

# Island in the Storm: Disturbance Ecology of Plant-Visiting Bats on the Hurricane-Prone Island of Puerto Rico

Michael R. Gannon and Michael R. Willig

## Introduction

The indigenous people of the West Indies, the Taíno, had many legends to explain common natural phenomena they encountered in their existence. One of the most interesting is that of the hurricane. According to Taíno legend,

in the beginning Atabei created the heavens, the Earth and other celestial bodies. Atabei had always existed. Atabei was the original mother. Atabei was the powerful creator.

She had two sons named Yucajú and Guacar. Yucajú created the sun and moon to illuminate the Earth. The Earth was fertile, and from it grew plants and trees. Yucajú then created animals and birds to live among the plants and trees. Yucajú created the first man, Locuo. Locuo was happy on earth, with all the beauty that surrounded him. He knelt before Yucajú to give thanks.

Guacar looked with envy on all his brother had created. He began to taint the creations of his brother. He changed his name, becoming the terrible god of evil, Juricán. Juricán carried the winds. Sometimes he carried them with such force that they destroyed what Yucajú had created. Juricán uprooted trees and killed animals. Locuo's happiness turned to fear. He could no longer enjoy the beauty of nature. (Muckley and Martínez-Santiago 1999)

Today, in the West Indies, hurricanes are still the most powerful and feared natural phenomena. They are large-scale, high-intensity disturbances that regularly occur throughout the region (Weaver 1989). The impact of these disturbances in the Caribbean is often great on plants (e.g., Brokaw and Walker 1992; Scatena et al. 1996; Lugo and Scatena 1996; Walker et al. 1991; Walker et al. 1996), animals (e.g., Secrest et al. 1996; Woolbright et al. 1996), and humans.

A hurricane is a tropical cyclone in which winds reach speeds greater than 119 km/h (74 mph, Neumann et al. 1993). The use of the term *hurricane* is restricted to storms occurring over the Atlantic Ocean. The same kind of storm in

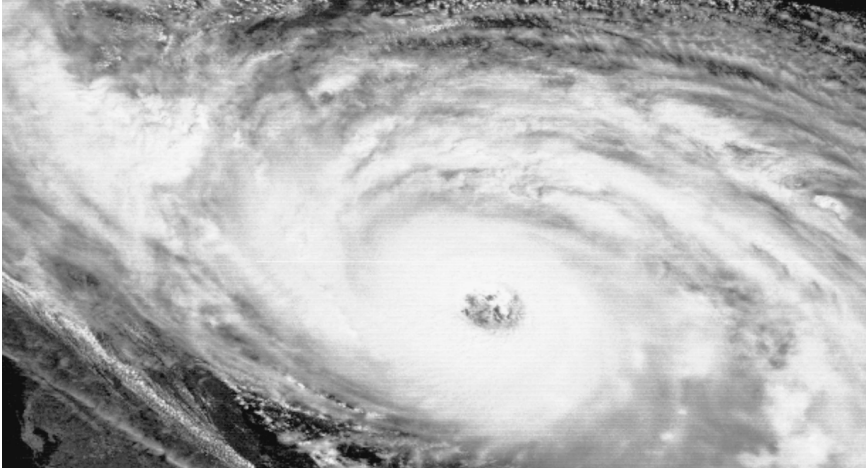


Figure 10.1. Photo of Hurricane Hugo as it passed through the Caribbean on September 1989. The circular shape and distinct eye of the storm are evident. (NOAA. Reprinted with permission.)

the Pacific Ocean is a typhoon. A tropical cyclone forming in the Atlantic first passes through two intermediate stages, a tropical depression and a tropical storm, before reaching hurricane strength (Neumann et al. 1993). A tropical depression forms from increasing low pressure that absorbs air and thermal energy from the ocean. The air rises by convection, while high pressure in the upper atmosphere pushes it outward. Wind currents rotate and usually spin the clouds in a tight circular pattern at speeds between 37 and 63 km/h (23 and 39 mph, Neumann et al. 1993). As winds increase between 64 and 118 km/h (40 and 73 mph), the depression becomes a tropical storm (Neumann et al. 1993). A mature hurricane (fig. 10.1) with wind speeds in excess of 119 km/h (74 mph) is nearly circular, and may be over 805 km (500 miles) in diameter (Neumann et al. 1993). As a result of the extremely low central pressure, surface air spirals inward (counterclockwise in the Northern Hemisphere and clockwise in the Southern Hemisphere), forming an eye that is about 30 km in diameter. The eye wall, located just outside the eye, is the region of heaviest precipitation and maximum wind speed. Inside the hurricane eye, weather is usually calm and clear, with little or no precipitation. In general, high winds are the primary cause of hurricane-inflicted damage and loss of life. Another cause is the flooding that results from the coastal storm surge and accompanying torrential rains (Neumann et al. 1993).

The Saffir-Simpson hurricane index of intensity (table 10.1) is used to classify hurricanes (Saffir 1973; Simpson 1974). The five categories in the hierarchy are defined by wind speed and potential to cause damage. These range from

Table 10.1. Saffir-Simpson index of hurricane intensity

Category	Wind speed	Storm surge	Damage
1—minimal	74–95 mph (119–153 km/h)	3–5 ft (1.0–1.7 m)	Some damage to vegetation and unanchored structures
2—moderate	96–110 mph (154–177 km/h)	6–8 ft (1.8–2.6 m)	Some trees blown over; widespread damage to unanchored buildings
3—extensive	111–130 mph (178–209 km/h)	9–12 ft (2.7–3.8 m)	Large trees blown over; structural damage to small buildings; flooding along the coastline
4—extreme	131–155 mph (210–249 km/h)	13–18 ft (3.9–5.6 m)	Severe damage to roofs, windows, and doors; complete destruction of unanchored buildings; major damage to structures along the shore; extensive flooding of low-lying areas
5—catastrophic	>155 mph (249 km/h)	>18 ft (5.6 m)	Complete failure of roofs on many buildings; complete destruction of small buildings; major damage to structures along the shore, extensive flooding of low-lying ground within 5–10 miles (8–16 km) of shore

Sources: Saffir 1973; Simpson 1974.

“minimal” at 119 km/h (74 mph) to “catastrophic” at >249 km/h (155 mph). Hurricanes originating in the eastern tropical Atlantic typically move westward, driven by easterly trade winds. These storms usually turn northwestward, and migrate into higher latitudes (Neumann et al. 1993). As a result, the West Indies, as well as the Gulf and East Coast of the United States, experience several hurricanes each year. Although any single location infrequently experiences tropical storm or hurricane forces, recorded storm paths over the last 150 years illustrate that no area within this region has been unaffected (fig. 10.2). Virtually all locations have been struck multiple times by intense storms during this period. Although hurricanes appear at irregular intervals and are difficult to predict in timing, intensity, or course of travel, mathematical models indicate that any area within this region is subject to storms of great magnitude at an average of approximately 60 years (Doyle 1981, 1982).

This chapter examines variation in bat population numbers over a 20-year period on Puerto Rico. During that time, two major hurricanes struck the island and provided a unique opportunity to examine responses to large-scale disturbances. Few studies on bat populations have persisted over such long time

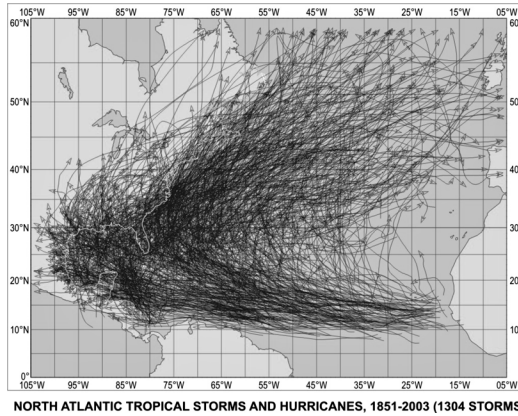


Figure 10.2. Map of the Caribbean showing pathways of hurricane and major storms for the last 150 years. (From NOAA 1999. Reprinted with permission.)

intervals. As such, this research provides a unique case study for quantifying long-term trends in response to disturbance.

### The Island

Puerto Rico (fig. 10.3) lies at a fulcrum ( $18^{\circ}35'–17^{\circ}55'N$  and  $67^{\circ}15'–65^{\circ}35'W$ ) between the Lesser and Greater Antilles. It is the fourth largest island in the Caribbean, with a land area of approximately  $8,900 \text{ km}^2$ . Its greatest length is slightly more than 170 km, west to east, whereas the greatest width is slightly less than 65 km, north to south.

Although it is an island, Puerto Rico has a diverse flora and fauna, which is due to a number of factors (Gannon et al. 2005). The tropical climate, high elevations, and strategic location of Puerto Rico, in the midst of the Caribbean basin, favor a diversity of organisms. In contrast, the small size of the island, distance from the mainland, and history of disturbance tend to reduce diversity. These interactions have resulted in a unique biota on Puerto Rico.

The topography of Puerto Rico rises from sea level to over 1,200 m in only 30 km, resulting in a landscape dominated by hills and low mountains. Less than one-quarter of total land area is level (Picó 1974). About 55% of its land is below 150 m in elevation, 21% is between 150 and 300 m, and 24% lies above 300 m (Wadsworth 1949). The island is divided into three major physiographic regions—a mountainous interior, a zone of coastal plains, and a karst region in the northwest (Mattson et al. 1990; Picó 1974). The interior is dominated by the Cordillera Central, a long mountainous tract in the center of the island that includes some of the highest peaks in Puerto Rico. Coastal areas consist of rocky outcrops, sand dunes, marshes, ponds, and low rolling hills. The karst region includes land that is mostly flat near the coast, but becomes irregular toward

the interior. It is underlain by limestone that slowly dissolves in rainwater (Lugo et al. 2001). Over time, this has caused development of caves, sinkholes, and hundreds of cone-shaped hummocks or haystacks called mogotes.

Many factors affect the climate of Puerto Rico. Compared with more temperate regions, the climate of Puerto Rico is consistently warm and wet. The island experiences large quantities of precipitation caused by convective cooling associated with mountains. A period of reduced precipitation occurs in winter. Tropical storms and hurricanes are most common in summer. Mean annual temperature ranges from almost 27°C in coastal areas to 20°C at mountain summits. August is usually the hottest month, and February is the coolest.

The native inhabitants of Puerto Rico (Borikén in their native language) were a group of Arawak Indians called the Taíno (Gannon et al. 2005). The Taíno of Borikén cleared small areas on the island for cultivation of crops. Taíno settlements were small and distributed across the island, and thus they caused little disturbance to the landscape. Christopher Columbus first came upon the northwestern shores of Borikén in 1493. Colonization of the island by the Spanish was slow at first and did not occur to any degree until Ponce de León began the conquest 15 years later (Gannon et al. 2005). As gold on the island was scarce, the main economic focus for the Spanish on Puerto Rico became sugar, ginger, coffee and tobacco. All were important cash crops at one time or another, and by 1768 the island was widely planted. In addition, raising livestock for domestic use and export contributed significantly to the Puerto Rican economy. These practices inevitably led to modifications of the island's ecosystems, unlike anything accomplished by the Taíno (Gannon et al. 2005).

The pace of deforestation under Spanish rule was slow but continual. By 1900 the island supported only 182,000 hectares of forest. By the mid-20th century, Puerto Rico was one of the most severely deforested and eroded regions on earth (Koenig 1953; Thomlinson et al. 1996). Recovery of Puerto Rican forests began in the 1950s as the economy of the island began to turn from agriculture

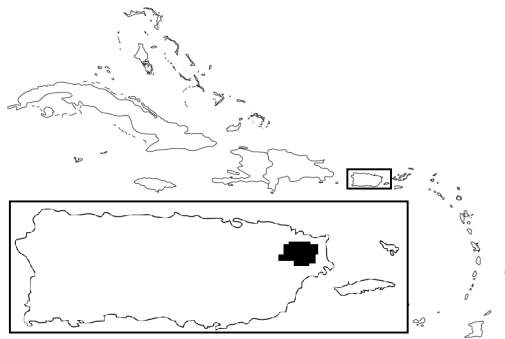


Figure 10.3. Map of the Caribbean showing the location of Puerto Rico as well as the location of the long-term study site in the Luquillo Experimental Forest (shown in black on island map).

to industry. By 1980, as pastures were reclaimed and replaced by secondary forests, as much as 30% of the island's area was forested (Birdsey and Weaver 1982). Between 1980 and 1990, secondary forests increased to greater than 75% of the timbered area on the island (Helmer et al. 2002). These new forests, however, are not identical in structure and composition to native forests (Lugo and Helmer 2004), and species composition of the resulting secondary forests often does not mimic that of native forests. Most new forests on the island occur in small patches. These highly fragmented forests typically have fewer endemic species, fewer large trees, and less organic matter in the soil than do native forests.

Although some damage may be wrought by a hurricane that only approaches Puerto Rico, the most destructive storms are those whose vortex strikes the island. Between 1893 and 1956, six hurricanes (San Roque, San Ciricao, San Felipe, San Nicolás, San Ciprián, and Santa Clara) passed directly over Puerto Rico, causing up to 3,000 human deaths and \$50,000,000 in damage. Since 1956 the frequency of major hurricanes has diminished considerably, although there was a recent resurgence of activity associated with hurricanes Hugo (1989) and Georges (1998).

The high winds and large rainfall caused by hurricanes can result in changes to the environment by altering both biotic and abiotic factors (Scatena and Larsen 1991; Waide 1991; Zimmerman et al. 1996). Rainfall accompanying a hurricane can initiate both landslides and floods (Walker 1991; Walker et al. 1996), whereas high winds result in damage to mature trees and partial or complete loss of the forest canopy. Canopy loss in turn leads to increased levels of temperature and light on the forest floor, as well increased amounts of forest litter from the dead and injured trees (Brokaw and Gear 1991; Fernández and Fetcher 1991). Damage to mature trees suppresses reproduction by these plants for months or years following a hurricane. Seedlings of trees that survive the storm can be injured by elevated sunlight that reaches them, or buried under debris from dead plants (You and Petty 1991). Seedlings from pioneer species, in contrast, often are favored by the overall increase in light intensity (Brokaw and Gear 1991; Fernández and Fetcher 1991).

It is unknown if ongoing recovery of Puerto Rico's forests will prevent extinction of species whose habitats were altered or fragmented in the past, but it is doubtful whether natural food webs ever will be restored completely (Lugo and Helmer 2004). As a consequence of habitat alteration or destruction by humans, over 500 species of endemic and nonendemic plants have been classified as rare or endangered, or as having a restricted distribution. For example, 13 endemic species of tree are classified as endangered, and 22 endemic species of tree are classified as threatened. Similarly, the future of wildlife supported by Puerto Rican forests is precarious: 27 species are considered highly endangered, 29 are endangered, and 15 are on the verge of endangerment (Birdsey and Weaver 1982; U.S. Department of Agriculture 1973, 1975).

Table 10.2. Species of bat on Puerto Rico

Family	Species	Common name	Main diet	Typical roost
Noctilionidae	<i>Noctilio leporinus</i>	Greater bulldog bat	Fish	Caves
Mormoopidae	<i>Mormoops blainvillei</i>	Antillean ghost-faced bat	Insects	Caves
	<i>Pteronotus quadridens</i>	Sooty mustached bat	Insects	Caves
	<i>Pteronotus parnellii</i>	Parnel's mustached bat	Insects	Caves
Phyllostomidae	<i>Brachyphylla cavernarum</i>	Antillean fruit bat	Fruit	Caves
	<i>Monophyllus redmani</i>	Greater Antillean long-tongued bat	Nectar	Caves
	<i>Erophylla sezekorni</i>	Brown flower bat	Nectar	Caves
	<i>Artibeus jamaicensis</i>	Jamaican fruit bat	Fruit	Caves
	<i>Stenoderma rufum</i>	Red fig-eating bat	Fruit	Foliage
Vespertilionidae	<i>Eptesicus fuscus</i>	Big brown bat	Insects	Caves
	<i>Lasiurus borealis</i>	Red bat	Insects	Foliage
Molossidae	<i>Molossus molossus</i>	Velvety free-tailed bat	Insects	Buildings
	<i>Tadarida brasiliensis</i>	Brazilian free-tailed bat	Insects	Caves

Source: Modified from Gannon et al. 2005.

## The Bats

Compared to mainland areas of similar size and habitat diversity, Puerto Rico harbors few mammal species, and population numbers are generally low except in areas in close proximity to large cave systems (Gannon et al. 2005). Bats, the only native mammals (Anthony 1918, 1925; Díaz-Díaz 1983; Gannon et al. 2005; Willig and Gannon 1996), compose the major portion of the Puerto Rican mammal fauna in terms of species richness and density (Gannon et al. 2005; Willig and Bauman 1984; Willig and Gannon 1996). Thirteen species of bats (table 10.2). are extant on Puerto Rico.

Bats are keystone species in many ecosystems in which they occur. In particular, plant-visiting bats such as frugivores and nectarivores can affect plant composition and structure. Indeed, frugivorous bats make a critical contribution to tropical forest succession by widely dispersing the seeds of early successional plants (e.g., Charles-Dominique 1986; de Foresta et al. 1984). Bats also have an important role in flower pollination in tropical systems (Baker et al. 1998; Machado et al. 1998). As such, frugivorous and nectarivorous bats can have a large impact on the distribution and genetic structure of tropical plant species (Willig and McGinley 1999). Bats likely colonized Puerto Rico via "stepping-stone dispersal." This involved emigration from the mainland to a nearshore island, then to more-distant islands (Griffiths and Klingener 1988).

The ancestral source of most extant species was most likely Central or North America (Gannon et al. 2005). As such, bats first arrived in the westernmost islands of the Greater Antilles, with some eventually moving further east to Hispaniola and Puerto Rico.

Whatever the origin, those species that successfully colonized and evolved on each island in the Caribbean were not there totally by chance. Present communities of bats are not random samples of the species available from mainland source pools (Rodríguez-Durán and Kunz 2001). Biogeographers have identified a core community of bats, the members of which are similar on most islands of the West Indies (Gannon et al. 2005). As such, much of what has been learned about bats on Puerto Rico can have implications and applications to other islands throughout the Caribbean.

### **The Effect of Hurricanes on Bat Populations**

There are several reasons why it is important to examine the effects of hurricanes on island populations of bats. First, an island is a somewhat isolated and closed system. The communities that develop or evolve there, in the presence of frequent large-scale disturbances, should differ considerably from those found in mainland settings. Second, bats that are endemic to Caribbean islands have relatively small geographic ranges and populations, when compared to sister taxa on the mainland. Therefore they may be more vulnerable to extirpation or extinction from disturbances such as hurricanes. Lastly, human development on islands is increasing. This is especially true for Puerto Rico, where expanding human alteration of the environment may decrease habitats that are crucial for bats' persistence.

The effects of hurricanes on bat populations is a culmination of a number of factors. Among them are hurricane size, intensity, path of travel, and the duration of time that a storm remains over land. As a result, hurricane severity can differ considerably in scope and timing. Effects of such disturbances can be short-term or long-term. Short-term effects are directly attributable to the hurricane (high winds, heavy rains) and cause individual mortality and alter spatial distributions. Long-term effects result in differential survivorship and reproductive success, with populations responding either positively or negatively to alterations that have occurred in abiotic conditions or in the composition and structure of relevant habitats (Willig and McGinley 1999).

Puerto Rico may be viewed as a case study for the evaluation of short-term and long-term effects of hurricanes on bats. Long-term population- and community-level studies of the bats have been ongoing on the island during the past 20 years. In that interval, two sizable hurricanes, Hurricane Hugo (1989) and Hurricane Georges (1998), struck Puerto Rico. The occurrence of these storms facilitated monitoring temporal changes in population numbers of several bat species. One site in particular, El Verde Field Station in the Luquillo

Experimental Forest (LEF), serves as a case study. It provides a useful insight into the ways in which different bat species are affected by and respond to hurricane-induced disturbances. In general, effects of hurricanes are inferred from the study of islands experiencing different disturbance regimes. However, extreme anthropogenic changes in flora, fauna, and geology that have occurred on almost all islands, as well as most other locations inhabited by humans over the course of human history, compromise the ability to distinguish short- and long-term hurricane effects from those related to other island characteristics. In this case we have the unique benefit of making observations over multiple years, during which two large-scale storms occurred over a relatively short period (nine years). Before and after these tropical storms we monitored bat populations within the LEF, a protected area that has been subject to less human disturbance than most islands of the Caribbean.

### **Case Study: The Luquillo Experimental Forest**

The LEF, also called El Yunque National Forest and the Caribbean National Forest (180°10'N, 65°30'W), is located in the northeast corner of Puerto Rico (fig. 10.3), in the Luquillo Mountains. Increasing elevation is accompanied by changes in climate, soil, and vegetation structure and composition, resulting in three distinct life zones (Brown et al. 1983; Ewel and Whitmore 1973). Tabonuco forest, the largest life zone, is located on lower mountain slopes below 650 m. Rainfall is substantial and varies between 2,000 and 4,000 mm annually. Palo Colorado forest occurs in valleys and on mountain slopes above cloud condensation level at 600 m; average rainfall is 4,700 mm. Dwarf forest occupies the highest mountain summits and ridge lines above 850 m. 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 differ in frequency and intensity, and include tree-fall gaps, landslides, droughts, and hurricanes. Substantial areas of the LEF remain virgin forest and are protected from human development. Nonetheless, anthropogenic disturbances have occurred in some areas and include roads, buildings, and agricultural legacies (coffee plantations and selective logging).

In September 1989, the eye of Hurricane Hugo, a category 4 storm with winds in excess of 220 km/h, passed close to the northeastern edge of Puerto Rico, within 10 km of the LEF (fig. 10.4). It was the first storm of this magnitude to pass directly over the LEF since 1932. It 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. Although the northeastern portions of the island were affected severely, most of Puerto Rico was relatively unaffected by this storm.

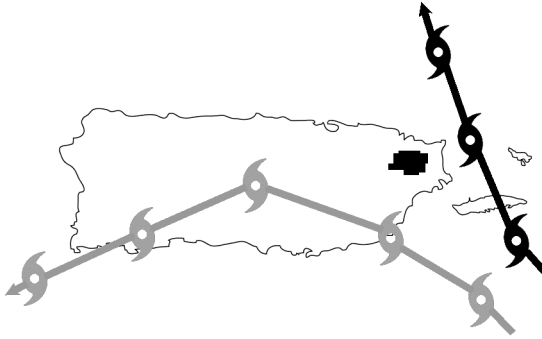


Figure 10.4. The island of Puerto Rico and the pathway for two hurricanes that struck the island in recent times. The pathway of Hurricane Hugo (1989) is *black* and that of Hurricane Georges (1998) is *gray*.

In September 1998 Hurricane Georges, a category 3 storm, passed directly over Puerto Rico (fig.10.4), with the path of the eye traveling through much of the center of the island. As a result, large-scale disturbances occurred throughout the island. Virtually all areas, including the LEF, were directly and extensively damaged by this storm.

Within the LEF, three plant-visiting species dominate the bat fauna, although some are common in certain habitats and rare or absent in others. These species include *Stenoderma rufum* and *Artibeus jamaicensis*, principally frugivores, and *Monophyllus redmani*, a nectarivore.

Prior to 1985, *S. rufum*, the red fig-eating bat, had been found only at two localities on Puerto Rico, and on the nearby islands of St. John and St. Thomas (Genoways and Baker 1972; Thomas and Thomas 1974). Until the late 1950s (Hall and Bee 1960), it was thought to be extinct. Studies conducted prior to Hurricane Hugo examined various aspects of the population biology and ecology of *S. rufum*, including foraging and home-range dynamics (Gannon 1991; Willig and Gannon 1996), reproduction (Gannon and Willig 1992), and diet (Willig and Bauman 1984; Willig and Gannon 1996).

The Jamaican fruit bat, *A. jamaicensis*, is distributed broadly throughout tropical and subtropical America (Ortega and Castro-Arellano 2001). Although extensive work had examined aspects of the ecology of several mainland populations (Handley et al. 1991; Morrison 1975, 1978a, 1978b, 1979), little was known about island populations in particular or about Puerto Rican populations specifically (see Kunz et al. 1983). Previous research in the LEF indicates that the Jamaican fruit bat represents at least 60% of the bat fauna in terms of numbers of individuals (Gannon and Willig 1994).

The Greater Antillean long-tongued bat, *Monophyllus redmani*, feeds primarily on flower nectar (Homan and Jones 1975). It has a distributional range that is restricted to the Greater Antilles and several islands in the Bahamas (Homan

and Jones 1975). Little is known of its ecology other than anecdotal observations. It is common on Puerto Rico, where it represents a substantial portion of the LEF bat fauna (Willig and Bauman 1984; Willig and Gannon 1996).

At El Verde Field Station, bat populations were monitored using mist nets twice a year from 1987 to 1995, once during the wet season (June–August) and once during the dry season (January–March). After 1995, mist-netting was conducted only once per year, during the wet season. Typically, mist nets were set between 17:00 and 24:00 hours at all locations. Netting from period to period was conducted in a similar manner and at the same location over the course of the study. Age, sex, and reproductive condition were determined for each captured bat. Before release each bat was marked by attaching either neck collars (Gannon 1994) or metal wing bands.

Individuals within populations are not equally catchable because of their ability to echolocate and avoid nets after previous encounters with such devices. This is true of the bats in the LEF, where the number of recaptures was extremely low. Therefore, capture-recapture estimates were not useful. Instead, we used several techniques to allow us to examine population trends and the manner in which they differed in response to hurricanes (Gannon and Willig 1994, 1998). In all cases, the different techniques demonstrated the same general trends, so we only report results based on the number of bats captured per net hour. Populations of the three dominant species of bats have been tracked using this approach since 1987.

### *Artibeus jamaicensis*

*Artibeus jamaicensis* exhibited stable numbers prior to Hurricane Hugo (fig. 10.5). Numbers declined to near zero immediately after Hurricane Hugo, remained low for almost two years, and then recovered to prehurricane levels the third year after Hurricane Hugo.

*A. jamaicensis* is a vigorous flier capable of moving large distances (Morrison 1978a, 1978b; Handley et al. 1991). Radio telemetry observations suggest that *A. jamaicensis* does not usually roost in the tabonuco forest at El Verde, but commutes longer distances from surrounding areas. Radio-tagged individuals were never located within the forest during the day (Gannon, unpublished). Suitable roost sites for this species within the LEF likely are rare. No known caves occur within the LEF, and rocky outcrops suitable for roosts are few and of only modest size. In the aftermath of Hurricane Hugo, changes in population numbers most probably reflect changes in foraging patterns toward areas of the island that were less severely disturbed and where food sources were more available, rather than a direct consequence of hurricane-induced mortality. Moreover, observations of fluctuating numbers of juveniles between early sampling periods after Hurricane Hugo, along with a decrease in reproductive females posthurricane (Gannon and Willig 1998), support the contention of a behavioral response rather than a demographic response to Hurricane Hugo.

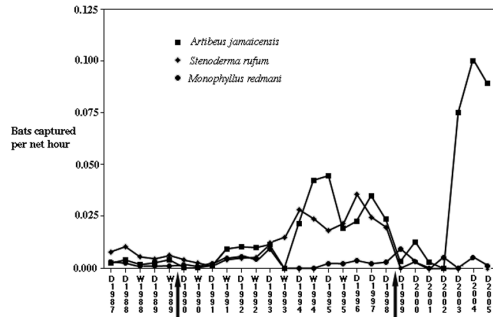


Figure 10.5. Long-term trends in abundance based on number of specimens captured per net hour of sampling effort for each of three common phyllostomid bats from a single netting locality in the Luquillo Experimental Forest. Squares represent *Artibeus jamaicensis*, diamonds represent *Stenoderma rufum*, and circles represent *Monophyllus redmani*.

Abundance of *A. jamaicensis* returned to prehurricane levels within two years of Hurricane Hugo's impact. As monitoring continued, the numbers of bats increased and eventually exceeded the number before Hurricane Hugo (fig. 10.5). After Hurricane Hugo, the forest was changing quickly, with many early successional plants on which bats feed, such as *Cecropia*, becoming established throughout the forest. This change likely provided elevated food abundance for *A. jamaicensis*. This was predictable, as the Jamaican fruit bat tends to exploit early successional plants as its food source. Abundance remained high until after Hurricane Georges. After Hurricane Georges (September 1998) numbers immediately declined in a fashion similar to that observed after Hurricane Hugo. *A. jamaicensis* again disappeared suddenly from the environs of El Verde. Numbers remained low for a period of about four years, until 2002. This prolonged recovery may have been a consequence of the differences between hurricanes in the extent of heterogeneity and damage. Although Georges was a smaller, category 3 hurricane, its islandwide extent was much more pervasive and devastating (Barlow et al. 2000; Jones et al. 2001). Its pathway down the center of Puerto Rico resulted in few areas of the island escaping impact. As a result, *A. jamaicensis* may have been unable to travel to less disturbed areas. Consequently, the effects of Hurricane Georges were greater on this species compared to those of Hurricane Hugo. The initial recovery took longer, but eventually recapitulated a pattern similar to that which occurred after Hurricane Hugo. Once the numbers of *A. jamaicensis* began to increase, recovery accelerated, and by 2003, abundance was twice that found after Hurricane Hugo.

### *Stenoderma rufum*

Prior to 2003, *Stenoderma rufum* was known from only three islands in the Caribbean, St. Thomas, St. John, and Puerto Rico. On Puerto Rico it was ini-

tially known from only two locations, one of which was the LEF (Genoways and Baker 1972). Telemetry studies prior to Hurricane Hugo (Gannon 1991; Gannon and Willig 1995; Willig and Gannon 1996) indicated that *S. rufum* roosted in the foliage of trees, close to its sources of food. It is a less vigorous, weaker flier than *A. jamaicensis*, traveling short distances, with a small home range averaging approximately 2.5 km<sup>2</sup>. Numbers in the LEF (fig. 10.5) were low before 1989, similar to those of *A. jamaicensis* at that time. After Hurricane Hugo, the abundance of *S. rufum* declined gradually over 18 months. Despite the vulnerability of this species to violent hurricane wind and rain (i.e., *S. rufum* roosts in the forest canopy), most individuals survived the immediate effects of the storm. However, changes associated with the loss of forest canopy had a greater long-term impact. Post-Hurricane Hugo changes in abundance and reproduction were substantial (Gannon and Willig 1994). Juveniles declined from between 30% and 40% of the population before Hurricane Hugo to about 10% after it. Similarly, the proportion of reproductively active adult females (pregnant or lactating) declined from about 55% pre-Hurricane Hugo to a low of 5%, two years after the hurricane's impact. In addition, foraging range increased to about four times the area after Hugo, but returned to prehurricane size within two years. *Stenoderma rufum* likely suffered from hurricane-induced alterations in the habitat (i.e., loss of canopy and roost sites, increased exposure to the elements, added energetic demands of finding food) than it did from direct hurricane mortality. The lag time for recovery (fig. 10.5) was greater for this species than for *A. jamaicensis*. Eventually the abundance of *S. rufum* exceeded pre-Hugo levels. It is doubtful that immigration or rescue effect had a substantial role in recovery. Other populations of *S. rufum* are separated from the Luquillo Mountains by many miles of urbanization (Gannon et al. 2005), and the biology of this species makes it unlikely that individuals frequently would cross those distances.

Hurricane Georges affected *S. rufum* in a much different manner than did Hurricane Hugo. Instead of a gradual decline in abundance over 18 months, the red fig-eating bat immediately disappeared from the LEF after Hurricane Georges. In fact, few individuals of *S. rufum* have been captured in the LEF since Hurricane Georges, so after almost ten years, abundance remains much less than prior to hurricane impact. The factors preventing the recovery of *S. rufum* after Hurricane Georges are unclear. Hurricane Georges took a direct path across Puerto Rico and spent more time in contact with the island than did Hurricane Hugo. We hypothesize that canopy removal in association with prolonged exposure to wind and rain during Hurricane Georges had a much greater impact on the mortality of *S. rufum* than did conditions during Hurricane Hugo.

Using the same methodology as in the LEF, over 100 locations were sampled throughout Puerto Rico between 1993 and 1999 (see Gannon et al. 2005). In particular, these data support the contention that Hurricane Georges's immediate impact on *S. rufum* was severe everywhere on the island. *Stenoderma rufum* was



Figure 10.6. Locations of 23 sites where *Stenoderma rufum* has been documented on Puerto Rico since Hurricane Hugo. Sixteen sites (circles and stars) were resurveyed after Hurricane Georges (sites shown as squares were not resurveyed). Circles indicate sites where *S. rufum* was located subsequent to Hurricane Georges. Stars indicate sites at which *S. rufum* was not captured after Hurricane Georges.

found at 23 of the sites sampled throughout the island (fig. 10.6). Four of these sites were within the LEF. During the summer of 1999, immediately after Hurricane Georges, we were able to resurvey 16 of the 23 localities that harbored *S. rufum*. The red fig-eating bat occurred at only 6 of those sites (38%). This suggests that local extirpation may have occurred over much of the island and raises considerable concern in the management and conservation of this species, as the frequency and intensity of hurricanes is predicted to increase in the Caribbean in the next few decades (Emanuel 2005; Emanuel et al. 2006). Almost 10 years after Hurricane Georges, numbers of *S. rufum* remain low in the LEF. This, along with islandwide range reduction in abundances and frequency of occurrence, raises significant concerns about the ability of *S. rufum* to persist on Puerto Rico. Much of the island has been developed, and forest patches are many miles apart, much farther than the distances typically traversed by this species. Isolation of populations may be a contributing factor that inhibits the recovery of this species.

It has long been theorized that storms and hurricanes in the Caribbean can act as dispersal agents for bats. This may happen in one of two ways: first, by directly moving organisms from island to island; second, and probably to a lesser extent, by causing such deterioration in habitat quality as to enhance the rewards of dispersal and minimize the risk. In 2002 and 2003, additional populations of *S. rufum* were discovered on Vieques (Rodríguez-Durán, unpublished data; Gannon 2003) and on St. Croix (Kwecinski and Coles 2007). Moreover, individuals were captured on St. John in 2003, more than 30 years after the last documented occurrence there. The recent discovery of *S. rufum* on St. Croix is of particular interest and supports the idea that, although hurricanes may negatively impact many bat populations in the Caribbean, they may also act as agents of dispersal. With the exception of St. Croix, all the islands that are now part of the commonwealths of Puerto Rico and the Virgin Islands are part of the Puerto Rican Bank. At one time, when ocean levels were lower, these islands were interconnected, and as a result they share much

of their flora and fauna. With effort, this bat may be found on other islands of the British Virgin Islands. However, St. Croix, located outside the Puerto Rican island bank, about 60 miles from Puerto Rico, was never connected to these other islands. Although bats are capable of flight between islands, such dispersal is probably a rare event. In the case of *S. rufum*, which is a weak flier with a small home range, it is even more unlikely. The presence of *S. rufum* on St. Croix supports the idea that hurricanes directly influenced dispersal and colonization of organisms in the Caribbean.

### *Monophyllus redmani*

The abundance of *Monophyllus redmani* increased slightly after Hurricane Hugo and after Hurricane Georges. The slight increase may be attributed to the rapid and sizable increase in the presence of flowering plants in the forest understory after both hurricanes. As *M. redmani* is primarily a cave-roosting species, most individuals likely commute from other areas of the island and feed within the LEF. As a result, increased capture rates may represent the presence of opportunistic individuals who exploit temporary increases in food supply. After both hurricanes, as the forest canopy closed, numbers of *M. redmani* returned to predisturbance levels (those in 1993 and 2001).

## Conclusions

Many factors, including intensity and path of the storm, geographic distribution of the species, roost characteristics, and food supply, influence how bats are affected directly by hurricanes and how they respond during subsequent succession (Willig and McGinley 1999).

Roost type readily can affect immediate survival of individuals during a hurricane. Bats such as *A. jamaicensis* or *M. redmani*, which roost in caves or other solid structures, are relatively buffered from direct effects of the storm. Bats that roost in trees, or other temporary structures (e.g., *S. rufum*), are more susceptible to direct mortality from storms. Most species are probably susceptible to long-term trajectories of change in habitat quality and resource distribution that follow major disturbances. Foliage-roosting bats such as *S. rufum* must contend with canopy loss and exposure to the elevated temperatures and exposure during early recovery. In addition, bats that depend on plants for food may be at greater risk of starvation as a consequence of increased energetic cost of foraging when resources are few and dispersed. In particular, fruit bats may be challenged to find sufficient food until early successional plants (e.g., *Cecropia*, *Ficus*, *Piper*, *Solanum*) begin to produce fruit.

The extent of damage caused by a hurricane can have an effect above and beyond that caused by local storm intensity. Although Hugo was a category 4 storm, it only brushed the island and affected a relatively small area. Bats had the opportunity to relocate to other less affected areas of the island. Those

that could do so (*A. jamaicensis*) recovered faster than those that could not (*S. rufum*). Hurricane Georges was a less severe storm (category 3), yet the disturbance it caused was more widespread. The recovery time of both bat species was considerably longer after Hurricane Georges, as few areas of the island were unaffected. However, *A. jamaicensis*, the stronger flier of the two species, recovered after several years, and its levels now exceed predisturbance levels. Eight years after Hurricane Georges, *S. rufum* had failed to recover and may be in a precarious situation.

Local extirpation or extinction of *S. rufum* in the LEF and Puerto Rico remain a concern. Jones et al. (2003) recently evaluated extinction risk in bats and noted that small geographic ranges were the greatest predictor of extinction. This may make *S. rufum* a prime candidate, as it has one of the smallest ranges of any bat species known. Island bats in general may be at greater risk to extinction. Many endemics in the Caribbean have small distributions and exist in an isolated environment in which movement between islands may be a rare event. Bats are not considered to be as mobile as birds.

Conservation and management protocols for populations in general, and keystone species such as plant-visiting bats in particular, need to consider consequences of catastrophic events on those populations. Conservation plans should manage for minimum numbers likely to occur over scores of years, and insure that the lowest likely densities (due to some catastrophic event, whether it be natural or anthropogenic) remain above estimated minimum viable population levels. Repeated hurricanes such as those observed in Puerto Rico over a decade are not unusual in the long-term. Indeed, the frequency of hurricanes in the Caribbean may be increasing because of mechanisms associated with global warming (Emanuel 2005; Emanuel et al. 2006). Demographic models for predicting population changes over time need to incorporate the likely impact of major disturbances such as hurricanes if they are to guide conservation action in an effective manner.

### Acknowledgments

We thank the University of Puerto Rico, U.S. Forest Service (Catalina), and U.S. Fish and Wildlife Service (Boquerón) for cooperation and support throughout the 20 years of this research. We are indebted to the staff of El Verde Field Station for the many years of logistic support. The number of students who contributed to field data collection is too great to list here. Without their hard work and dedication this work could not have been completed.

This research was partially supported by grants BSR-8811902, DEB9411973, DEB 0080538, DEB 0218039, and DEB 0620910 from the National Science Foundation to the Institute for Tropical Ecosystem Studies, University of Puerto Rico, and to the International Institute of Tropical Forestry, U.S. Forest Service. Additional support was provided by the Forest Service (U.S. Department of

Agriculture), the University of Puerto Rico, U.S. Fish and Wildlife Service (U.S. Department of Interior), Sigma Xi, the American Museum of Natural History (Theodore Roosevelt Fund), the Department of Biological Sciences and the Graduate School of Texas Tech University, the American Society of Mammalogists, Oakridge Associated Universities (U.S. Department of Energy), and Penn State University.

### Literature Cited

- Anthony, H. E. 1918. Indigenous land mammals of Porto Rico, living and extinct. *Memirs American Museum Natural History, new series*, 2:331–435.
- Anthony, H. E. 1925. Mammals of Porto Rico, living and extinct. *Scientific Survey of Porto Rico and Virgin Islands. New York Academy of Sciences*, 9:1–96.
- Baker, H. G., I. Baker, and S. A. Hodges. 1998. Sugar composition of nectars and fruits consumed by birds and bats in the tropics and subtropics. *Biotropica*, 30:559–586.
- Barlow, K. E., N. Vaughan, K. E. Jones, A. Rodríguez-Durán, and M. R. Gannon. 2000. Are bats which pollinate and disperse forest plants particularly sensitive to disturbance? A case study on the effects of Hurricane Georges on bats of Puerto Rico. *Bulletin of the British Ecological Society*, 31:36–37.
- Birdsey, R. A., and P. L. Weaver. 1982. The Forest Resources of Puerto Rico. Resource Bulletin SO-85. U.S. Department of Agriculture, Forest Service, Southern Forest Experimental Station.
- Brokaw, N. V. L., and J. S. Gear. 1991. Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains, Puerto Rico. *Biotropica*, 23:386–392.
- Brokaw, N. V. L., and L. R. Walker. 1992. Summary on the effects of Caribbean hurricanes on vegetation. *Biotropica*, 23:442–447.
- Brown, S., A. E. Lugo, S. Silander, and L. Liegel. 1983. Research history and opportunities in the Luquillo Experimental Forest. General Technical Report SO-44. U.S. Department of Agriculture, Forest Service, New Orleans, LA.
- Charles-Dominique, P. 1986. Inter-relations between frugivorous vertebrates and pioneer plants: *Cecropia*, birds and bats in French Guiana. Pp. 119–135 *in*: *Frugivores and Seed Dispersal* (A. Estrada and T. H. Fleming, eds.). Dr W. Junk Publishers, The Hague, The Netherlands.
- Crow, T. R. 1980. A rain forest chronicle: a 30 year record of change in structure and composition at El Verde, Puerto Rico. *Biotropica*, 12:42–55.
- de Foresta, H., P. Charles-Dominique, C. Erard, and M. F. Prevost. 1984. Zoocorie et premiers stades de la régénération naturelle après coupe en forêt guyanaise. *Revue de Écologie*, 39:369–400.
- Díaz-Díaz, C. 1983. Compendio enciclopédico de los recursos naturales. Vol. 1. Los mamíferos de Puerto Rico. Departamento de Recursos Naturales, Area de Investigaciones Científicas.
- Doyle, T. W. 1981. The role of disturbance in gap dynamics of a montane rain forest: an application of a tropical forest succession model. Pp. 56–73 *in*: *Forest Succession: Concepts and Applications*. (D. C. West, H. H. Shugart, and D. B. Botkin, eds.). Springer-Verlag, New York.

- Doyle, T. W. 1982. A description of FORICO, a tropical montane dynamics model of lower montane rain forest of Puerto Rico. Environmental Sciences Division, Publication no. 1875. Oak Ridge National Laboratory, Oak Ridge, TN.
- Emanuel, K. A. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. *Nature*, 436:686–688.
- Emanuel, K. A., S. Ravela, E. Vivant, and C. Risi. 2006. A statistical-deterministic approach to hurricane risk assessment. *Bulletin American Meteorological Society*, 87:299–314.
- Ewel, J. J., and J. L. Whitmore. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. Research Paper, ITF-18:1–72. U.S. Department of Agriculture, Forest Service, Institute of Tropical Forestry, Río Piedras, Puerto Rico.
- Fernández, D. S., and N. Fetcher. 1991. Changes in light availability following Hurricane Hugo in a subtropical montane forest in Puerto Rico. *Biotropica*, 23:393–399.
- Gannon, M. R. 1991. Foraging ecology, reproductive biology, and systematics of the red fig-eating bat (*Stenoderma rufum*) in the tabonuco rain forest of Puerto Rico. PhD dissertation, Texas Tech University.
- Gannon, M. R. 1994. A new method for marking bats. *Bat Research News*, 34:88–89.
- Gannon, M. R. 2003. Survey of bats on Puerto Rico after Hurricane Georges, with special emphasis on *Stenoderma rufum*. Unpublished report for U.S. Department of Agriculture, Forest Service, Caribbean Field Office, Boquerón, Puerto Rico.
- Gannon, M. R., A. Kurta, A. Rodríguez-Durán, and M. R. Willig. 2005. Bats of Puerto Rico. Texas Tech University Press, Lubbock.
- Gannon, M. R., and M. R. Willig. 1992. Bat reproduction in the Luquillo Experimental Forest of Puerto Rico. *Southwestern Naturalist*, 37:414–419.
- Gannon, M. R., and M. R. Willig. 1994. The effects of Hurricane Hugo on the bats of the Luquillo Experimental Forest of Puerto Rico. *Biotropica*, 26:320–331.
- Gannon, M. R., and M. R. Willig. 1995. Ecology of ectoparasites from tropical bats. *Journal of Environmental Entomology*, 24:1495–1503.
- Gannon, M. R., and M. R. Willig. 1998. Long-term monitoring protocol for bats: lessons from the Luquillo Experimental Forest. Pp. 271–291 *in*: *Forest Diversity in North, Central, and South America, and the Caribbean: Research and Monitoring* (F. Dallmeier and J. Comiskey, eds.). Man and Biosphere series, vol. 21. UNESCO and Parthenon Publishing Group, Carnforth, Lancashire, UK.
- Genoways, H. H., and R. J. Baker. 1972. *Stenoderma rufum*. *Mammalian Species*, 18: 1–4.
- Griffiths, T. A., and D. Klingener. 1988. On the distribution of Greater Antillean bats. *Biotropica*, 20:240–251.
- Hall, E. R., and J. W. Bee. 1960. The red fig-eating bat *Stenoderma rufum* found alive in the West Indies. *Mammalia*, 24:67–75.
- Handley, C. O. Jr., D. E. Wilson, and A. L. Gardner, eds. 1991. Demography and natural history of the common fruit bat, *Artibeus jamaicensis*, on Barro Colorado Island, Panama. *Smithsonian Contributions to Zoology*, 511. Smithsonian Institution Press, Washington, DC.
- Helmer, E. H., O. Ramos, T. del M. López, M. Quiñones, and W. Diaz. 2002. Mapping the forest type and land cover of Puerto Rico, a component of the Caribbean biodiversity hotspot. *Caribbean Journal of Science*, 38:165–183.

- Homan, J. A., and J. K. Jones, Jr. 1975. *Monophyllus redmani*. Mammalian Species, 57:1–2.
- Jones, K. E., K. E. Barlow, N. Vaughan, A. Rodríguez-Durán, and M. R. Gannon. 2001. Short-term impact of extreme environmental disturbance on the bats of Puerto Rico. *Animal Conservation*, 4:59–66.
- Jones K. E., A. Purvis, and J. L. Gittleman. 2003. Biological correlates of extinction risk in bats. *American Naturalist*, 161:601–614.
- Koenig, N. 1953. A comprehensive agricultural program for Puerto Rico. U.S. Department of Agriculture and Commonwealth of Puerto Rico, Washington, DC.
- Kunz, T. H., P. V. August, and C. D. Burnett. 1983. Harem social organization in cave roosting *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Biotropica*, 15:133–138.
- Kwincinski, G. G., and W. C. Coles. 2007. Presence of *Stenoderma rufum* beyond the Puerto Rican bank. *Occasional Papers of the Museum, Texas Tech University*, 226:1–9.
- Lugo, A. E., and E. Helmer. 2004. Emerging forests on abandoned land: Puerto Rico's new forests. *Forest and Ecology Management*, 190:154–161.
- Lugo, A. E., L. Miranda Castro, A. Vale, T. del Mar López, E. Hernández Prieto, A. Garcia Martínó, A. R. Puente Rolón, A. G. Tossas, D. A. MacFarlane, T. Miller, A. Rodríguez, J. Lundberg, J. Thomlinson, J. Colón, J. H. Schellekens, O. Ramos, and E. Helmer. 2001. Puerto Rican Karst: A Vital Resource. Technical Report, WO-65:1–100. U.S. Department of Agriculture, Forest Service.
- Lugo, A. E., and F. N. Scatena. 1996. Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica*, 28:585–599.
- Machado, I. C. S., I. Sazima, and M. Sazima. 1998. Bat pollination of the terrestrial herb *Irlbachia alata* (Gentianaceae) in northeastern Brazil. *Plant Systematics and Evolution*, 209:231–237.
- Mattson, P., G. Draper, and J. F. Lewis. 1990. Puerto Rico and the Virgin Islands. Pp. 112–120 *in*: The Geology of North America, vol. H, The Caribbean Region (G. Dengo and J. E. Case, eds.). Geological Society of America, New York.
- Morrison, D. W. 1975. The foraging behavior and feeding ecology of a Neotropical fruit bat, *Artibeus jamaicensis*. PhD dissertation, Cornell University.
- Morrison, D. W. 1978a. Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. *Ecology*, 59:716–723.
- Morrison, D. W. 1978b. Influence of habitat on the foraging distances of the fruit bat *Artibeus jamaicensis*. *Journal of Mammalogy*, 59:622–624.
- Morrison, D. W. 1979. Apparent male defense of tree hollows in the fruit bat, *Artibeus jamaicensis*. *Journal of Mammalogy*, 60:11–15.
- Muckley, R. L., and A. Martínez-Santiago. 1999. *Stories from Puerto Rico*. Passport Books, Chicago.
- Neumann, C. J., B. R. Jarvinen, C. J. McAdie, and J. D. Elms. 1993. Tropical Cyclones of the North Atlantic Ocean, 1871–1992, Prepared by the National Climatic Data Center, Asheville, NC, in cooperation with the National Hurricane Center, Coral Gables, FL.
- NOAA–National Environmental Satellite, Data, and Information Service. 1999. Tropical Cyclones of the North Atlantic Ocean, 1871–1998. Historical Climatology Series 6-2. National Climatic Data Center (NESDIS), October.
- Ortega, J., and I. Castro-Arellano. 2001. *Artibeus jamaicensis*. Mammalian Species, 662: 1–9.

- Picó, R. 1974. *The Geography of Puerto Rico*. Aldine Publishing, Chicago.
- Rodríguez-Durán, A., and T. H. Kunz. 2001. Biogeography of West Indian bats: an ecological perspective. Pp. 355–368 *in*: *Biogeography of the West Indies: Patterns and Perspectives* (C. A. Woods and F. E. Sergile, eds.). CRC Press, Boca Raton, FL.
- Saffir, H. S. 1973: Hurricane wind and storm surge. *Military Engineer*, 423:4–5.
- Scatena, F. N., and M. C. Larsen. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. *Biotropica*, 23:317–323.
- Scatena, F. N., S. Moya, C. Estrada, and J. D. Cjomea. 1996. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley experimental watersheds, Luquillo Experimental Forest, Puerto Rico. *Biotropica*, 424–440.
- Secrest, M. F., M. R. Willig, and L. L. Peppers. 1996. The legacy of disturbance on habitat associations of terrestrial snails in the Luquillo Experimental Forest. *Biotropica*, 28:502–514.
- Simpson, R. H. 1974. The hurricane disaster potential scale. *Weatherwise*, 27:169–186.
- Thomas, K. R., and R. Thomas. 1974. Notes on *Stenoderma rufum* Desmarest. *Bat Research News*, 15:24–25.
- Thomlinson, J. R., M. I. Serrano, T. del M. Lopez, T. M. Aide, and J. Zimmerman. 1996. Land-use dynamics in a post-agricultural Puerto Rican landscape. *Biotropica*, 28:525–536.
- U.S. Department of Agriculture, Soil Conservation Service, and Commonwealth Department of Natural Resources. 1973. *Rare and Endangered Animal Species of Puerto Rico*. Committee Report. San Juan, Puerto Rico.
- U.S. Department of Agriculture, Soil Conservation Service, and Commonwealth Department of Natural Resources. 1975. *Rare and Endangered Animal Species of Puerto Rico*. Committee Report. San Juan, Puerto Rico.
- Wadsworth, F. H. 1949. *The development of the forest land resources of the Luquillo Mountains, Puerto Rico*. PhD dissertation, University of Michigan, Ann Arbor.
- Waide, R. B. 1991. The effect of Hurricane Hugo on bird populations in the Luquillo Experimental Forest, Puerto Rico. *Biotropica*, 23:475–480.
- Walker, L. R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. *Biotropica*, 23:379–385.
- Walker, L. R., D. J. Lodge, N. V. L. Brokaw, and R. B. Waide. 1991. An introduction to hurricanes in the Caribbean. *Biotropica*, 23:313–316.
- Walker, L. R., D. J. Zarin, N. Fetcher, R. W. Myster, and A. H. Johnson. 1996. Ecosystem development and plant succession on landslides in the Caribbean. *Biotropica*, 28:566–576.
- Weaver, P. L. 1989. Forest changes after hurricanes in Puerto Rico's Luquillo Mountains. *Interciencia*, 14:181–192.
- Willig, M. R., and A. Bauman. 1984. Notes on bats from the Luquillo Mountains of Puerto Rico. Center for Energy and Environment Research, San Juan, Puerto Rico, CEER-T-194:1–12.
- Willig, M. R., and M. R. Gannon. 1996. Mammals. Pp. 399–431 *in*: *The Food Web of a Tropical Rain Forest* (D. P. Reagan and R. B. Waide, eds.). University of Chicago Press, Chicago.
- Willig, M. R., and M. A. McGinley. 1999. Animal responses to natural disturbance and roles as patch generating phenomena. Pp. 633–657 *in*: *Ecosystems of Disturbed Ground* (L. R. Walker, ed.). Elsevier Science, Amsterdam.

- Woolbright, L. L. 1996. Disturbance influences long-term population patterns in the Puerto Rican frog, *Eleutherodactylus coqui* (Anura: Leptodactylidae). *Biotropica*, 28:491–501.
- You, C., and W. H. Petty. 1991. Effects of Hurricane Hugo on *Manilkara bidentata*, a primary tree species in the Luquillo Experimental Forest of Puerto Rico. *Biotropica*, 23:400–406.
- Zimmerman, J. K., M. R. Willig, L. R. Walker, and W. L. Silver. 1996. Introduction: disturbance and Caribbean ecosystems. *Biotropica*, 28:414–423.