively high numbers and dominance prior to Hurricane Hugo. Numbers of *A. jamaicensis* declined to near zero immediately after the hurricane, remained low for almost two years, and then recovered to prehurricane levels in year three. Numbers of *S. rufum* declined more gradually after the impact of Hurricane Hugo, reaching the lowest level in 1991. It has remained at densities far below those maintained prior to the disturbance. The dominance values of *M. redmani* fluctuated both before and after Hurricane Hugo; however, actual numbers of individuals have remained relatively stable, with only a slight increase soon after Hurricane Hugo.

HOME RANGE AND FORAGING.—Statistical comparisons of MCP home ranges were made by two-way ANOVA to assess effects of hurricane (pre-Hugo versus 1 year post-Hugo versus 2 years post-Hugo), sex (adult male versus adult female), and their interaction (Table 2, Fig. 2a). Both home range and foraging range exhibited a consistent significant difference associated with the hurricane treatment, but no difference related to sex of individuals. As a consequence, the sexes were combined in subsequent *a posteriori* comparisons to evaluate mean differences between all possible pairs of levels of hurricane treatments. Pre-Hugo (mean = 2.1 ha) and 2 year post-Hugo (mean = 3.6 ha) home range sizes were statistically indistinguishable based upon Welsch's step-up procedure; however, each was statistically distinguishable from the 1 year post-Hugo home range size (mean = 13.4 ha). The same pattern of significance was obtained for MCP foraging ranges (means were 1.2 ha, 9.3 ha, and 2.3 ha for pre-Hugo, 1 year post-Hugo, and 2 years post-Hugo, respectively). Thus, size of home range and foraging range were significantly affected by Hurricane Hugo, but the effect was no longer detectable after 2 years (Fig. 3).

For analyses based on MAP, statistical comparisons were made with two-way ANOVA for effects due to hurricane (pre-Hugo versus 1 year post-Hugo versus 2 years post-Hugo), sex (adult male versus adult female), and their interaction. For MAP 95 home range and foraging range, we detected significant differences due only to Hurricane Hugo, and these differences were experienced by the sexes in the same manner (*i.e.,* no significant interaction effect, Table 1, Fig. 2b). As a consequence, males and females were combined in subsequent *a posteriori* comparisons to evaluate mean differences between all possible pairs of levels of hurricane treatment. Pre-Hugo (mean = 2.1 ha) and 2 year post-Hugo (mean = 3.3 ha) home range sizes (MAP 95) were statistically indistinguishable based upon Welsch's step-up procedure; however, each was statistically distinguishable from the 1 year post-Hugo home range size (mean = 9.7 ha). Although the same trend toward recovery from hurricane effects was reflected in the analyses of foraging range using MAP 95 techniques (means are 1.5 ha, 8.5 ha, and 3.4 ha for pre-Hugo, 1 year post-Hugo, and 2 years post-Hugo, respectively), each hurricane treatment level was different from the others (Welsch's step-up procedure). Although MAP 95 foraging ranges are smaller 2 years after the hurricane than they were 1 year after the hurricane, they have not yet returned to the prehurricane sizes.

Results for the more stable MAP 50 home range and foraging range showed significant differences due only to Hurricane Hugo, and these differences were experienced by males and females in the same manner (*i.e.,* no significant interaction effect, Table 2, Fig. 2c). As a consequence, males and females were combined in subsequent *a posteriori* comparisons to evaluate mean differences between all possible pairs of levels of hurricane treatment. Pre-Hugo (mean = 0.7 ha) and 2 year post-Hugo (mean = 1.1 ha) home range sizes were statistically indistinguishable based upon Welsch's step-up procedure; however, each was statistically distinguishable from the 1 year post-Hugo home range size (mean = 3.0 ha). Although the same trend toward recovery from hurricane effects is seen when attention is restricted to foraging range using MAP 50 techniques (means are 0.5 ha, 2.9 ha, and 1.2 ha for pre-Hugo, 1 year post-Hugo, and 2 years post-Hugo, respectively), each hurricane treatment level was different from the others (Welsch's step-up procedure). Foraging ranges (MAP 50) were smaller 2 years after the hurricane than they were 1 year after the hurricane; nonetheless, they have not returned to the prehurricane sizes.

Comparisons of pre-, 1 year post-, and 2 year posthurricane home range and foraging ranges based upon MAP methods can be facilitated by three dimensional plots of space-use (Fig. 4), which are, in effect, a series of histogram bars throughout the plane where an animal may be found (*i.e.,* real space). The height of the bar, or z-axis, is the probability of locating that individual at each point at any given time. Higher peaks indicate higher probability. These figures can be used to qualitatively assess the pattern of space use for each bat. Similar figures were obtained for ranges based on 95 percent and 50 percent approaches; consequently, only 95 percent results are illustrated (Fig. 4). These figures consistently suggest that bats forage and roost within larger areas 1 year after the hurricane, and that the utilization of space is more diffuse or homogeneous (less steep topographies in MAP plots). Space utilization 2 years after Hurricane Hugo were similar, and in some cases indistinguishable from those prior to the hurricane.

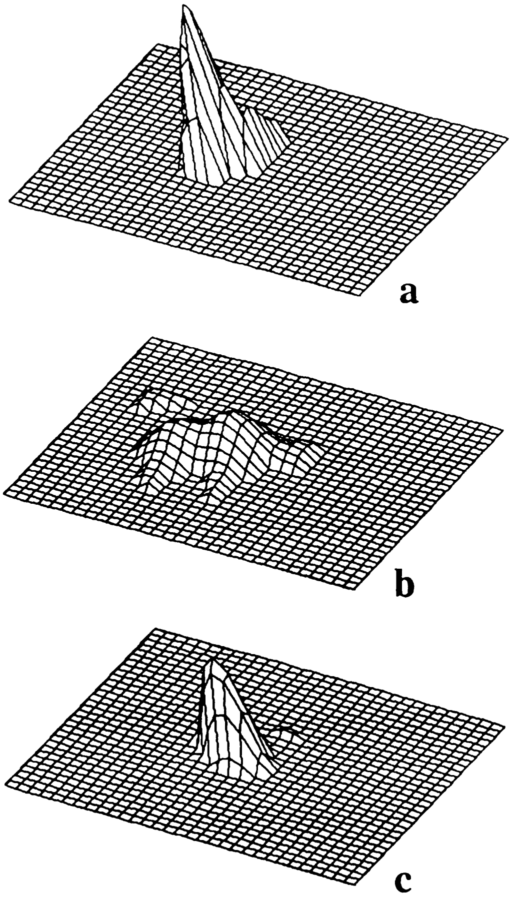

FIGURE 4. Schematic representation of home range of *Stenoderma rufum* based on the 95 percent Minimum Area Probability method (a) before, (b) 1 year after, and (c) 2 years after Hurricane Hugo. Three different individuals were used to construct Minimum Area Probabilities; comparisons are illustrative and do not represent a change of space use by a single individual. Similar results were obtained for 95 percent Minimum Area Probability foraging range and both 50 percent Minimum Area Probability home and foraging range.

DISTRIBUTION.—The proportional representation of species (*i.e.,* the number of individuals of a particular species divided by the total number of indi-

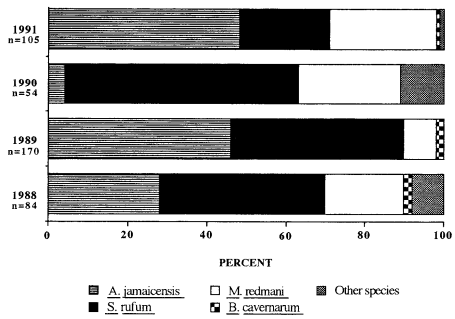

FIGURE 5. Proportional representation of species in the bat fauna of the tabonuco rain forest at El Verde from 1988 to 1991 (Various netting sites are pooled; dry and rainy seasons are pooled).

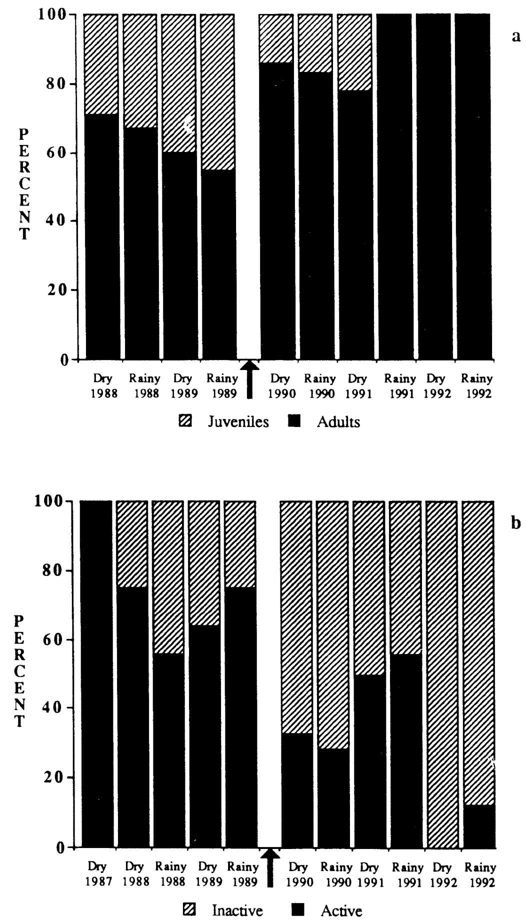

FIGURE 7. Histograms representing (a) the demographic structure, and (b) the proportion of breeding females, of the population of *Stenoderma rufum* in the tabonuco rain forest at El Verde. An arrow represents the occurrence of Hurricane Hugo.

viduals regardless of species) at all sites within a particular forest type represents the community composition of that forest type (four years [1988–1991] in the tabonuco rain forest [Fig. 5] as well as for tabonuco, palo colorado, and dwarf forest during 1991 [Fig. 6]). The proportional composition of the bat fauna in the tabonuco rain forest was altered because of the effects of Hurricane Hugo (Fig. 5). In particular, the originally dominant *A. jamaicensis* became a less important component of the fauna within a year of Hurricane Hugo's impact; however, it presently occupies a position of dominance equal to that during prehurricane periods. Although the abundance of *S. rufum* declined after the hurricane, it declined less than the other species, consequently assuming a position of higher dominance within a year of Hurricane Hugo's impact. The subsequent increase in density of *A. jamaicensis,* coupled with a decrease in density of *S. rufum* resulted in an appreciable decrease in the dominance of the latter during 1991.

Current distributional patterns of bats in the LEF (Fig. 6) suggest that the tabonuco rain forest is the most diverse zone in terms of bats because it contains a larger number of bat species and those species have a relatively even distribution. Moreover, this forest is unique in harboring a population of *S. rufum.* The palo colorado forest is almost as diverse in bat species as the tabonuco rain forest, but does not contain *S. rufum,* and *B. cavernarum* occurs there in a much higher density than elsewhere in the LEF. The dwarf forest is the least diverse zone with respect to bats, as its fauna comprises

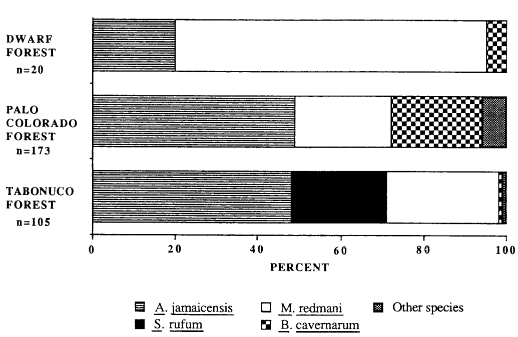

FIGURE 6. Proportional representation of species in the bat fauna within each of three life zones (tabonuco rain forest, palo colorado forest, and dwarf forest) of the Luquillo Experimental Forest.

only three species and is dominated by the nectarivorous bat, *M. redmani*.

DEMOGRAPHIC STRUCTURE.—The effect of recent perturbations on demographic parameters of *S. rufum* can be estimated by examining the proportion of captured individuals which are juveniles (Fig. 7a). This proportion is a measure of recent reproductive success, as well as an index of the potential of the population to increase in density in the near future. The effect of Hurricane Hugo on *S. rufum* in the tabonuco rain forest is evident from examination of trends in demographic structure from 1987 to 1992. Juveniles represented between 30 percent and 40 percent of the population before Hurricane Hugo (dry season 1988 to rainy season 1989), with a substantial decline in juvenile representation (to about 10%) after Hugo, during the dry season of 1990. Although slight increases in the sample proportion of juveniles were recorded during the next year (to about 20%), these do not represent statistical differences from the initial posthurricane proportions (*i.e.*, the 95% confidence intervals overlap). Most dramatically, we did not detect any juveniles in the population since the rainy season of 1991. This represents a statistically real alteration in demographic structure of the population compared to prehurricane and earlier posthurricane situations.

Changes in female reproductive patterns occurred as well (Fig. 7b). Prior to Hurricane Hugo, at least 55 percent of the adult female *S. rufum* were reproductively active (pregnant or lactating). Since the hurricane, we have noted a decline in the proportion of females that are breeding, with relatively few individuals producing young. This decline has persisted into 1992, with less than 5 percent of the females exhibiting reproductive activity.

DISCUSSION

Hurricane Hugo had a variety of effects on the bats of the LEF. These effects were best documented in the tabonuco rain forest, and to some extent, they were species-specific.

Artibeus jamaicensis was negatively affected by Hurricane Hugo, with a severe decrease in numbers, as well as in relative importance. Its levels remained low for two years posthurricane. Because prehurricane telemetry data indicated that this bat is a strong flier that moves large distances (M. Gannon, pers. obs.; Handley *et al.* 1991), reduced numbers may reflect movement of individuals to less affected areas of the island. Data collected since the rainy season of 1991 indicate that this species has returned to the level of dominance prior to Hurricane Hugo, in terms of both proportional representation of the fauna and in terms of captures per net hour.

Monophyllus redmani appeared positively affected by Hurricane Hugo. Both its biomass dominance and numerical dominance in the tabonuco rain forest increased compared to prehurricane levels. However, only a slight increase occurred in actual numbers of captured individuals. This relative increase is mostly due to the decrease of the other two previously dominant species. The small increase in actual numbers may also be attributed, in part, to the rapid and sizable increase in the presence of flowering plants in the open forest understory after Hurricane Hugo.

The most striking results are for *S. rufum;* it was negatively affected by the hurricane, although apparently less so initially than other bat species. However, it decreased in numbers in a steady fashion after Hurricane Hugo and experienced its lowest level during the dry season of 1991. Inability to disperse out of the tabonuco rain forest, as suggested by its limited foraging and home ranges, combined with increased exposure to high temperature, precipitation, and wind at roost sites (tree canopy), as well as decreased availability of fruit, may account for its gradual decline after Hurricane Hugo.

The impact of Hurricane Hugo on potential reproductive status of *S. rufum* occurred in two stages. The first stage reflects the greater susceptibility of juveniles to hurricane-induced alteration of resource and refuge characteristics (on average, proportions of juveniles decreased from 40 percent before to 17 percent immediately after Hurricane Hugo; none have been found since the dry season of 1991). The second stage reflects reduced fertility of adult females as well as reduced survivorship of pregnant females and their offspring; few of the posthurricane females have been reproductively active (on average, proportions decreased from 93% before to 29% after the hurricane). These trends appear to be continuing, and the future will probably see a further reduction in density of this sensitive species. Our surveys, along with historical records, indicate that *S. rufum* is restricted to this forest life zone. Its absence from both palo colorado and dwarf forest suggests that immigration from surrounding areas (the rescue effect: Brown & Kodric-Brown 1977, Willig & Moulton 1989) cannot countermand its decline. The localized occurrence of *S. rufum* in the tabonuco rain forest, its decline in density after the hurricane, and the dramatic reduction in juvenile representation in the population suggest that this species may be in danger of extirpation.

We recognize that the alteration of the forest as a result of the hurricane could potentially alter our net-capture success. However, because the disturbance resulted in an almost complete removal of the forest canopy, the only remaining food source for frugivorous bats was early successional shrubs on the forest floor. In this case, with our nets located in close proximity to 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.

Bats have been implicated as major dispersers of important species of tree in the tabonuco rain forest (Devoe 1990), and for some species, such as *Manilkara bidentata,* they appear to be the only dispersal agent (You 1991). Within the tabonuco rain forest, *S. rufum* is the only frugivorous bat known to consume *Manilkara* in appreciable amounts, where it comprises approximately 23 percent of the diet of *S. rufum* (Willig & Gannon 1994). The extirpation of *S. rufum* could have long-term and far reaching adverse effects on the life history of this tree species in particular. Moreover, the absence of *A. jamaicensis* from the tabonuco rain forest immediately after the hurricane suggests that *S. rufum* initially may play a critical role in recovery as the only bat dispersal agent of some early successional plants. It is presently unclear how many other plants could be adversely affected, or how the absence of *S. rufum* could affect the structure of the forest as it recovers from the hurricane.

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THE ASSOCIATION FOR TROPICAL BIOLOGY STUDENT PAPER AWARD

At the 1994 annual meeting, in Guadalajara, Mexico, The ATB awarded the first Alwyn Gentry Award, for the best paper presented by a student, to Elaine Joyal, of the Department of Botany, Arizona State University. Her presentation was titled, "Traditional Resource Management and Conservation Biology: An Ethnoecological Case Study from Sonora, México." Honorable mentions were awarded to Juan Francisco Ornelas (Department of Ecology and Evolutionary Biology, University of Arizona) for the paper, "Evolution of Nectar Robbing among Hummingbirds: A Phylogenetic Test," and to C. T. Sahley (Department of Biology, University of Miami) for the paper, "Reproductive Biology of *Weberbauerocereus* Cacti in Southwestern Peru: The Role of Bats and Hummingbirds as Pollinators."

The Award for the best paper presented by a student at the annual meeting of the Association for Tropical Biology was named after Alwyn H. Gentry, in honor of his outstanding contributions to tropical biology and to the Association for Tropical Biology. He is remembered especially for his support for students and their research. He was killed in an airplane crash in 1993, while assessing botanical diversity in Ecuador.

The first selection committee was chaired by Mercedes Foster. In subsequent annual meetings, the ATB plans to provide awards for both the best paper and best poster presented by students. The 1995 ATB annual meeting will be with the AIBS, in San Diego. Applications for consideration for the Alwyn Gentry Award and Best Student Poster award will be available with the call for papers.