

Bats of Montserrat: Population Fluctuation and Response to Hurricanes and Volcanoes, 1978–2005

Scott C. Pedersen, Gary G. Kwiecinski, Peter A. Larsen,
Mathew N. Morton, Rick A. Adams, Hugh H. Genoways,
and Vicki J. Swier

Introduction

The British Crown Colony of Montserrat is a small 100 km² island located in the northern Lesser Antilles (16°45'N, 62°10'W; fig. 11.1). Long before Christopher Columbus discovered and named the island in 1493, humans knew that bats existed on Montserrat, as indicated by the presence of bat bones (*Brachyphylla cavernarum*) in Amerindian trash middens ca. 200 AD (Steadman et al. 1984a; Steadman et al. 1984b; Wheeler 1988). The first written account concerning the presence of bats on the island alludes to the habits of *Stenoderma montserratense* (*sic*; now *Ardops nichollsi montserratensis*), which “is said to hang all day under the branches of trees, and not take refuge in holes and crannies as most other species do” and may be responsible for “much damage to the cacao plantations” (Thomas 1894). Since the late 1970s, Montserrat has received a great deal of attention from bat biologists, including 12 surveys that have established a database including 2,602 captures of 10 species of bats from over 60 locations around the island (fig. 11.2; J. K. Jones and R. Baker in 1978; D. Pierson et al. in 1984; S. Pedersen in 1993–1994; M. Morton and D. Fawcett in 1995; Pedersen and others in 1997–1998, 2000–2002, 2004–2006; G. Kwiecinski in 2003).

Montserrat has a relatively simple chiropteran fauna (genus-to-species ratio 1:1), including one piscivore (*Noctilio leporinus*), one omnivore (*Brachyphylla cavernarum*), one nectarivore (*Monophyllus plethodon*), four frugivores (*Ardops nichollsi*, *Artibeus jamaicensis*, *Chiroderma improvisum*, *Sturnira thomasi*), and three insectivorous species (*Natalus stramineus*, *Tadarida brasiliensis*, *Molossus molossus*), representing four families—Noctilionidae, Phyllostomidae, Natalidae, and Molossidae. Two of these, *S. thomasi* and *C. improvisum*, are very rare endemic species that had been previously reported only from Guadeloupe (Baker and Genoways 1978), 55 km southeast (*upwind*) of Montserrat.

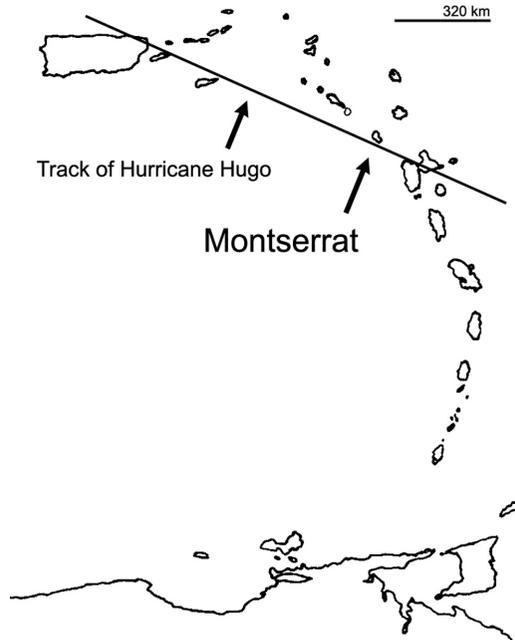


Figure 11.1. Map of the Lesser Antilles showing the position of Montserrat ($16^{\circ}45'N$, $62^{\circ}10'W$).

Montserrat is one of several volcanic islands in the archipelago that have been created by the subduction of the Atlantic tectonic plate beneath the Caribbean plate. Most of these islands are dominated by andesitic stratovolcanoes (steep-sided symmetrical cones) that are the result of explosive eruptions and extensive pyroclastic flows that generate a cone composed of alternating layers of volcanic debris. Stratovolcanoes are quite different from the gently sloping shield volcanoes, such as those in Hawaii, which are typically nonexplosive and which produce fluid lavas that can flow great distances from active vents. There are three volcanic massifs on Montserrat—Silver Hills in the north, Centre Hills, and, largest and youngest, the Soufrière Hills, which occupy the southern half of the island (fig. 11.2).

Due to its location on a fault line, earthquakes are not uncommon on Montserrat, with several periods of activity reported from the 1890s, 1930s, and 1960s (e.g., Perret 1939). Renewed seismic activity and pyroclastic flows from the Soufrière Hills volcano, which began in 1995, have progressively reduced the eastern and western flanks of the volcano to an ecological wasteland and have buried much of the southern half of the island under varying amounts of volcanic ash.

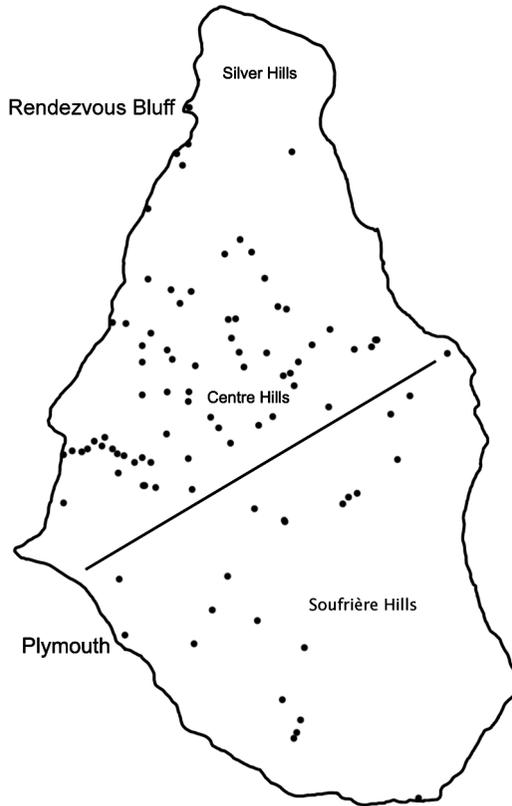


Figure 11.2. Map of Montserrat indicating the three volcanic massifs and all collection localities visited from 1978 to 2006. The region south of the line has been badly damaged if not destroyed by volcanic activity since 1995.

Located in the middle of the “hurricane belt,” Montserrat has also been battered by 28 hurricanes in the last 359 years, 12 of them severe, with Hurricane Hugo (1989) being the most destructive in recent history (<http://stormcarib.com> 2006; UNDRO-PCDPPP 2001). Thus Montserrat has undergone dramatic ecological changes resulting from two very different types of natural disaster during the last 20 years: hurricanes Hugo (1989) and Louis (1995), and recent eruptions of the Soufrière Hills volcano. Therefore Montserrat provides a dynamic setting and a unique opportunity to monitor a natural experiment in island biogeography and bat biodiversity.

This chapter has four sections. The first presents a wide range of issues encountered during a long-duration study involving numerous investigators and then outlines how best to frame the study of a single island within the

context of the entire archipelago. The next two sections concern the impact that hurricanes and volcanic activity have had on bat abundance and perceived biodiversity over the last 20 years. The last section covers in some detail the incidence of several sublethal pathologies that have been observed in fruit bats associated with ingestion/contact with volcanic ash during the recent volcanic activity on the island.

Value and Complications of Long-Term Studies

Montserrat's ecological fortunes have fluctuated dramatically over the last 20 years, and our efforts at tracking changes in its biota over time have provided a unique insight into island biogeography and underscore the great value of long-term surveys (Barlow et al. 2000; Gannon and Willig 1998; Jones et al. 2001; Rodríguez-Durán and Vázquez 2001; present authors; Rodríguez-Durán, chapter 9; Gannon and Willig, chapter 10; both in this volume). However, a difficulty arises when one tries to incorporate data from the older literature that primarily dealt with species inventories rather than with animal ecology or physiology per se (e.g., Baker and Genoways 1978; Genoways and Jones 1975).

Such inventory work throughout the region usually combined roost visits with ground-level mist-netting, as all surveys performed on Montserrat have done. There has been some variation in effort among surveys, but typically, five to eight mist nets of varying lengths have been deployed each evening at 100 m intervals along roads, covered flyways, and streams so as to snare bats while they were commuting or foraging. Net sizes were selected so as to block as much of a flyway as possible, but a combination of 6 m and 9 m nets have been quite adequate for such locations. Diverse netting localities were readily available, as Montserrat is covered with bamboo thickets, open meadows, small freshwater streams, and a wide range of cultivated and wild fruit trees. This protocol is standard for inventory work, but how do we evaluate fluctuations in bat abundance over time?

Measures of Bat Abundance

We could try to account for every bat in every roost across the entire island, but this is clearly impossible given the wide range and degree of permanency of various roost types differentially employed by each species of bat. It is also nearly impossible to account for every bat within a complex roost space, or to locate every roost on a given island. Given the difficulty in accurately quantifying bat abundance and animal activity, we have used a simple metric—BNN, bats captured per net-night—to approximate activity levels at our sampling sites on various islands throughout the region (Genoways et al. 2007a; Genoways et al. 2007b; Genoways et al. 2007c; R. J. Larsen et al. 2005; R. J. Larsen et al. 2006; R. J. Larsen et al. 2007; Pedersen et al. 1996; Pedersen et al. 2003; Pedersen et al. 2005; Pedersen et al. 2006; Pedersen et al. 2007).

However, data collected in 2005 and 2006 regarding mist-net capture bias indicate that less than 5% of bats flying along traditional flyways (e.g., trails, roads, rivers) actually become snared in a mist net (R. J. Larsen et al. 2005; R. J. Larsen et al. 2006; R. J. Larsen et al. 2007). These data closely mirror data collected by Lang et al. (2004) in Panama, and if generally true, then mist-netting surveys may very well be underestimating species diversity and bat activity (Simmons and Voss 1998). Although we could include additional variables (e.g., net dimensions, net-hours, etc.), we feel that these would introduce false precision to the data and make a bad situation (net bias) even worse. For example, if one is netting a road 7 to 8 m wide, a 6 m net does not fill the gap and portions of a 9 m net would be wasted/blocked by foliage unless one placed the longer net at an angle to the flyway, but this in turn creates a very different set of problems regarding bat-net detection and netting success. In addition, BNN is all too often the only statistic that can be culled from the older literature (Findley and Wilson 1983). Indeed, details concerning net size, habitat type, or observations concerning animal behavior relative to the net itself are often left to the imagination of the reader of the older literature.

BNN would seem therefore to be the most pragmatic metric with which to evaluate long-term studies at a single location by numerous investigators and protocols (Fenton et al. 1992; LaVal 2004; Pedersen et al. 2005). We use the BNN metric conservatively, not as an estimate of population size per se, but as an approximation of bat activity at a particular location. If we compare trends in BNN over time for any single location, however, we use BNN (with some trepidation) as a crude estimate of bat abundance. Given that islands adjacent to Montserrat have been relatively undamaged by natural disasters over the last 25 years, our survey activities on Antigua, St. Kitts, Nevis, Saba, and St. Eustatius (Statia) (Pedersen team 1993–2002) provide excellent controls/comparisons for our work on Montserrat. However, how does Montserrat activity data compare with that reported from other islands in the region?

If capture data from all feeding guilds are combined, bat captures on Montserrat have varied considerably during the last 28 years (table 11.1). We record an average capture rate of 3.08 BNN (range 1.46–11.29), which is typically higher than those rates that we have reported from other islands in the region (average 2.70: range 1.55–3.75; P. A. Larsen et al. 2006a; P. A. Larsen et al. 2006b; Pedersen et al. 2003; Pedersen et al. 2005; Pedersen et al. 2006; Pedersen et al. 2007), but falls below capture rates reported from mainland populations (4.53 BNN; range 2.71–6.65). If we restrict the analysis to fruit bats, average capture rates on Montserrat are the highest (2.10 BNN; range 1.00–10.59) of those we have reported from other islands in the region (1.88 BNN; range 0.65–2.10) and are comparable to fruit bat capture rates in Central America (4.15 BNN; range 2.20–5.93; table 11.1). In summary, given the existing sampling protocols, sampling efforts, and its relative size, Montserrat would appear to be species-rich and its bat populations would appear larger than those on neighboring islands.

Table 11.1. Mist-net capture rates of Neotropical bats

| Localities | Fruit bat BNN | Total BNN |
|--|---------------|-----------|
| Northern Lesser Antillean faunas | | |
| St. Eustatius (2002, 2003, 2004) ^a | 1.55 | 3.75 |
| Montserrat (1994–1995, 1997–1998, 2000–2004) ^{a, b} | 2.10 | 3.08 |
| Saba (2002, 2003) ^b | 0.65 | 2.47 |
| St. Kitts (1999, 2001) ^b | 1.11 | 2.11 |
| Antigua (1994, 1998, 2000, 2003) ^b | 1.45 | 2.04 |
| St. Maarten (2002, 2003, 2004) ^b | 0.92 | 1.63 |
| Nevis (1999, 2001) ^b | 1.34 | 1.55 |
| Average | 1.88 | 2.70 |
| Mainland faunas | | |
| San Vito, Costa Rica (1971) ^c | 5.93 | 6.65 |
| Osa, Costa Rica (1973) ^c | 5.68 | 5.87 |
| La Pacifica, Costa Rica (1970) ^c | 4.11 | 4.46 |
| BCI, Panama (1977) ^c | 2.85 | 2.98 |
| Canal Zone, Panama (1977) ^c | 2.20 | 2.71 |
| Average | 4.15 | 4.53 |
| Disturbed-site faunas | | |
| Akumal, Mexico ^d (undisturbed) | 4.20 | 5.33 |
| Akumal, Mexico ^d (disturbed) | 3.29 | 3.91 |
| St. Kitts: 1999 ^b (disturbed?) | 0.43 | 1.30 |
| St. Kitts: 2001 ^b (recovery?) | 1.47 | 2.54 |
| Montserrat: 1978 pre-Hugo ^e (undisturbed) | 44.40 | 86.40 |
| Montserrat: 1984 pre-Hugo ^f (undisturbed) | 10.59 | 11.29 |
| Montserrat: 1993–1994 ^b (disturbed) | 1.95 | 3.51 |
| Montserrat: 1995 ^a (disturbed) | 1.42 | 1.78 |
| Montserrat: 1997–1998 ^a (disturbed) | 1.00 | 1.46 |
| Montserrat: 2000–2001 ^a (disturbed) | 1.60 | 2.68 |
| Montserrat: 2002 ^a (disturbed) | 3.43 | 3.54 |
| Montserrat: 2003–2004 ^a (disturbed) | 3.45 | 3.51 |

Source: Pedersen et al. 2005.

Note: BNN = bats captured/net-night.

^aUnpublished survey data collected during 1993–2004 by Pedersen et al.

^bPublished survey data from Pedersen et al. 1996; Pedersen et al. 2003; Pedersen et al. 2005; Pedersen et al. 2006; or Genoways et al. 2007a, 2007b.

^cData from Findley 1983.

^dData from Fenton et al. 1992.

^eData from Jones and Baker 1979.

^fData from Pierson et al. 1986.

Species-Accumulation Curves

Islands north of Guadeloupe in the Lesser Antillean archipelago share a similar bat fauna, what we term the northern Lesser Antillean fauna. The fauna on any one of these islands is nearly the same regardless of rainfall, habitat diversity, or island size—Saba being the best example (Genoways et al. 2007a).

Our ability to report an accurate species inventory for an island has been hampered by the inadequacy of ground-based netting strategies, something that has been painfully obvious to field biologists who study species-specific

Table 11.2. Species accumulation curve data

| Location | Species | Nights | Nets | Captures |
|-----------------------|---------|--------|------|----------|
| Belham River (Lower) | 9 | 5 | 41 | 564 |
| Belham River (Sappit) | 7 | 5 | 51 | 281 |
| Paradise Estate | 7 | 2 | 27 | 177 |
| Collins River, etc. | 6 | 6 | 46 | 85 |
| Hope Springs | 6 | 5 | 25 | 73 |
| Soldier ghaut | 5 | 4 | 33 | 44 |
| Lawyers Tank | 5 | 3 | 17 | 48 |
| Runaway ghaut | 5 | 3 | 11 | 9 |
| Lawyers lower | 5 | 2 | 10 | 31 |
| Dick Hill farm | 3 | 1 | 6 | 15 |
| Cassava ghaut | 2 | 2 | 11 | 8 |
| Average effort | 5.5 | 3.5 | 25.3 | 121.4 |

Note: Entries indicate minimum effort to document complete site-specific species rosters for 11 typical sites on Montserrat (1978–2004 data; see also figs. 11.3–11.5). Subsequent efforts, some of which have been considerable, have not increased the species list at any of these sites.

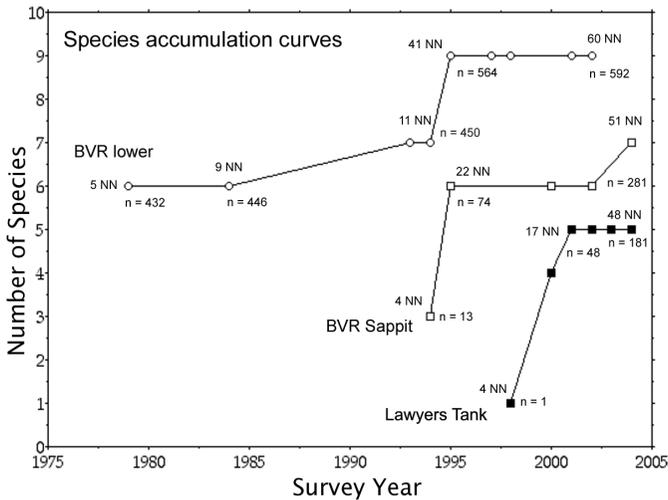


Figure 11.3. Species accumulation curves for three typical netting localities on Montserrat, 1978–2004. Vertical axis is number of species, and horizontal axis is survey year. n = individual bats captured; NN = net-nights.

responses to mist nets (detection) and species-specific ability to avoid mist nets (maneuverability; Barber et al. 2003; Berry et al. 2004; R. J. Larsen et al. 2005; R. J. Larsen et al. 2006; R. J. Larsen et al. 2007). Added to this, the sheer amount of effort, financing, and materiel required to adequately sample an island's habitat and fauna can be daunting (35 trips to 12 islands). However, we will limit our discussion herein to the island of Montserrat.

Study sites on Montserrat vary considerably in terms of habitat and species diversity, but an average number of species at an average locality on Mont-

Montserrat typically required three to four nights of effort (25 nets) and captures of approximately 120 bats (table 11.2, figures 11.3, 11.4). However, no more than eight species of bat have ever been collected during any single survey on Montserrat (1978–2004, fig. 11.5), that is, until 2005 when all ten species were captured for the first time during a single field season. Species that do not

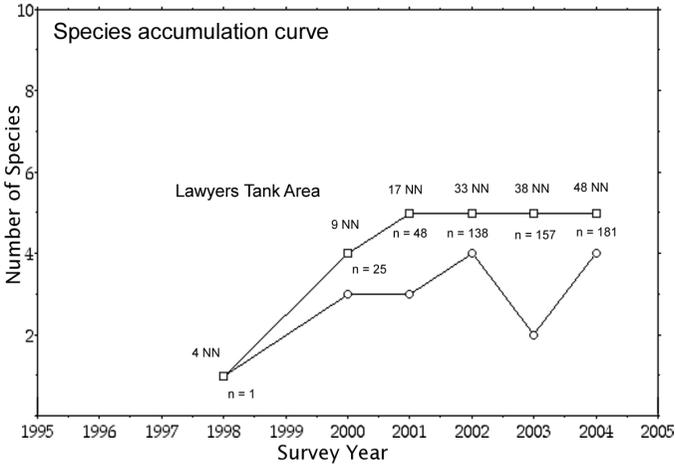


Figure 11.4. Species accumulation curve and species tally for the Lawyers Tank site, 1978–2004 (from fig. 11.3). Vertical axis is number of species, and horizontal axis is survey year. Note that the yearly species tally falls short of the known species inventory at this site. *n* = individual bats captured; NN = net-nights.

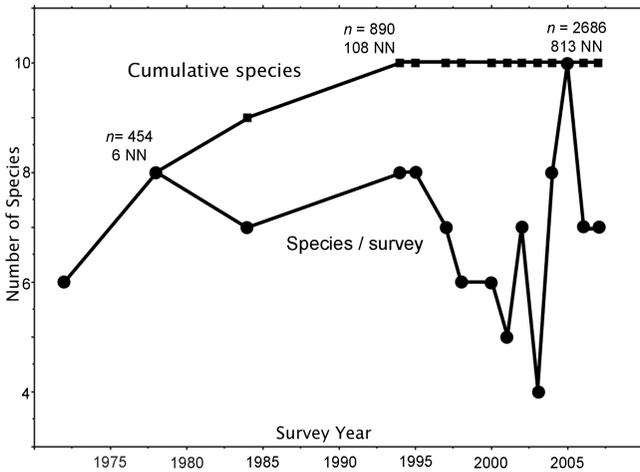


Figure 11.5. Species accumulation curve and species tally for the entire island of Montserrat, 1978–2004. Vertical axis is number of species, and horizontal axis is survey year. Note that the yearly species tally falls short of the known species inventory of the island. *n* = individual bats captured; NN = net-nights.

show up on a regular basis may simply be able to avoid mist nets, or fly where we cannot place mist nets, or are uncommon (*Chiroderma improvisum*, *Sturnira thomasi*, *Natalus stramineus*, *Noctilio leporinus*, and *Tadarida brasiliensis*).

Species-Area Curves

The number of species found on an island is correlated with the size (area) of the island, the distance from a source area (continental area), and the diversity of habitats available, which in most cases is directly affected by elevation of the island (see Willig et al., chapter 8, this volume). Increased elevation usually results in increased rainfall and more diverse vegetation (MacArthur and Wilson 1967). Morgan and Woods (1986) found that 69% of the variance in West Indian mammalian faunal diversity could be explained by island area alone whereas the “remaining 31% of the variance is dependent upon other variables such as habitat diversity and distance from source areas.” Following models that have been applied to amphibians and reptiles (Preston 1962), birds (Hamilton et al. 1964), and West Indian bats and other mammals (Griffiths and Klingener 1988; Morgan and Woods 1986), we constructed a species-area curve for the Antillean bat fauna (fig. 11.6; see Pedersen et al. 2006). The relative position of an island above the curve may be attributed to a wealth of sufficient habitat that supports a high level of bat diversity, close proximity to source islands, or a long history of survey efforts. The relative position of an island below the curve may be attributed to a dearth of sufficient habitat to support bat diversity, the presence of an insurmountable biological barrier beyond which bats cannot move, or a simple case of undersampling.

Montserrat with its ten species of bat falls well above the regression line relative to other islands of similar size (fig. 11.6) due primarily to the presence of two very rare species, *Sturnira thomasi* and *Chiroderma improvisum*. We hypothesize that Montserrat’s bat diversity is related to (1) its downwind position and proximity to a larger, more diverse island, Guadeloupe (12 species; Baker et al. 1978; Genoways and Baker 1975; Genoways and Jones 1975; Masson and Breuil 1992); (2) Montserrat’s tall mountains and varied topography; and (3) the fact that Montserrat has never been developed as a tourist destination, that is, it has not suffered from land development and overpopulation by humans. One could also argue that the location of Montserrat above the curve might reflect the amount of attention paid to this island; however, the species-accumulation curve for Montserrat plateaued at ten species after 100 net-nights of effort—the same amount of effort that has been expended by the authors on a dozen islands of various sizes throughout the region. Montserrat is simply unique.

If we compare Guadeloupe and Montserrat, it is interesting to note that two species of insectivorous bat (*Myotis nigricans*, *Eptesicus guadeloupensis*) remain unaccounted for on Montserrat despite extensive efforts. Given our radio-tracking data (to be published elsewhere), we argue that the primary agent behind the interisland movement of bats is tropical storms. Is there something

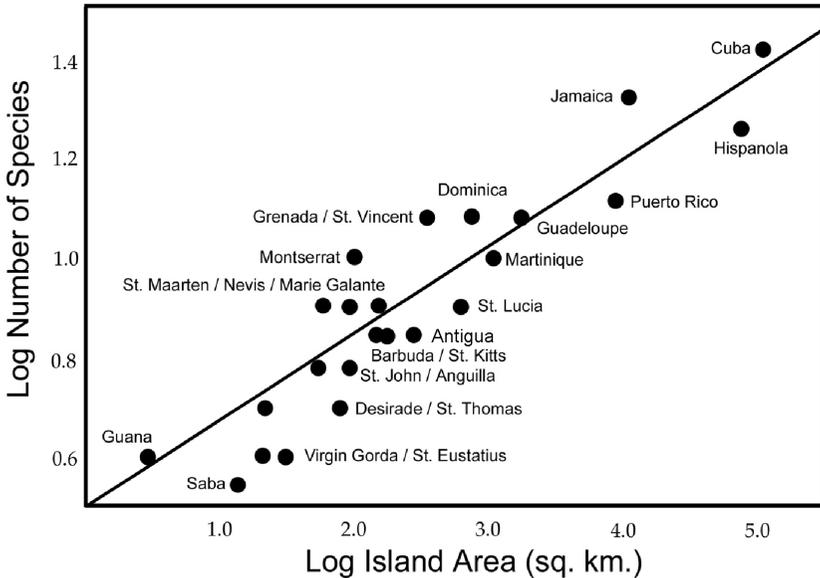


Figure 11.6. Species-area curve (Pedersen et al. 2005 after Genoways et al. 2001). Linear regression of log-transformed data: $y = 0.17x + 0.49$ ($R^2 = 0.81$).

unique about these two species that limits their dispersal abilities, such as cave resources, island altitude, habitat diversity, or flight ability?

There are several interesting aspects of and problems associated with the development of a species-area curve for bats. For example, what is the appropriate slice of time that should be used when constructing species-area curves—should recent fossils be included in an island's fauna (Pedersen et al. 2006) and should human impacts be factored into species-area curve analyses (Steadman et al. 1984a; Steadman et al. 1984b)? Given the accelerated rate of development and deforestation on several neighboring islands during the last 25 years (e.g., Anguilla, Antigua, St. Maarten; Genoways et al. 2007a; Genoways et al. 2007b; Genoways et al. 2007c; Pedersen et al. 2006), how should conservation officers best utilize species-area curves in their management decisions? Should elevation be factored into species-area curves? Should insectivorous and frugivorous guilds be treated separately?

We will not expand on these particular questions here in any detail, however; we have shown that the inclusion of recent fossils and treating frugivores separately is productive (Pedersen et al. 2005, 2006), but we showed that species-altitude curves do not do as well at predicting bat biodiversity as species-area curves (i.e., northern Lesser Antilles: Genoways et al. 2007a).

As our group has compiled survey data for the Antilles (Genoways et al. 2005; Genoways et al. 2007a; Genoways et al. 2007b; Genoways et al. 2007c; P. A.

Larsen et al. 2006a; Pedersen et al. 1996; Pedersen et al. 2003; Pedersen et al. 2005; Pedersen et al. 2006; Pedersen et al. 2007), the slopes of our published species-area curves have decreased. Others (Davies and Smith 1997; Wilcox 1980) have interpreted these flatter curves to mean that a particular fauna has a propensity for dispersal and colonization, or alternatively, that the fauna in question has a low extinction rate relative to other West Indian animals. Our work has negated the prediction that smaller islands will always have fewer species of bats—*islands in the northern Lesser Antilles basically share the same number of species regardless of island size (Genoways et al. 2007a)*. However, two lines of evidence appear to argue for the propensity of Antillean bats to disperse/colonize. The bat fauna on the smallest island that we have surveyed (Saba) matches the diversity of other islands in the northern Lesser Antilles and is best explained by over-water dispersal by these bats. The Caribbean archipelago exhibits levels of endemism and taxonomic composition that are characteristic of more isolated, oceanic island systems (Hedges 1996). However, none of the species of bats occurring in the northern Lesser Antilles is endemic to the region, and this would argue against isolation and in favor of sufficient dispersal to maintain populations of at least eight species on the majority of islands in the region.

Natural Disasters on Montserrat

Caribbean islands are subject to strong meteorological and geological extremes, the effects of which can be so intense that the exposed biota is commonly reconfigured for years to come (Schoener et al. 2001). Montserrat is no exception. Although earthquakes and volcanic eruptions have been responsible for the greatest loss of human life in the Caribbean (Tomblin 1981), tropical storms and hurricanes are a yearly threat that can devastate the landscape and economy of affected islands; for example, damage resulting from Hurricane Hugo amounted to the loss of nearly five years of Montserrat's gross domestic product (UNDRO-PCDPPP 2001).

Hurricanes and volcanic activity differ fundamentally in both their immediate and long-term effects on ecosystems. Typically, hurricane-force winds strip the standing fruit crop and defoliate trees, reducing primary production and leaving fruit bats to forage on harder, more robust fruits that may have survived the initial wind damage, or to shift food choice, or to starve to death (see Gannon and Willig, chapter 10, this volume). We have no data concerning how strong storms impact insectivorous bats or insect communities on Montserrat, but extensive flooding and landslides associated with hurricanes impact the general landscape and biota. With regard to roost sites, severe storms often knock down older cavity-rotted trees, thereby destroying roost sites for tree-cavity and foliage-roosting species. It is unlikely that hurricanes are capable of directly damaging cave roosts that are located inland; however, obvious storm

surge effects were noted by one of us (SCP) in a sea cave at Rendezvous Bluff on Montserrat due to Hurricane Lenny (1999).

The ecological effects of hurricanes contrast sharply with those of pyroclastic eruptions (landslides of superheated rock, gas, and volcanic ash [tephra] capable of 400 km/h and 300–500°C) produced by the Soufrière Hills volcano that incinerated, suffocated, or buried everything in their paths. Gases vented from the volcano on Montserrat generated acid rain that adversely affects terrestrial vertebrates (e.g., blistering of frog skin and eyes), vegetation, and groundwater, thus affecting the aquatic life in the rivers and streams (transitory pH of 2–3 in many streams). Unconsolidated volcanic ash eventually forms massive mudflows (lahars) so extensive that they have filled entire valleys and have buried Montserrat's abandoned capital, Plymouth. Over the last decade, repeated eruptive events have covered substantial portions of the southern half of Montserrat with sterile volcanic ash (fig. 11.2). Such absolute destruction of watercourses, foraging areas, and roost sites has insured that primary production and food-web dynamics in these affected ecosystems will remain in this disrupted state for the foreseeable future. Of interest here is that variation in the local fruit bat populations has accurately reflected the environmental damage caused by each natural disaster.

Hurricane Hugo and Its Effects

On September 13, 1989, Hurricane Hugo officially became the sixth hurricane of the season, with sustained winds of 224–240 km/h (category 4) and gusts over 290 km/h. Hurricane Hugo was a classic Cape Verde hurricane that moved across the Atlantic Ocean and then around the Caribbean for 12 days, killing 49 people, injuring hundreds of others, severely damaging Dominica, Guadeloupe, Montserrat, and Puerto Rico, and causing more damage than any other hurricane on record up to that time. Hugo hit Montserrat on September 17 near midnight with 224 km/h winds that left the vast majority of Montserratians homeless. Hugo devastated forested areas on Montserrat with near-complete canopy defoliation, and 20% of the large trees were either uprooted or severely damaged/broken, not unlike damage sustained on Puerto Rico (Stuedler et al. 1991; Walker 1991). One of us (SCP) lived on Montserrat in 1993–1994 and made numerous inquiries as to the environmental damage incurred by Hugo, and by all local accounts, plantation fruit production for human use (papaya, banana, guava, etc.) had mostly recovered by 1993, but many native fruits had not yet recovered because they either came from long-lived trees that had not yet recovered from Hugo, or from smaller trees and shrubs that had been destroyed outright by Hugo.

Before Hugo, two mist-netting surveys were conducted, one by J. Knox Jones Jr. and Robert J. Baker in 1978 (Jones and Baker 1979) and the other by Elizabeth Pierson in 1984 (Pierson et al. 1986; Pierson and Warner 1990). Jones and Baker captured six species (432 bats with 5 nets/2 nights: 86.4 BNN) within a gallery

forest along the Belham River valley replete with cultivated fruit, a flowing stream, and pools of water; Pierson et al. captured seven species (180 bats with 17 nets/3 nights: 11.3 BNN) from a wide variety of forested habitats with native vegetation. The 13-hole golf course that Jones and Baker netted is well known to one of us (SCP), and the very high capture rates of *Artibeus* (200+) may very well be attributed to the fact that the almond and mango trees along Belham River reach their peak fruit production at this time of year (July).

The stream and pools associated with Belham River as it meanders through the golf course were also the main source of fresh drinking water (other than swimming pools) for insectivorous bats (*Molossus molossus*, *Tadarida brasiliensis*), and it is not surprising that large numbers (200+ *M. molossus*) were captured during the two nights of that 1978 study. These two evenings in 1978 represent an unusual opportunity/site and an unprecedented rate of capture (overall, 86.4 BNN; fruit bats, 44.4 BNN; table 11.1). As such, it is difficult to incorporate the 1978 data into the present analysis. However, the 1984 pre-Hugo survey (Pierson et al. 1986) netted at locations that bracket the range of habitat types and elevations surveyed in subsequent years (1993–2005); as a result, the 1984 data are a better estimate of pre-Hugo bat abundance levels and will be treated separately from the 1978 data. Of interest, the 1984 data set (all bats, 11.3 BNN; fruit bats, 10.6 BNN) is comparable to survey work performed by the authors on much larger islands (e.g., St. Vincent, 2005, unpublished data: all bats, 11.3 BNN; fruit bats, 9.1 BNN).

When the first post-Hugo survey (1993–1994) is compared with the pre-Hugo survey of 1984, we observe nearly a threefold decrease in bat abundance (eightfold decrease if the 1978 and 1984 pre-Hugo data are combined; fig. 11.7). Conservatively speaking, the threefold decrease is likely related not only to fatalities that occurred during the storm, but also to starvation resulting from forest defoliation and habitat destruction by the hurricane, and to slow recovery due to the low reproductive potential of some species (Gannon and Willig, chapter 10, this volume).

Hurricane Hugo and the Frugivore Guild

The frugivore guild (Gardner 1977) on Montserrat is composed of *Artibeus jamaicensis*, *Monophyllus plethodon*, *Ardops nicholli*, *Brachyphylla cavernarum*, *Sturnira thomasi*, and *Chiroderma improvisum*. Before Hurricane Hugo, this guild was dominated by *A. jamaicensis* (90% of all fruit bat captures in 1978 and 52% in 1984), but the first post-Hugo survey (1993–1994) indicated that the *A. jamaicensis* population was reduced (32% of fruit bat captures; 17% of all captures; table 11.3). Because *M. plethodon* feeds predominantly on small-sized native and cultivated fruits that are found at higher elevations, it was not surprising that Jones and Baker did not net these bats along the Belham River in 1978. However, the number of *M. plethodon* captured in 1994 (17% of all fruit bat captures) was significantly reduced in comparison to collections at the same sites before Hugo in 1984 (41%; Pierson et al. 1986).