Mammals

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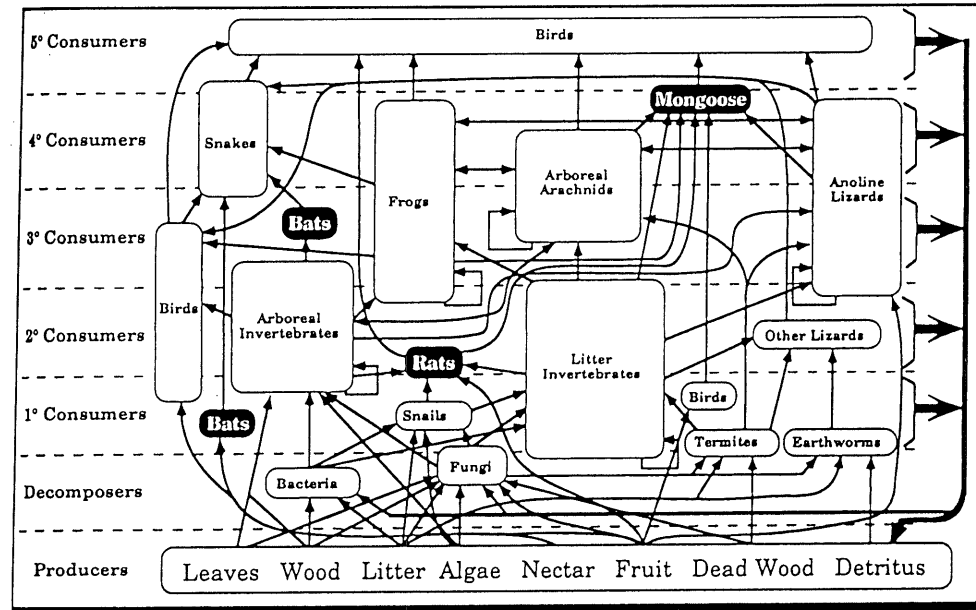
MAMMALS make important contributions to the food web at El Verde. They do so in the usual manner, by affecting pathways of energy flow and nutrient cycling. Perhaps equally important, they affect the spatial heterogeneity of nutrients, as well as the spatial distribution and genetic structure of plant populations. Indeed, because of their role in pollination, and fruit or seed dispersal, a number of mammal species may be keystone mutualists in the tabonuco forest.

Terrestrial mammals (mongooses and rats) in the food web are highly omnivorous, consuming prey from all but the quinary trophic level. Their large individual biomasses and high metabolic rates suggest that they may play important functional roles in the tabonuco forest. The recent introduction of terrestrial mammals to Puerto Rico may have had a disruptive effect on the structure of the food web at El Verde, in part by contributing to the extinction of previous links in the food web, and in part by assuming trophic positions not previously represented by any of the native animals. The long-term consequences of such disruptions on the dynamics of the food web at El Verde are unclear.

Bats are prominent nocturnal components of the food web at El Verde. They occupy three trophic groups: frugivores, nectarivores, and insectivores. The frugivores consume fruits of both early successional shrubs and late successional trees, whereas the insectivores primarily consume invertebrates that occur in or above the forest canopy. Because of their role in recovery from disturbance during secondary succession, frugivorous and nectarivorous bats may be especially important in maintaining the spatial integrity of the food web.

ZOOGEOGRAPHIC CONSIDERATIONS

The composition of the mammalian community of the tabonuco forest at El Verde is the product of a variety of biogeographic and human-mediated events. In general, the mammal fauna of Puerto Rico is depauperate compared to tropical mainland areas of similar size and habitat diversity (table 12.1). Low species richness is affected in part by well-documented biogeographic processes related to the island's size and distance from potential sources of colonization. Moreover, Griffiths and Klingener (1988) observed that, compared to other islands in the Greater Antilles, the bat fauna of Puerto Rico is well below its equilibrial species richness based upon the MacArthur-Wilson model of island biogeography (MacArthur and Wilson 1967). This observation is consistent with the hypothesis that colonization from Central and North America was differentially directed to Cuba and Jamaica because of extensive land bridges (e.g., the Grand Bahama, Rosilind, Seranillas and Pedro banks in the Caribbean) and an enlarged mainland (e.g., the Nicaraguan Plateau and the southern Florida peninsula) during Pleistocene glacial maxima. Puerto Rico was relatively isolated even during periods of the Pleistocene when sea level was lower than it is presently, and insufficient time has elapsed since the last glacial maximum to allow dispersal of North and Central American–derived stock to Puerto Rico. In addition, Puerto Rico has experienced a number of mammalian extinctions since the end of the Pleistocene (Anthony 1918, 1926; Baker and Genoways 1978; Best and Castro 1981; Choate and Birney 1968; Morgan and Woods 1986) that include one insectivore (Nesophontes edithae), three bats (Macrotus waterhousii waterhousii, Monophyllus plethodon frater, and Phylloncyteris major), two edentates (Acratocnus odontrigonus and A. major), and six rodents (the heptaxodontids, Heptaxodon bidens and Elasmodontomys obliquus; the capromyid, Isolobodon portoricensis, possibly introduced to Puerto Rico from Hispaniola by Amerindians; and the echimyids, Heteropsomys insulans, Homopsomys [= Heteropsomys] antillensis, and Proechimys corozalos). Moreover, the fossil mammalian fauna of Puerto Rico is depauperate for the island's present size, compared to other fossil faunas on islands in the West Indies, a discrepancy further magnified if the island's larger size during the last glacial interval is considered (Morgan and Woods 1986). Unfortunately, the fossil record does not indicate the range of habitats that these extinct mammals occupied, making it impossible to determine which, if any, species occurred in the tabonuco forest.

Other than domesticated animals, three rodents (Rattus rattus, the black rat, R. norvegicus, the Norway rat, and Mus musculus, the house mouse) and one carnivore (Herpestes auropunctatus, the Indian mongoose), have been introduced to Puerto Rico by Europeans in post-Columbian times. Of these, two (R. rattus and H. auropunctatus) are found at El Verde and represent the entire nonvolant mammal fauna. Regardless of the causes of nonvolant mammal extinctions, the composition of the mammal community of the tabonuco forest is clearly of recent origin in evolutionary and perhaps ecological time.

The only extant native mammals in Puerto Rico are bats. Thirteen species representing five feeding guilds presently are found on the island. The piscivore guild is represented by only one species, Noctilio leporinus mastivus, the greater bulldog bat. The aerial insectivore guild comprises five species:

Table 12.1. Species richness of various mammalian assemblages

	Puerto Rico	Costa Rica							Panama		Colombia			Brazil	
Taxon		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Marsupialia	0	6	8	7	5	5	0	6	5	6	—	—	—	4	—
Insectivora	0	0	0	2	2	0	2	2	0	0	—	—	—	0	—
Chiroptera	13	86	81	82	60	45	16	34	29	32	14	16	29	34	25
Emballonuridae	0	9	9	7	4	0	0	0	2	2	0	0	2	1	1
Noctilionidae	1	2	2	2	0	0	0	0	—	—	0	0	0	—	—
Mormoopidae	3	4	4	4	3	1	0	2	1	1	0	0	0	1	1
Phyllostomidae	5	48	44	47	35	34	11	25	22	24	11	12	25	21	14
Natalidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	—
Furipteridae	0	1	2	0	0	0	0	0	0	0	1	0	0	1	0
Thyropteridae	0	1	1	1	0	1	0	1	2	2	1	2	2	0	0
Vespertilionidae	2	9	9	10	10	8	5	6	1	2	1	2	2	2	4
Molossidae	2	9	10	10	8	1	0	0	2	3	1	2	0	7	3
Primates	0	3	4	3	2	3	0	3	2	4	—	—	—	2	—
Edentata	0	6	7	5	6	3	0	4	5	—	—	—	—	3	—
Lagomorpha	0	1	1	2	1	1	1	1	1	1	—	—	—	1	—
Rodentia	0	17	20	15	16	10	10	16	14	13	—	—	—	10	—
Carnivora	0	13	17	19	12	10	7	14	10	10	—	—	—	3	—
Artiodactyla	0	3	4	3	3	0	1	3	2	2	—	—	—	1	—
Perissodactyla	0	1	1	1	0	0	1	1	0	0	—	—	—	0	—

Sources: Costa Rica (Wilson 1983), Panama (Fleming 1973), Colombia (Thomas 1972), and Brazil (Mares et al. 1981, Willig 1983, Willig and Mares 1989).

Notes: Introduced and domesticated mammals are not included in the species richness of any site. Site code: 1 = La Selva, 2 = Osa, 3 = Guanacaste, 4 = San Jose, 5 = San Vito, 6 = Cerro de la Muerte, 7 = Monteverde, 8 = Balboa, 9 = Cristobal, 10 = Hormiguero, 11 = Pance, 12 = Zabaletas, 13 = Caatinga, 14 = edaphic Cerrado.

Table 12.2. Relative importance of bat species at El Verde

Taxon	Mean wet weight (g)	Guild	Numerical dominance	Bioma[ss] domina[nce]
Phyllostomidae				
A. jamaicensis	46.8	Frugivore	0.40	0.6
S. rufum	22.7	Frugivore	0.37	0.2
M. redmani	9.3	Nectarivore	0.15	0.0
B. cavernarum	49.6	Frugivore	0.02	0.0
E. sezekorni	19.1	Frugivore	0.02	0.0
Vespertilionidae				
E. fuscus	15.8	Aerial Insectivore	0.02	0.0
P. parnellii	12.5	Aerial Insectivore	<0.01	<0.0
P. quadridens	5.6	Aerial Insectivore	<0.01	<0.0
L. borealis	10.0	Aerial Insectivore	<0.01	<0.0

Note: Estimates of relative importance are based upon numerical dominance and biomass dominance. See text for details and discussion of dominance indexes.

Pteronotus quadridens fuliginosus, the sooty mustached bat; *P. parnellii [p]toricensis,* Parnell's mustached bat; *Mormoops blainvillii cuvieri,* Blainvi[llii] ghost-faced bat; *Eptesicus fuscus wetmorei,* the big brown bat; and *Lasi[urus] borealis minor* (= *L. minor*), the red bat. The nectarivore guild contains [one] species, *Monophyllus redmani portoricensis,* the Puerto Rican long-tong[ued] bat. The frugivore guild contains four species: *Brachyphylla cavernarum [in]termedia,* the Antillean fruit-eating bat; *Artibeus jamaicensis jamaicensis,* [the] Jamaican fruit-eating bat; *Stenoderma rufum darioi,* the red fig-eating [bat]; and *Erophylla sezekorni sezekorni* (reported as *E. bombifrons* by some [au]thors), the buffy flower bat. The molossid insectivore guild contains two s[pe]cies, *Tadarida brasiliensis antillularum,* the Brazilian free-tailed bat; [and] *Molossus molossus debilis,* Pallas' free-tailed bat. Only nine species (f[our] frugivores, one nectarivore, four aerial insectivores; table 12.2) have b[een] recorded from the tabonuco forest at El Verde (Tamsitt and Valdivieso 19[;] Jones et al. 1971; Genoways and Baker 1975; and this report for *L. b. mi[nor]* and *P. q. fuliginosus*).

BATS

Foraging Ecology

In general, the population biology and foraging ecology of bats are poo[rly] known; this is especially true of tropical species. The paucity of data is att[rib]utable in part to nocturnal activity patterns, as well as to the rapid rat[e] which bats process food, making identification of dietary constituents d[iffi]cult (Willig et al. 1993). More specifically, little ecological information of [this] sort has been published concerning bats in the tabonuco forest of Puerto R[ico] prior to 1990. Density estimates are not known for any bat species in

forest; however, the relative importance of each species (compared to other bats in the community) can be assessed from netting records in two ways. Numerical dominance (ND) for each species can be measured as n_i/N, where n_i is the number of captured specimens of species i and $N (= \Sigma\, n_i)$ is the total number of captured specimens regardless of taxonomic identity. Biomass dominance (BD) for each species is given 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. Both ND and BD for each species are listed in table 12.2. As a consequence of faunal depauperization associated with low origination (immigration and speciation) and high extinction rates, island species may frequently experience competitive release and enjoy elevated local densities compared to mainland taxa (MacArthur and Wilson 1967). Bats at El Verde do not demonstrate this phenomenon, although other vertebrates (e.g., *Eleutherodactylus coqui* and anoline lizards) clearly maintain high densities. In fact, netting success for bats in the tabonuco forest is considerably less (5 to 10%) than that of tropical or subtropical mainland sites.

Frugivores

Four species of frugivorous bat (*A. jamaicensis, S. rufum, E. sezekorni,* and *B. cavernarum*) have been captured at El Verde. Together, they constitute the bulk of the bat fauna in terms of numbers and biomass (total ND = 0.81; total BD = 0.94; see table 12.2).

The Jamaican fruit-eating bat, *A. jamaicensis* (fig. 12.1), has a wide distribution in tropical and subtropical habitats of the New World. Moreover, it is the predominant bat species at El Verde (ND = 0.40; BD = 0.62). Its population biology has been studied intensively in moist tropical forest of Panama and dry tropical forest of Mexico (Morrison 1978a,b,c,d, 1979, 1980). A summary of its foraging ecology is provided by Fleming (1982) and Handley et al. (1991). Although figs are a major dietary item elsewhere, these bats primarily consume *Cecropia schreberiana* (table 12.3) at El Verde. Preliminary data from the wet season, based upon telemetrically monitored bats, suggest that *A. jamaicensis* does not exhibit foraging site fidelity at El Verde (Gannon and Willig unpublished).

The reproductive biology of *A. jamaicensis* is geographically variable (Wilson 1979; Willig 1985a,b) throughout its range and is poorly documented on Puerto Rico in general and at El Verde in particular. The proportion of reproductively active females during the wet season is statistically variable from year to year (G-Test of Independence: $G = 6.16$, d.f. $= 20$,

Figure 12.1. Photograph (courtesy of R. J. Baker) of an adult male *Artibeus jamaicensis,* the Jamaican fruit-eating bat, from Puerto Rico

$.025 > p > .01$): 68% were pregnant or lactating ($N = 45$ adult females) in 1982 (Willig and Bauman 1984), whereas 36.6% ($N = 30$) were reproductively active in 1988 and 1989 (Gannon 1991; Gannon and Willig 1992). In part, this difference may be a methodological bias because the 1988–1989 data are based solely upon field palpation of live females (underestimates of true reproductive activity) whereas the 1982 data are based upon necropsy. Data for the dry season are few (33.3% of six adult females were reproductively active in 1988 and 1989) but do not suggest seasonal differences in reproductive activity beyond the variation characteristic of the wet season alone.

The red fig-eating bat, *S. rufum* (fig. 12.2), is endemic to Puerto Rico and the nearby islands of St. John and St. Thomas. Although generally reported to be rare, it was almost as abundant as *A. jamaicensis* at El Verde prior to Hurricane Hugo (table 12.2) and during the wet season was more abundant at some locations. Genoways and Baker (1972) summarized published information concerning the biology of this species. Although its common name implies a diet of figs, neither published (Scogin 1982; Willig and Bauman 1984) nor current data (table 12.3) indicate that this species eats figs. The

Table 12.3. Diet of frugivorous bats at El Verde

Dietary Item	Bat Species		
	A. jamaicensis (N = 40)	S. rufum (N = 36)	E. sezekorni (N = 5)
Cecropia schreberiana	0.65	0.38	—
Piper aduncum	—	—	0.80
Piper hispidum	—	0.04	—
Piper glabra	0.05	—	—
Manilkara bidentata	0.03	0.23	—
Prestoea montana*	0.05	0.27	0.20
Unknown plant material	0.23	0.08	—

Notes: Consumption of each dietary item is reported as the percentage of digestive tracts that contain that item. N = number of bats with stomach contents.

*Tentative identification of fruit pulp.

bulk of the diet of *S. rufum* at El Verde (88% of the stomachs containing food) comprises *Cecropia schreberiana, Manilkara bidentata,* or *Prestoea montana* (table 12.3). All of the adult females collected in June and July (1983) at El Verde ($N = 12$) were pregnant or lactating (Willig and Bauman 1984). When all data from that study are combined with similar reproductive records from 1989–1990 (Gannon 1991; Gannon and Willig 1992; museum records for El Verde prior to 1989 [specimens deposited in Carnegie Museum of Natural History or The Museum, Texas Tech University]), it appears that reproductive activity during the wet season (72.3% of sixty-five adult females pregnant or lactating) is statistically indistinguishable (G-Test of Independence: $G = 0.58$, d.f. $= 1$, $.5 > p > .1$) from that during the dry season (80% of twenty-five adult females pregnant or lactating). Although the presence of simultaneously pregnant and lactating specimens indicates that *S. rufum* is polyestrous, the statistical comparison suggests that the population is asynchronous, with an invariant and high proportion of adults reproductively active throughout the year. Such asynchronous polyestry is characteristic of species whose food does not vary greatly in abundance on a seasonal basis (Wilson 1979).

Detailed consideration of space use by *S. rufum* prior to Hurricane Hugo (Gannon 1991; Gannon and Willig unpublished) is available only for the wet season (June-August). Neither total home range nor foraging home range size differ between sexes, but consistent differences for each exist between adults and subadults (table 12.4). More specifically, adults have consistently smaller total home ranges than do subadults (fig. 12.3). These differences are consistent with a number of behavioral hypotheses. Subadults are less experienced than adults and as a consequence may traverse larger areas in search for food, or may at times be excluded by adults from feeding on trees with
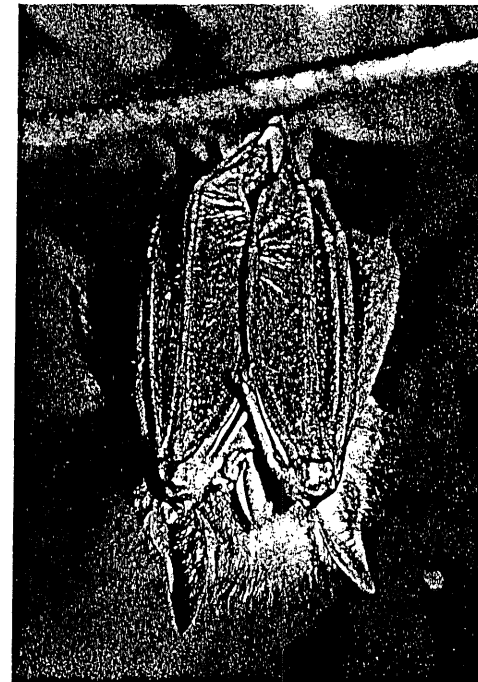

Figure 12.2. Photograph (courtesy of M. R. Gannon) of an adult male (*A*) and juvenile female (*B*) *Stenoderma rufum*, the red fig-eating bat, from Puerto Rico

Table 12.4. Two-way analysis of variance (sex versus age) of minimum convex polygon home range size for captures of Stenoderma rufum

Source	d.f.	Total Home Range[a]			Foraging Home Range[b]		
		MS	F	P	MS	F	P
Age (A)	1	44815.2	7.36	0.01	4638.4	11.23	0.03
Sex (S)	1	9.5	0.02	0.90	1080.3	2.62	0.12
A × S	1	69.9	0.12	0.74	543.4	1.32	0.26
Within	22	609.0			412.1		

Note: All captures during wet season.

[a] All captures.

[b] Night captures.
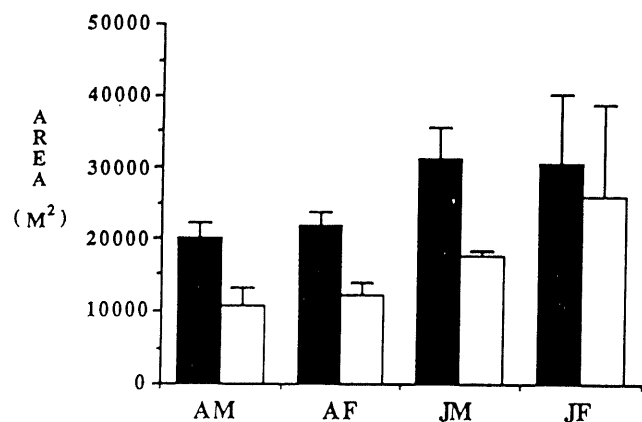
Figure 12.3. Bar diagram of the minimum convex polygon estimates of total home range (solid bars) and foraging home range based upon activity only during the night (open bars) for Stenoderma rufum at El Verde (AM = adult males, AF = adult females, SM = subadult males, and SF = subadult females). Vertical lines represent standard errors.
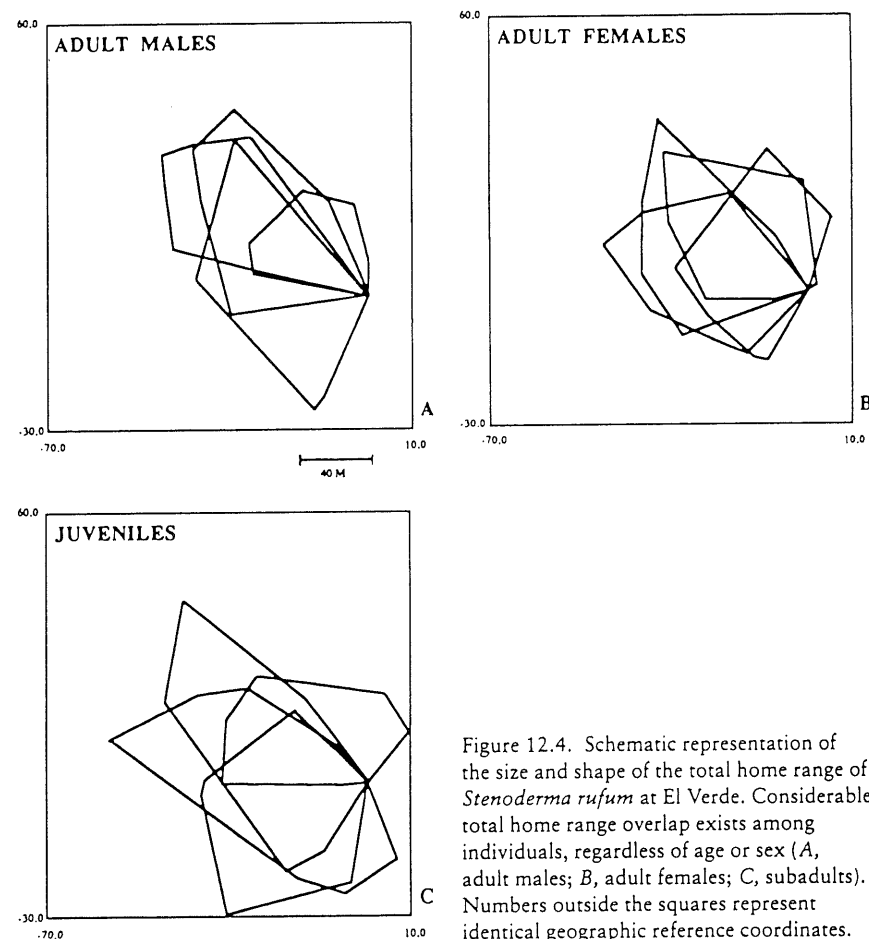

Figure 12.4. Schematic representation of the size and shape of the total home range of Stenoderma rufum at El Verde. Considerable total home range overlap exists among individuals, regardless of age or sex (A, adult males; B, adult females; C, subadults). Numbers outside the squares represent identical geographic reference coordinates.

through fruit set. Both scenarios result in larger total home range size in subadults than in adults. The social system of S. rufum, as revealed from telemetry, is one in which both males and females are solitary in roosting behavior with no evidence of polygeny or harem formation. Moreover, considerable overlap in space use by all age-sex categories exists (fig. 12.4). These two characteristics suggest the absence of factors promoting sex-specific differences in foraging, especially in light of the relatively even year-round abundance of Cecropia and other bat fruits (most fruit falls to the forest floor uneaten) in the tabonuco forest (Devoe 1990).

A log of nightly movement patterns of focal bats, with each individual's position recorded at five-minute intervals over a four- to eight-hour period, can be superimposed on long-term home range data (fig. 12.5). Consideration of the results suggests that day roosts are scattered throughout the total home range with only a few located outside the foraging area. Thus, commuting time is negligible. Although a major night roost may exist in which a bat repeatedly returns to a single tree after foraging, most sites are visited only once. The area used on a particular night rarely encompasses more than 75% of the entire foraging home range, but occasional forays outside the total home range suggest that S. rufum exhibits a foraging strategy sensitive to the detection of fruiting trees in surrounding habitat. The emerging view of the total home range of an individual is one in which space is used hetero-
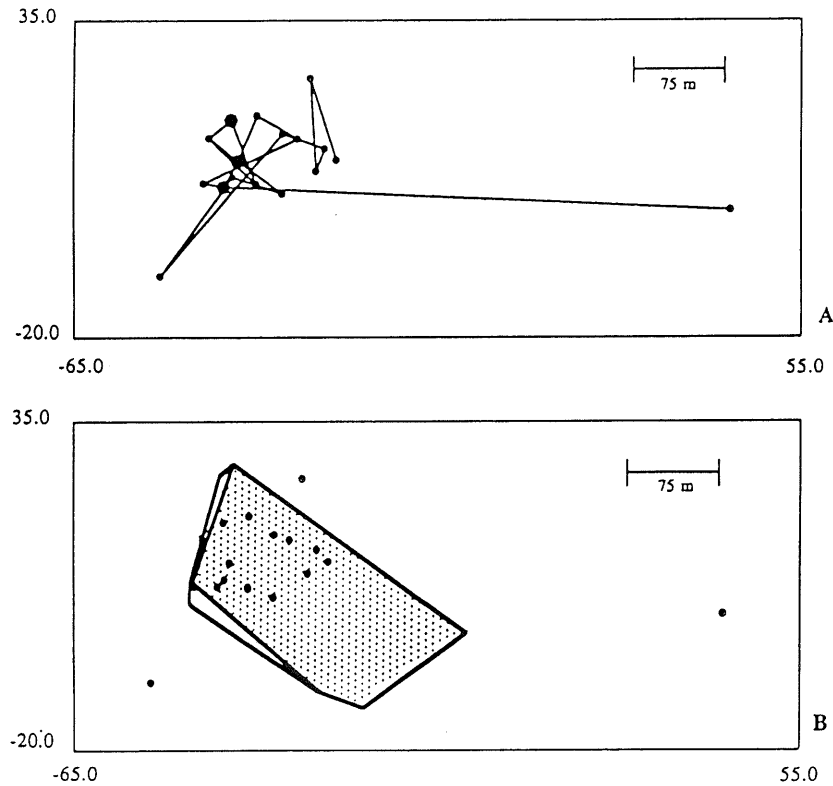
Figure 12.5. Detailed records of movements (lines) every 5 m (over an eight-hour period) for an adult male *Stenoderma rufum* (A) indicates repeated use of three focal night roosts (larger dots) and many singly used minor night roosts (small dots). When these detailed data are superimposed (B) upon the total home range and foraging home range (shaded area) of the same individual over a longer time period, it is clear that most minor and all major roosts occur within the estimated ranges, but that occasional long-distance sorties outside the total home range occur.

Figure 12.6. A minimum area probability plot or space utilization distribution (Anderson 1982) representing the total home range (in the shaded x-y plane) with its frequency of use plotted on the vertical z-axis. This gives rise to a topographic representation of space use for an adult female *Stenoderma rufum*. Areas of intense space-use in the background (peaks) are distinct from the isolated areas of minor use in the foreground.

Table 12.5. Statistical comparison (analysis of variance) of the effects of lunar phase and age-sex categorie on movement parameters of the red fig-eating bat at El Verde

Movement Parameter	d.f.	Lunar		Age-Sex		Lunar × Age-Sex	
		F	P	F	P	F	
Mean Distance Per Hour	10	0.004	0.95	0.341	0.72	0.163	0.
Maximum Distance	10	0.096	0.76	0.128	0.88	0.390	0.
Minimum Distance	10	2.501	0.15	0.177	0.84	0.051	0.
Mean Distance Per Move	10	0.545	0.48	0.508	0.62	0.022	0.
Number of Moves Per Hour	10	0.550	0.48	0.102	0.90	0.173	0.
Percent Time Roosting	10	0.061	0.81	0.031	0.97	1.007	0.

geneously for particular behaviors. A few areas of intense use (peaks) may be contrasted with areas of infrequent use (valleys), giving rise to a varied behavioral topography (fig. 12.6) even during short time periods.

Comparison of the details of nightly movement parameters as they relate to age or sex characteristics, as well as to lunar illumination (table 12.5) substantiates that the way in which total home ranges are used does not differ among adult males, adult females, or subadults (age-sex is not significant for any parameter) even though the terrain over which subadults forage is greater than that of adults (table 12.4). Mainland bat populations may suffer

appreciable predation pressure, resulting in modification of foraging behavior during periods of high lunar illumination (i.e., lunar phobia). The tabonuco forest harbors few nocturnal predators capable of subduing bats. As a result, *S. rufum* should not experience severe selection to reduce foraging activity during high lunar illumination even though closely related taxa exhibit such behavior on the mainland (Morrison 1978b). The absence of a significant lunar effect for each foraging parameter (table 12.5) corroborates this prediction and further indicates that the absence of lunar phobia is consistently exhibited by subadults as well as by adult males and females.
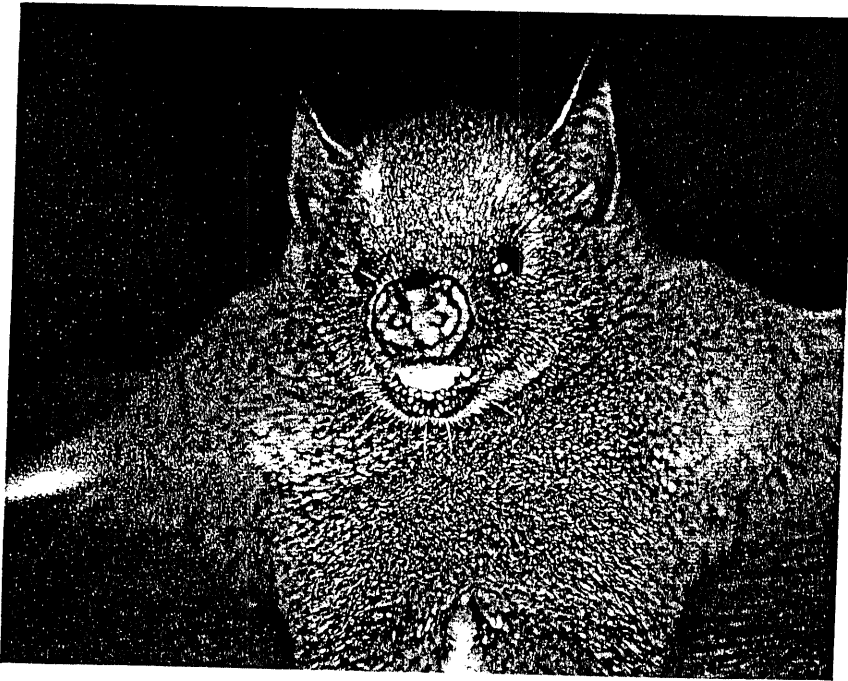
Figure 12.7. Photograph (courtesy of M. R. Gannon) of an adult female *Brachyphyllum cavernarum*, the Antillean fruit-eating bat, from Puerto Rico

Figure 12.8. Photograph (courtesy of M. R. Gannon) of an adult female *Erophylla sezekorni*, the buffy flower bat, from Puerto Rico

The Antillean fruit-eating bat, *Brachyphylla cavernarum* (fig. 12.7), occurs on Puerto Rico, the Virgin Islands, and throughout the Lesser Antilles to St. Vincent and Barbados. Netting records suggest that it is uncommon in the tabonuco forest (table 12.2). Swanepoel and Genoways (1983) summarized published information on the biology of *B. cavernarum;* Nellis (1971) and Nellis and Ehle (1977) provided the most detailed information concerning its behavior and natural history (see also Silva-Taboada and Pine 1969). None of the digestive tracts of *B. cavernarum* that were captured at El Verde ($N = 8$) contained food; however, a number of reports summarized in Swanepoel and Genoways (1983) have indicated that it consumes fruit, flowers, pollen, and insects. *Manilkara* fruit and the flowers of palms (*Prestoea montana*) are likely dietary constituents at El Verde, as they are consumed in other tropical and subtropical habitats.

The buffy flower bat, *E. sezekorni* (fig. 12.8), is endemic to the Greater Antilles and associated islands. It is an uncommon species at El Verde (table 12.2). Its general biological features are summarized by Baker et al. (1980); few ecological data are available. The diet appears to consist mostly
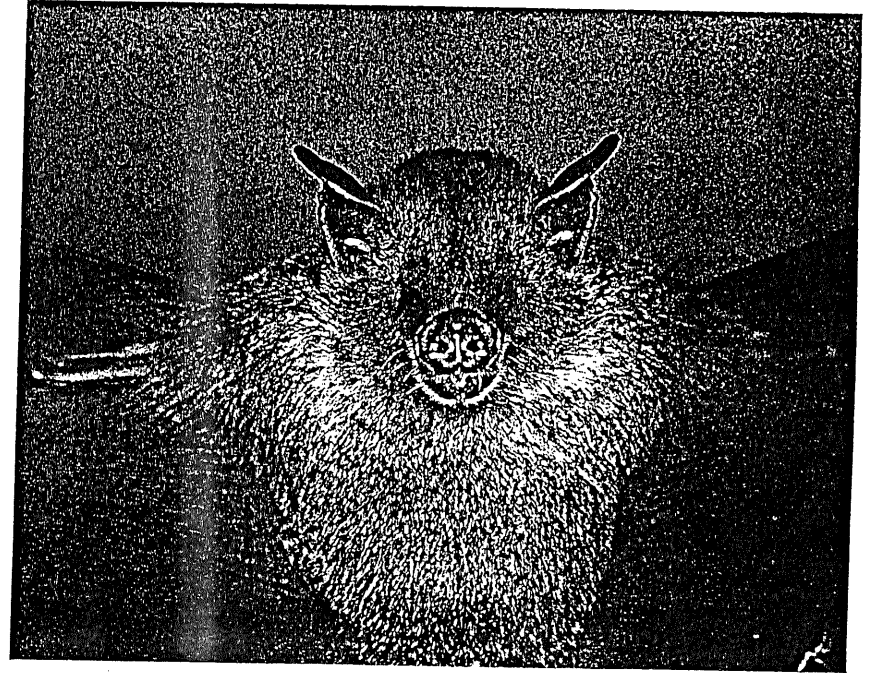
of *Piper aduncum* fruits at El Verde (table 12.3); however, this observation is based on analysis of the stomach contents of only five specimens.

Nectarivores

The nectarivore guild at El Verde is represented by only one species, *M. redmani* (fig. 12.9), the Puerto Rican long-tongued bat. The distribution of *M. redmani* includes the Greater Antilles and some of the southern Bahama Islands. It is common in the tabonuco forest, but never was caught in large numbers at any one site (table 12.2). Homan and Jones (1975) summarized published biological information on this species; ecological data are few, but suggest a diet of nectar, soft fruit, and possibly insects. None of the digestive tracts from specimens collected at El Verde contained seeds or insect remains, although a viscous liquid (= nectar or fruit pulp?) was found in the stomach of some specimens. Of the four adult females collected in the dry season (March), one was pregnant (Gannon 1991; Gannon and Willig 1992).

Figure 12.9. Photograph courtess of M. R. Gannon of an adult male *Monophyllus redmani*, the Puerto Rican long-tongued bat, from Puerto Rico

Figure 12.10. Photograph (courtess of M. R. Gannon) of an adult female *Eptesicus fuscus*, the big brown bat, from Puerto Rico

Aerial Insectivores

Although four bat species (*E. fuscus, P. parnellii, P. quadridens,* and *L. borealis*) constitute the insectivore guild at El Verde, they represent a minor portion of the bat fauna as assessed by ground netting (table 12.2). However, insectivorous bats were frequently seen foraging in open areas (7 to 12 m above the ground) near El Verde Field Station throughout the night, but especially at dusk. Netting records probably provide underestimates of the guild's importance in the tabonuco forest. Frugivores and nectarivores would more frequently encounter ground nets while foraging in the understory of the forest, whereas aerial insectivores would infrequently encounter ground nets while foraging.

The big brown bat, *E. fuscus* (fig. 12.10), has a cosmopolitan distribution in the New World and although rare at El Verde compared to species in other guilds was more frequently caught than other insectivores (table 12.2). Based upon analyses of four digestive tracts which contained food, a variety of insect taxa constitute the diet (Blattodea [a blattelid, *Cariblatta* sp.]; Homoptera [a cixiid, *Pintalia* sp.; a cicadellid leafhopper; a flatid, *Colpoptera*
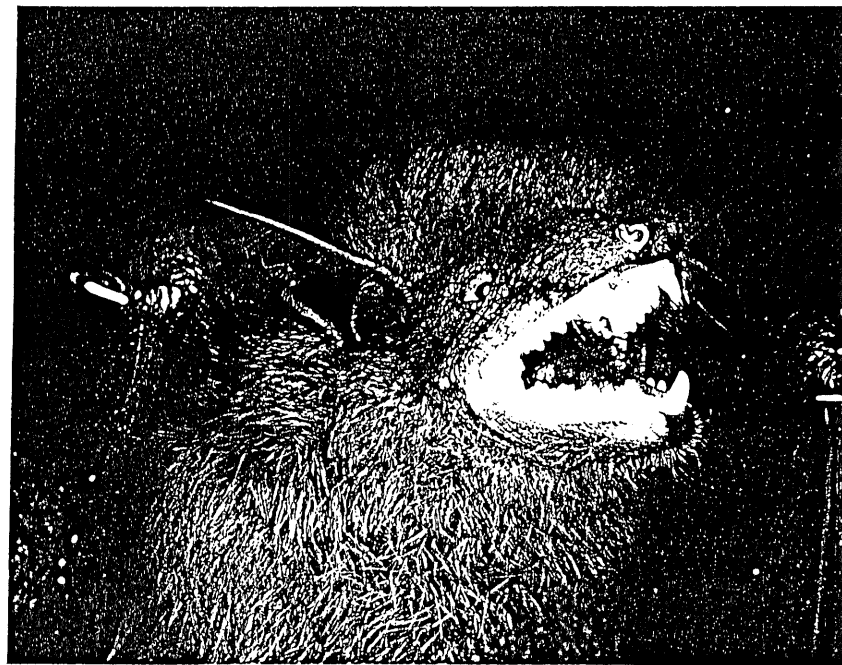
sp. or *Neocolpoptera* sp.]; Hemiptera [a lygaeid, probably *Ozophora* sp.]; Coleoptera [a scarabaeid, probably *Phyllophaga* sp.]; Hymenoptera [a formicid, probably *Iridomyrmex melleus*]; and Isoptera [a termitid, *Nasutitermes* sp.]).

Parnell's mustached bat, *P. parnellii* (fig. 12.11), is distributed throughout much of the tropical and subtropical New World, including the Greater Antilles. The most recent systematic analysis of the relationship of this species to other mormoopids (ghost-faced bats) is provided by Smith (1972). It is rare in the tabonuco forest at El Verde (table 12.2). A general summary of the biology of *P. parnellii* is provided by Herd (1983); its diet includes Lepidoptera (moths), but mainly comprises Coleoptera (beetles).

The sooty mustached bat, *P. quadridens* (fig. 12.12), is endemic to the Greater Antilles, with *P. q. fuliginosus* occurring on Puerto Rico, Hispaniola, and Jamaica (Silva-Taboada 1976). It is rare at El Verde (table 12.2), and most information concerning the biology of the species is based upon the study of specimens associated with caves outside of the tabonuco forest (Rodriguez-Duran and Kunz 1992). In Puerto Rico, *P. quadridens* are known to forage
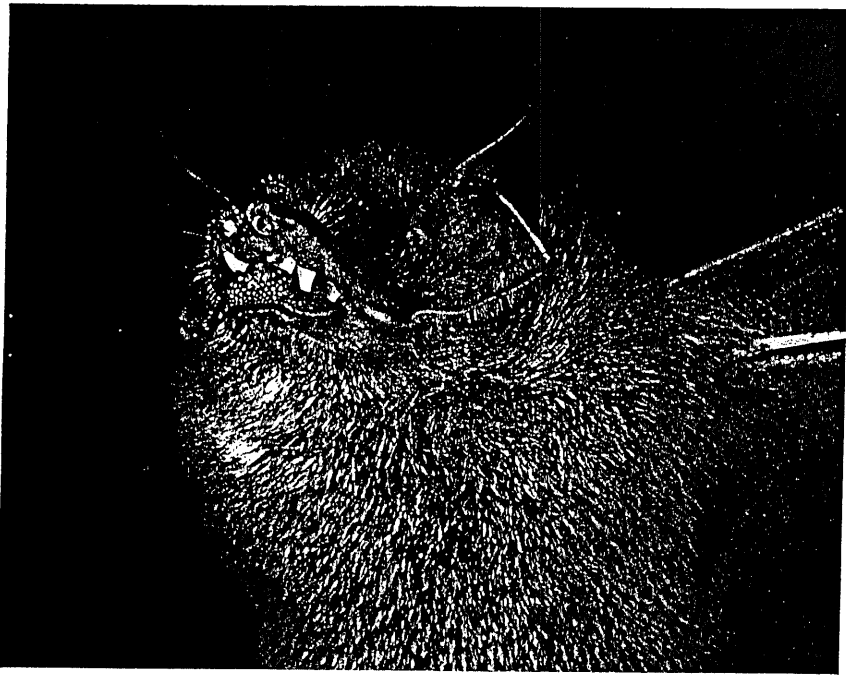
Figure 12.11. Photograph (courtesy of M. R. Gannon) of an adult female *Pteronotus parnellii*, the Parnell's moustached bat, from Puerto Rico

Figure 12.12. Photograph (courtesy of M. R. Gannon) of an adult male *Pteronotus quadridens*, the sooty moustached bat, from Puerto Rico

as far as 9 km from their day roost (Rodriguez-Duran 1984), and in Cuba it evinces the ability to home from distances of up to 30 km (Silva-Taboada 1979). The species feeds primarily on insects in the forest understory, with Coleoptera, Lepidoptera, Orthoptera, Hymenoptera, Diptera, Hemiptera, and Homoptera composing the bulk of the diet (Rodriguez-Duran 1984; Silva Taboada 1979)

The red bat, *L. borealis,* is migratory and occurs from temperate North America to temperate South America. Shump and Shump (1982) provide a summary of its biology, but most data are derived from temperate North America. Specimens roost in trees and shrubs, at times on or near the ground. Based upon records from ground netting, it is rare at El Verde (table 12.2). The contents of a single stomach included many flying male formicids, probably carpenter ants, *Camponotus ustus.*

Bat Ectoparasites

It is no more clear for bats in the tabonuco forest than for most animals in general whether parasites have an effect on population-level processes of

their hosts (Anderson 1982; Holmes 1983a; May 1983). Bat ectoparasites (Webb and Loomis 1977) and endoparasites (Ubelaker et al. 1977) have received varied attention, but mostly for New World leaf-nosed bats from a systematic perspective. Even so, prior to 1990, documentation of the ectoparasite fauna at El Verde was limited, based on data for only a few bat specimens, fewer than ten individuals in the case of most bat species. Herein, we provide an updated list of ectoparasites from bats captured at El Verde. We augment published records of ectoparasite infestation with those recently (1989–90) obtained from moderate samples (*A. jamaicensis, N* = 86; *S. rufum, N* = 42; *M. redmani, N* = 22; *E. sezekorni, N* = 4; and *Eptesicus fuscus, N* = 3) by Gannon (1991) and Gannon and Willig (1994b, unpublished) in the tabonuco forest. Flies (Streblidae) and mites (Labidpocarpidae, Macronyssidae, Spinturnicidae, Spelaeororhynchidae) are the predominant ectoparasites of bats from El Verde, whereas ticks (Argasidae) are rare and only known from *E. sezekorni* (table 12.6).

Incidence (percentage of bats with parasites), prevalence (mean number of parasites per bat), and density (mean number of parasites per infested bat) of ectoparasites of *S. rufum, A. jamaicensis,* and *M. redmani* at El Verde have

Table 12.6. Host-parasite associations for bats at El Verde

Host	Ectoparasite	Family
A. jamaicensis	Megistopoda aranea [a,c,g,*]	Streblidae
	Paralabidocarpus foxi [a]	Labidocarpidae
	Paralabidocarpus artibei [d,*]	Labidocarpidae
	Periglischrus iheringi [a,b,c,e,g,*]	Spinturnicidae
	Periglischrus vargasi [a,b,*]	Spinturnicidae
	Sphelaeorhynchus praecursor [a,c,f,g,*]	Spelaeorhynchidae
	Aspidoptera phyllostomatus [g,*]	Streblidae
	Trichobius intermedius [a,g,*]	Streblidae
	Trichobius robynae [a]	Streblidae
B. cavernarum	Lawrenceocarpus micropilus [a,d]	Labidocarpidae
	Lawrenceocarpus puertoricensis [a]	Labidocarpidae
	Radfordiella oudemansi [a,c]	Macronyssidae
	Trichobius truncatus [a,c,g,*]	Streblidae
	Periglischrus cubanus [g,*]	Spinturnicidae
E. fuscus	Spinturnix bakeri [g,*]	Spinturnicidae
E. sezekorni	Trichobius robynae [a]	Streblidae
	Trichobius truncatus [c]	Streblidae
	Ornithodoros viguerasi [c]	Argasidae
	Ornithodoros sp. [g,*]	Argasidae
	Periglischrus cubanus [g,*]	Spinturnicidae
M. redmani	Spelaeorhynchus monophylli [a,b,c,f,g,*]	Spelaeorhynchidae
	Trichobius cernyi [g,*]	Streblidae
	Trichobius robynae [a,g,*]	Streblidae
	Trichobius truncatus [a,c]	Streblidae
	Trichobius sp. (near sparsus Kessel) [h,*]	Streblidae
	Nycterophilia parnelli [g,*]	Streblidae
	Periglischrus vargasi [g,*]	Spinturnicidae
S. rufum	Paralabidocarpus artibei [a,d,*]	Labidocarpidae
	Paralabidocarpus foxi [a,*]	Labidocarpidae
	Paralabidocarpus stenodermi [a,*]	Labidocarpidae
	Periglischrus iheringi [a,b,c,g,*]	Spinturnicidae
P. Parnellii	Cameronieta thomasi [h,*]	Spinturnicidae

Sources: After Gannon and Willig 1994b.

[a] Webb and Loomis 1977.

[b] Tamsitt and Valdivieso 1970.

[c] Tamsitt and Fox 1970a.

[d] Tamsitt and Fox 1970b.

[e] Rudnick 1960.

[f] Fain et al. 1967.

[g] Gannon and Willig 1994b.

Note: Some ectoparasite records are from Puerto Rico in general, without documented occurrence on specimens from El Verde in particular; only parasites documented from El Verde are indicated with an asterisk.

been recorded by Gannon and Willig (unpublished). Prevalence differed consequence of host age, but not sex, with juveniles harboring higher r bers of ectoparasites in the cases of S. rufum and A. jamaicensis. In cont prevalence did not differ between seasons for any bat species. Significa different parasite assemblages occurred on adult male, adult female, an venile A. jamaicensis. Moreover, S. rufum, A. jamaicensis, and M. redr each had statistically distinctive ectoparasite assemblages.

TERRESTRIAL CONSUMERS

Excluding domesticated or feral mammals (dogs and cats), two terres consumers (R. rattus and H. auropunctatus) occur at El Verde. Although additional commensal species, Mus musculus and Rattus norvegicus, o on Puerto Rico, no museum specimens or published records document t occurrence at El Verde. Moreover, no long-term studies of the ecology c rattus or H. auropunctatus have been undertaken in the tabonuco fo Nonetheless, six vertebrate species (Puerto Rican short-eared owl, Asio f meus portoricensis; the Puerto Rican boa, Epicrates inornatus; Puerto R parrot, Amazona vittata; the snake Alsophis portoricensis; and possibly t the Key West quail-dove, Geotrygon chysia, and the Puerto Rican w poor-will, Caprimulgus noctitherus) are considered to be endangered pa because of the introduction of rats or mongooses to Puerto Rico (Raff et al. 1973). The endangered birds construct ground or exposed nests wl are vulnerable to predation by terrestrial mammals. Moreover, the declin extinction of the mammalian insectivore, Nesophontes edithae, is circ stantially associated with competitive or predatory interactions with Ra during post-Columbian times (Morgan and Woods 1986).

The black rat, R. rattus (fig. 12.13), is a common omnivore at El Verd was most likely inadvertently introduced to the island by Ponce de Leo 1508 (Snyder et al. 1987). Population studies suggest a density of appro mately 40 individuals ha^{-1} in tabonuco forest (see Weinbren et al. 19 Brown et al. 1983), whereas up to 281 individuals ha^{-1} have been estima in Puerto Rican parrot habitat in the palo colorado forest (Layton 19: Immatures compose up to 35% of the population at El Verde, with Dec ber through February representing the months with the smallest propor of immature individuals; recapture records indicate low survival rates e though few predators occur at El Verde (Weinbren et al. 1970).

Massive infestations of the liver parasite, Capillaria hepatica, charac ized the specimens obtained by Weinbren et al. (1970). However, it is uncl how such parasitism is related to demographic properties of tabonuco fo: populations of black rats. In a later study, 50% of the adults and 22% of juveniles from a tabonuco forest population of black rats (N = 25) w infected with parasites, a rate of parasitism similar to that of populati
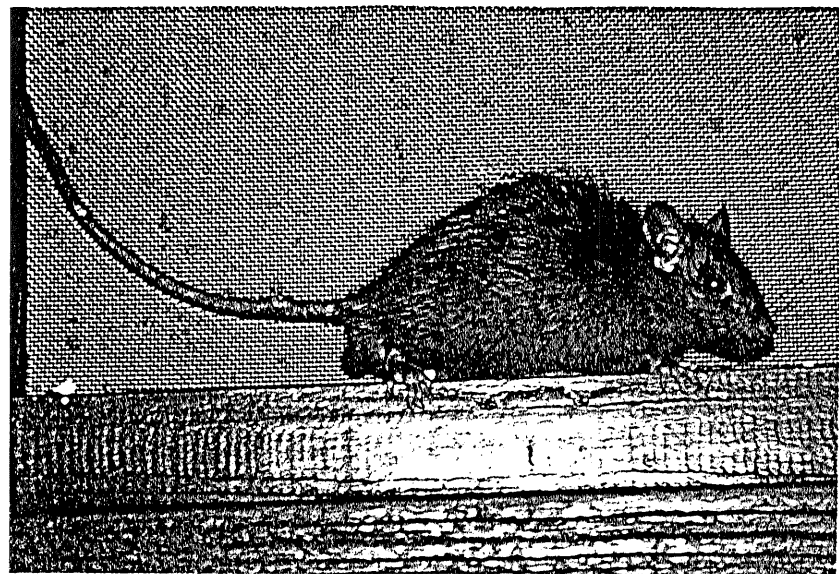
sumption of *C. schreberiana* and *C. borinquensis* was indistinguishable from that of all fruits; and the six other species constituted a group of most preferred fruits. Sastre-De Jesus (1979) reported that rats consume and disperse seeds of the late successional tree, *Buchenavia capitata*, in the tabonuco forest. Similarly, both immature and mature fruits of *Inga vera* were consumed by black rats at El Verde (Muniz-Melendez 1978). Additional studies of black rat foraging ecology under natural conditions are needed to confirm the existence of preferences when resource abundance reflects the ecological conditions in the tabonuco forest.

In addition to mongooses, which are almost exclusively diurnal, terrestrial predators of black rats (Pimentel 1955), red-tailed hawks (*Buteo jamaicensis*) and broad-winged hawks (*B. platypterus*) prey upon rats during the day (Layton 1986). Although aggregations of the Puerto Rican boa (*Epicrates inornatus*) have been observed feeding on bats as they leave caves at dusk (*B. cavernarum* and *M. redmani,* Rodriguez and Reagan 1984; *E. sezekorni,* Armando Rodriguez-Duran pers. comm., July 1994), the geomorphology of the Luquillo Mountains makes this phenomenon unlikely in the vicinity of El Verde. Nonetheless, the Puerto Rican boa has been found to consume adult rats in the tabonuco forest at El Verde (Reagan 1984; Thomas and Gaa Kessler, this volume).

Indian mongoose, *H. auropunctatus,* was introduced into Puerto Rico in 1877 in an attempt to control the rat population (Wadsworth 1949). Its density in the tabonuco forest is low, consistent with the observation that mongooses are not tree-climbers and avoid forested areas because they offer little chance to obtain food or adequate shelter (Pimentel 1955). Mongooses forage during the day and are relatively inactive during the night. They occupy burrows located near boulders, logs, or roots.

Mongooses may be among the most omnivorous species at El Verde. Pimentel (1955) reported that the diet of mongooses contained approximately 11% plant material, 56% insects, 17% reptiles, 12% myriapods, 8% arachnids, 3% mammals, 1% asteroids, and 1% amphibians by volume; in some areas, *Anolis* lizards constituted a major portion of the diet. Vilella (unpublished) provides the only dietary information concerning mongooses at El Verde; subsequent analyses are entirely based on that data. Stomach content analysis of thirteen male and six female mongooses from the tabonuco forest revealed exceptionally euryphagic diets, including both terrestrial and aquatic components. Males consumed a greater variety of food types (mean = 3.2; standard deviation = 1.5; range, 1–5) than did females (mean = 2.2; standard deviation = 1.0; range, 1–3). Nonetheless, most individuals that contained three or more food items in the stomach had vertebrates, invertebrates, and plant material as dietary constituents. Based on the percent of examined mongooses ($N = 18$) with food items in the stomach, dietary constituents included birds (11%); lizards in the genus *Anolis* (50%);

Figure 12.13. Photograph (courtesy of M. R. Gannon) of *Rattus rattus,* the black rat, from Puerto Rico

palo colorado forest, but different from that within elfin forest (Layton 1986). These data certainly imply a possible regulatory effect by endoparasites on rat populations in the tabonuco forest. Regardless of the identity of the regulatory agent, maximum survival of rats is about two years, but mean survival is usually one year or less (Weinbren et al. 1970).

The black rat is arboreal in the tabonuco forest; it is frequently observed foraging in vines and trees throughout the night as well as in the day. Similarly, *Rattus* activity in palo colorado forest appears to be primarily arboreal, with diurnal denning sites located in the canopy (Layton 1986). Laboratory experiments showed that *R. rattus* will consume a variety of fruits from the tabonuco forest, including *Byrsonima coriacea, Cecropia schreberiana, Dryes glauca, Ormosia krugii, Allophylus occidentalis, Inga vera, Dacryodes elsa, Prestoea montana, Palicourea riparia, Tetragastris balsamifera,* and *rdia borinquensis* (Weinbren et al. 1970). Snyder et al. (1987) suggest that ra palm (*Prestoea montana*) is an important food source for rats and that r nests are associated with the vine, *Marcgravia sintenesii.* A statistical lysis (reported herein) of the consumption data from the laboratory le 6 in Weinbren et al. 1970) indicates that all foods are not equally preed (analysis of variance; $V_1 = 10$, $V_2 = 33$; $F = 5.18$; $p < .001$). An a teriori Student-Neuman-Keuls Test (experiment-wise error rate = 0.05) aled that *D. excelsa* and *T. balsamifera* were least preferred fruits; con-

frogs in the genus *Eleutherodactylus* (11%); crabs in the genus *Epilobocera* (17%); freshwater shrimp in the genus *Attia* (17%); centipedes in the genus *Scolopendra* (33%); coleopterans (28%); orthopterans (33%); spiders (6%); and plant (fruits, seeds) material (61%), especially fruits from taxa in the Flacourtiaceae and Melastomataceae.

RESPONSE TO DISTURBANCE

Natural disturbances can have large effects on ecosystem structure and function depending on their scale, intensity, and frequency. On 18 September 1989, the eye of Hurricane Hugo passed within 10 km of El Verde, providing a rare opportunity to evaluate the effects of an infrequent but large-scale and high-intensity disturbance (Walker et al. 1991) on tropical bat species. Gannon and Willig (1994a) compare demographic parameters of the three most common phyllostomid bats (*A. jamaicensis, S. rufum,* and *M. redmani*) before and after the hurricane; their work forms the basis for the discussion that follows. In general, population levels, as estimated by numerical dominance (ND), biomass dominance (BD), and captures per net hour for the three species were affected by Hurricane Hugo in a species-specific fashion.

Artibeus jamaicensis was negatively affected by Hurricane Hugo, with a severe decrease in numbers, as well as in relative importance (fig. 12.14). Its numbers remained low for two years after the hurricane. Because it is a strong flier that moves large distances (Handley et al. 1991), immediate reduction in numbers may reflect movement of individuals from severely affected areas to less affected areas of the forest, or alteration of foraging patterns by cave-dwelling individuals. Data collected since the rainy season of 1991 indicate that *A. jamaicensis* has returned to the level of dominance it evinced prior to Hurricane Hugo.

Relative to other species, *M. redmani* was affected positively by Hurricane Hugo. Both its biomass dominance and numerical dominance at El Verde increased compared to pre-hurricane levels (fig. 12.14). However, only a slight increase occurred in actual numbers of captured individuals. This relative increase is due mostly to the decrease of the other two, previously dominant species. Nonetheless, the small increase in actual numbers may be attributed, in part, to the rapid and sizable increase in the presence of flowering plants in the open forest understory after Hurricane Hugo.

Numbers of *S. rufum* declined to about 30% of pre-hurricane levels and did not recover after three years (fig. 12.14). Moreover, analyses of telemetry data (two years before and two years after Hurricane Hugo) indicate that foraging and total home range size of individuals expanded to encompass an area approximately five times larger than its pre-hurricane size (fig. 12.15). The cost of foraging, in terms of time and energy, may be considerably elevated over pre-hurricane scenarios. The protracted decline in numbers of *S. rufum*
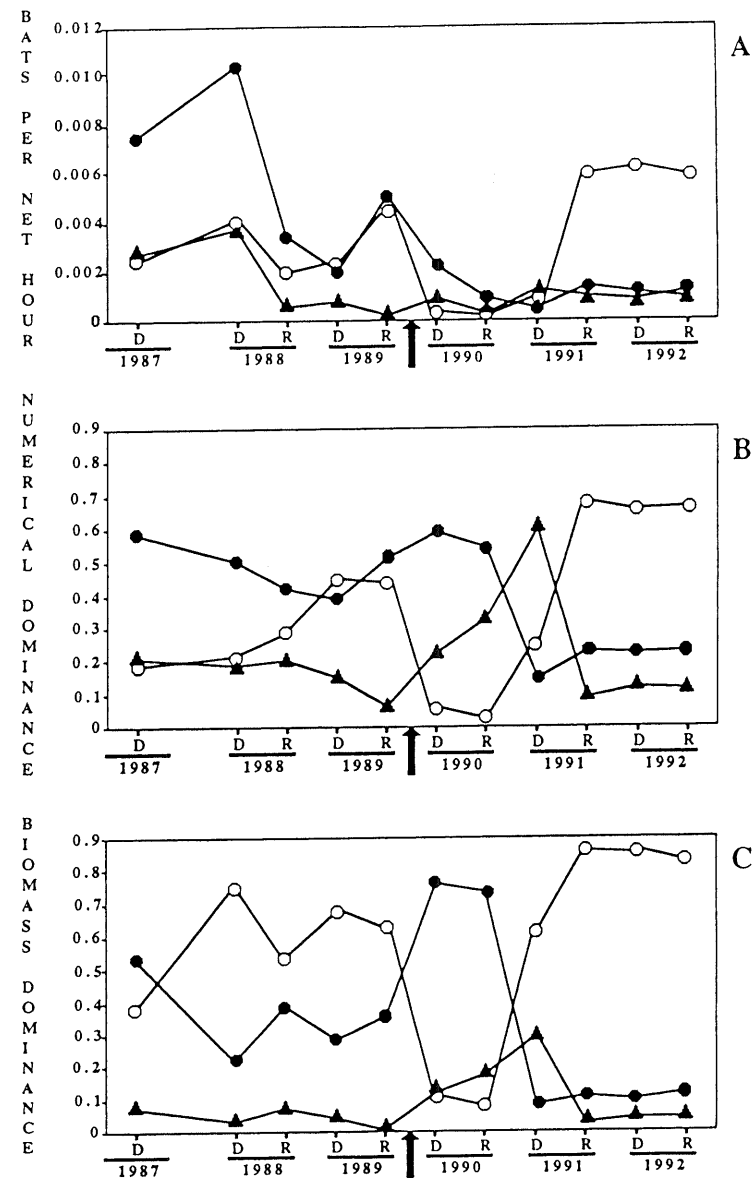

Figure 12.14. Long-term population trends of three common phyllostomid bats (*Artibeus jamaicensis,* open circles; *Stenoderma rufum,* closed circles; *Monophyllus redmani,* closed triangles) from a single netting locality in the tabonuco forest at El Verde based on number of specimens per net hour of sampling effort (*A*), numerical dominance (*B*), and biomass dominance (*C*). An arrow indicates the occurrence of Hurricane Hugo. Modified from Gannon and Willig (1994a).
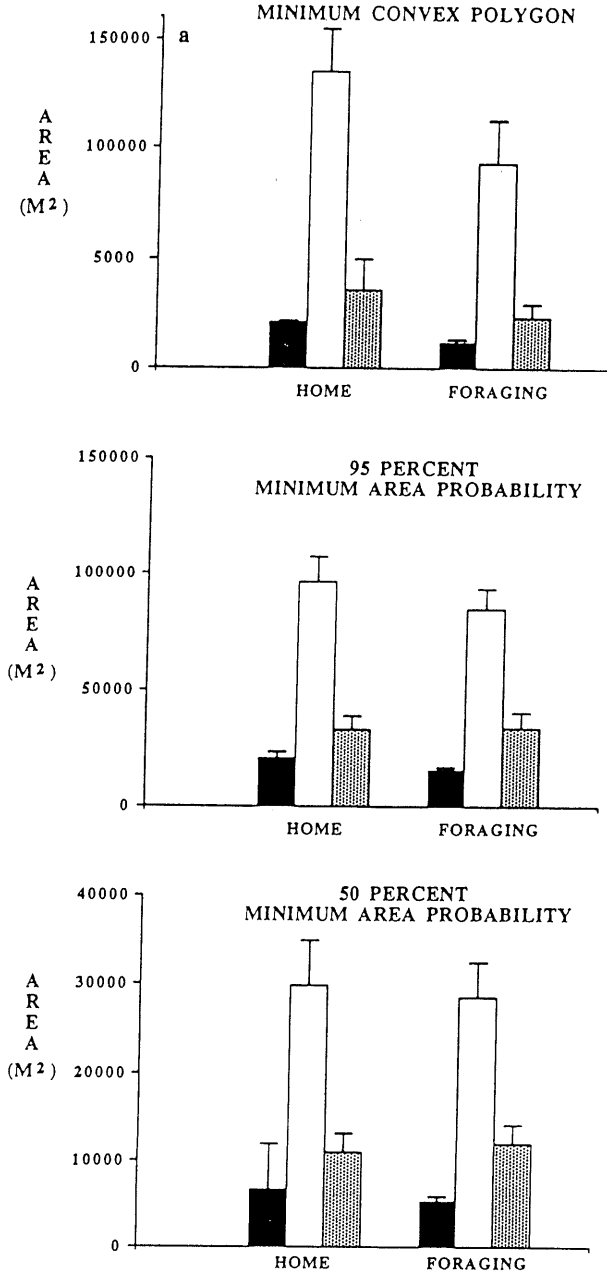
MINIMUM CONVEX POLYGON

95 PERCENT MINIMUM AREA PROBABILITY

50 PERCENT MINIMUM AREA PROBABILITY

Figure 12.15. A comparison of mean total home range and foraging home range of *Stenoderma rufum*, before (solid bars) and after Hurricane Hugo (one year post-Hugo, shaded bars; two years post-Hugo, stippled bars). Modified from Gannon and Willig 1994a).

may be related to four factors. First, increased exposure to high temperature, precipitation, and wind at roost sites (tree canopy) during and immediately after Hurricane Hugo likely caused immediate reductions in density. Second, the inability to disperse out of the tabonuco forest subsequent to the hurricane, as indicated by small foraging and total home range sizes, may have resulted in continued exposure to severe or detrimental microclimatic conditions, resulting in additional mortality and reduced fecundity. Third, decreased availability of fruit, especially that of *Cecropia*, for an extended period after the hurricane may have exacerbated microclimatic effects. Finally, the local population at El Verde could not be rescued by immigration from other demes because of the fragmented geographic distribution and low population levels of the species on Puerto Rico (Willig, Stevens, and Gannon unpublished).

The impact of Hurricane Hugo on reproduction 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% before to 17% immediately after Hurricane Hugo). The second stage reflects reduced fertility of adult females, as well as reduced survivorship of pregnant females and their offspring; few of the post-hurricane females were reproductively active (on average, proportions decreased from 93% before to 29% after the hurricane).

TROPHIC COMPARISONS

A recent study by Stevens and Willig (unpublished) has examined the composition of seven bat guilds from a variety of mainland communities throughout the New World; each has been netted on a monthly basis for at least twelve consecutive months (fig. 12.16). The bat community at El Verde is sufficiently well studied that one can be confident of its composition as well, making comparison with mainland tropical sites meaningful. Moreover, the clearly delimited species pool of potential bat colonists from Puerto Rico makes the distinction between island and tabonuco forest effects possible.

Most tropical bat communities from the mainland contain representatives of all (six of eleven sites) or at least six (ten of eleven sites) of the seven bat guilds, whereas El Verde harbors representatives of only three guilds (fig. 12.16). The absence of sanguinivores is an island-specific consequence of their inability to disperse to or persist on oceanic islands rather than a unique attribute of the tabonuco forest. Most of the islands of the Caribbean do not support blood-feeding bats. It is unlikely that any of the vampire bats could maintain sufficiently large populations to persist in the tabonuco forest given the absence of suitable nonvolant mammalian prey or suitable caves for roost sites. Similarly, the island of Puerto Rico does not harbor any species of gleaning carnivore (e.g., bat species in the Phyllostominae); their
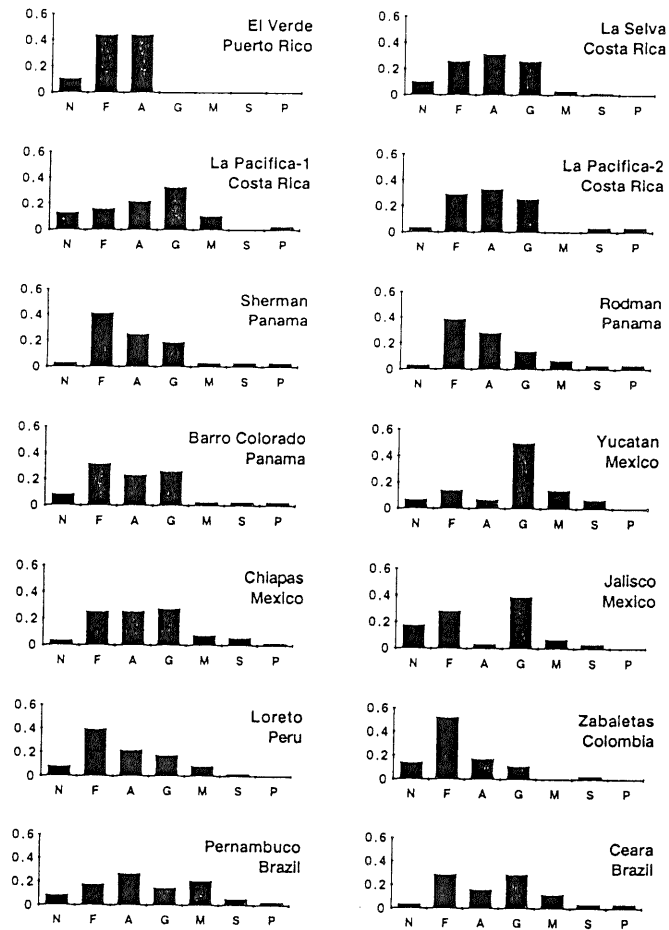
Figure 12.16. Guild structure (on the ordinate, proportion of species represented by a particular guild) of the bat community in the tabonuco forest of El Verde, as well as at eleven other tropical sites throughout Central and South America (La Selva, Costa Rica, La Val and Fitch 1977; La Pacifica-1, Costa Rica, Fleming et al. 1972; La Pacifica-2, Costa Rica, La Val and Fitch 1977; Sherman, Panama, Fleming et al. 1972; Rodman, Panama, Fleming et al. 1972; Barro Colorado, Panama, Bonaccorso 1975; Zabalatas, Colombia, Thomas 1972; Yucatan, Mexico, Bowles et al. 1990; Chiapas, Mexico, Medellin 1993; Jalisco, Mexico, Iniguez Davalos 1993; Loreto, Peru, Ascorra unpublished.; Pernambuco, Brazil, Willig 1982; Ceara, Brazil, Willig 1982). Guild codes (on the abscissa) are N, nectarivore; F, frugivore; A, aerial insectivore; G, gleaning carnivore; M, molossid insectivore; S, sanguinivore; P, piscivore.

absence from the community is likely an island biogeographic artifact. absence of piscivores and molossid insectivores is not primarily an is attribute because the species pool of bats on Puerto Rico does comprise cies in these guilds. Their absence from the tabonuco forest is more lik consequence of the ecological characteristics of the forest. Streams are sī fast running, and contain few fish (Covich and McDowell, this volume); consequence, *Noctilio,* the fish-eating bat, would have to rely almost e> sively on insects to persist at El Verde. Molossid insectivores (e.g., *Tadä* or *Molossus*) have never been recorded from El Verde or the Luquillo perimental Forest (Willig, Stevens, and Gannon unpublished); the densi insect prey above the forest canopy may be insufficient to support a l population of these species.

Compared to mainland tropical communities, the three feeding gɪ present at El Verde (nectarivore, frugivore, and aerial insectivore) comɪ larger percentages of the faunas primarily as a consequence of the absenɑ species in each of the other four guilds. Nonetheless, mainland commun are commonly dominated by species in the frugivore or aerial insecti guild. The aerial insectivore guild at El Verde may be limited because oí abundant diurnal and nocturnal predators (frogs and lizards) that rec available prey (Reagan, this volume; Stewart and Woolbright, this voluı

DISCUSSION

A discussion of the impact and role of mammals at El Verde is difficul develop in the absence of detailed information from throughout the yea the population biology and foraging ecology of the common mammal cies. In particular, three species (*A. jamaicensis, S. rufum,* and *R. rattus*) serve future study because their relatively large size, high metabolic ɪ probable high biomass, and mobility suggest an important role in affec energy and nutrient budgets of the tabonuco forest ecosystem, or in shaɪ landscape patterns. All three species may be important seed-dispersal age For example, *Manilkara bidentata* is a dominant tree in the tabonuco est and appears to be exclusively dispersed by bats (You 1991), most lil *S. rufum* (table 12.3; Gannon and Willig 1994a). In addition, both *A.* *maicensis* and *S. rufum* consume fruit of *Cecropia schreberiana,* a domir tree in the tabonuco forest that produces fruit throughout the year. In ɡ eral, *Cecropia* plays a major role in secondary succession and forest reɡ eration after disturbance (e.g., tree falls, landslides, or hurricanes). Con erable evidence suggests that as a result of coevolution, bats and *Cecrɑ* are mutualists (for a review, see Heithaus 1982). Fruits obtained from a ᵕ may be dispersed several hundred meters to several kilometers (Fleming . Heithaus 1981). Moreover, food transit time in the digestive system of ᵗ

is short (usually less than twenty minutes) and defecation usually occurs in flight. The many tiny seeds contained within *Cecropia* fruit lose their cohesiveness after passing through the digestive system, and because of air turbulence, the seeds fall to the ground in a trail up to 400 × 30 cm (Charles-Dominique 1986). Seed germination of *Cecropia* is enhanced by passage through the digestive tract of bats (Fleming and Heithaus 1981).

Adult *A. jamaicensis* require 43.9 kJ d^{-1} to support basal metabolic needs and minimum maintenance flight (Morrison 1978a) whereas *C. schreberina* fruit contains 4,675 calories (and 32.6 mg nitrogen) g^{-1} dry weight (Scogin 1982). Discounting costs of foraging (which cannot be estimated because search and travel time are not known for *A. jamaicensis* in the tabonuco forest) and assuming an assimilation efficiency of 20% (see Morrison 1978a, 1980), then an adult *A. jamaicensis* must consume at least 11.2 g dry weight of *Cecropia* a night to maintain a positive energy balance, and perhaps substantially more, because much of the caloric value of *Cecropia* is contained within the seeds, which for the most part pass intact through bat digestive systems.

Like *Cecropia,* a number of species of *Piper* contribute to forest regeneration as early successional species in light gap areas. Moreover, bats are important seed-dispersal agents for *Piper* and have been considered keystone mutualists in some tropical forests (Fleming 1985). Although the data are few from the tabonuco forest, they suggest a one-to-one correspondence between bat consumers and *Piper* species in that *P. glabra* is consumed only by *A. jamaicensis, P. hispidum* is consumed only by *S. rufum,* and *P. aduncum* is consumed only by *E. sezekorni*. These bat species also consume fruit from other species, and the common bats (*A. jamaicensis* and *S. rufum*) consume appreciable quantities of *Cecropia* as well. This may facilitate the deposition of later successional seeds (*Cecropia*) in light gap areas that are in early stages of secondary succession (dominated by *Piper* species).

The two common frugivores at El Verde appear to have similar diets. Each consumes five food types, four of which are shared dietary constituents. Nonetheless, the proportional contribution of the various components (after combining the three *Piper* species with *M. bidentata* to obtain sufficiently large sample sizes) are significantly different (G-Test of Independence; $G = 13.78$; d.f. = 3; $p = 0.003$), indicating real dietary differences between *A. jamaicensis* and *S. rufum* at El Verde.

Because *R. rattus* is a large abundant consumer in the tabonuco forest, it potentially has a significant impact on food web structure and function. Moreover, its euryphagic habits suggest a broad range of primary producers upon which it may have an effect via seed dissemination or predation. Unlike the scenario for bats, time may not have permitted coevolutionary adjustment between the black rat and its prey. The manner in which the black rat affects the abundance and distribution of its prey could have disruptive effects on any equilibrial conditions which may have existed among components of the food web in pre-Columbian times.

SUMMARY

The mammal fauna of Puerto Rico is depauperate compared to equivalent areas of the mainland or to other islands in the Caribbean as a consequence of biogeographic and anthropogenic factors. In the same manner, the tabonuco forest at El Verde contains fewer mammal species than it might otherwise support because the pool of colonist species on the island is small and functionally different than that on the mainland. With the exception of feral animals (i.e., cats and dogs), the mammal community at El Verde comprises two introduced terrestrial mammal species (Indian mongooses and black rats) and nine bat species, the only native mammals.

Mongooses and rats are relatively large, mobile omnivores; they have been implicated in the extinction of a number of bird species in the food web at El Verde. Black rats in particular may occupy a dominant role in the food web because they forage on the ground as well as in the canopy, they have high population densities (281 individuals ha^{-1}), and they consume a variety of fruits, invertebrates, and vertebrates. Although the density of mongooses is relatively low, they are among the most omnivorous species in the food web, feeding on all but the quinary consumer trophic level. The high mobility of both of those terrestrial mammals suggests that they may transport seeds a considerable distance from parent trees, thereby affecting survivorship and spatial distribution of seedlings.

Bats are highly mobile, nocturnal consumers and occupy frugivore (four species), nectarivore (one species), and insectivore (four species) feeding guilds at El Verde. The absence of some bat guilds (e.g., sanguinivores) from El Verde is a consequence of island biogeographic phenomena, whereas the absence of others (e.g., foliage gleaning carnivores) may be a consequence of the elevated density of arboreal frogs and lizards. Because of bat behavior, accurate estimates of population density are not possible using conventional multiple mark and recapture techniques. Nonetheless, numerical or biomass dominance, based on netting records prior to Hurricane Hugo, indicate that frugivorous species (ND = 0.81; BD = 0.94) are far more abundant than insectivorous (ND = 0.03, BD = 0.02) or nectarivorous (ND = 0.15, BD = 0.05) counterparts. In particular, two frugivores, *A. jamaicensis* (ND = 0.40, BD = 0.62) and *S. rufum* (ND = 0.37, BD = 0.28), are the most dominant bat species in the forest. Unfortunately, estimates of biomass and numerical dominance for insectivorous bats are biased. Insectivorous species consume prey that occur in or above the forest canopy; as a consequence, these species are less likely to be caught in ground nets than are frugivorous or nectarivorous bats.

Many bats are keystone mutualists in tropical ecosystems, primarily as a consequence of their role in seed dispersal and pollination. In fact, a number of early successional shrubs (e.g., *Piper* spp.) and late successional trees (e.g., *Manilkara*) in the tabonuco forest rely on bats for pollination or seed dispersal. These activities may be particularly important because recurrent hurricanes and tropical storms continually create patches (e.g., landslides and treefalls) within the forest that undergo secondary succession.

The effect of Hurricane Hugo on bat populations was species specific. *Artibeus jamaicensis* exhibited an immediate and drastic decline in captures, followed by relatively rapid recovery. In contrast, *S. rufum* declined more gradually and has not yet (1992) recovered to pre-hurricane levels. The considerable demographic data available on *S. rufum* suggests that philopatric and canopy-roosting species are particularly susceptible to large-scale and intense disturbances such as hurricanes and tropical storms.

In conclusion, mammals consume prey from a variety of trophic levels in the food web at El Verde and are represented by herbivorous (frugivores, granivores, nectarivores) and carnivorous species. Although primarily nocturnal, they forage at a diversity of vertical strata within the forest, including the litter, the shrub, subcanopy, and canopy levels, and even above the canopy. Mongooses are highly omnivorous and consume prey from four trophic levels in the grazing circuit. Rats are similarly omnivorous, prey on a variety of decomposers, producers, and consumers, and consequently occupy trophic positions in grazing and detrital circuits. Bats are more stenophagic, with particular species being either herbivores, consuming fruit and nectar, or insectivores, consuming arboreal invertebrates.

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