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

Scott C. Pedersen

South Dakota State University, scott.pedersen@sdstate.edu

Gary G. Kwiecinski

University of Scranton

Peter A. Larsen

Texas Tech University, peter.larsen@duke.edu

Matthew N. Morton

Durrell Wildlife Conservation Trust

Rick A. Adams

University of Northern Colorado

See next page for additional authors

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Authors

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

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

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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.

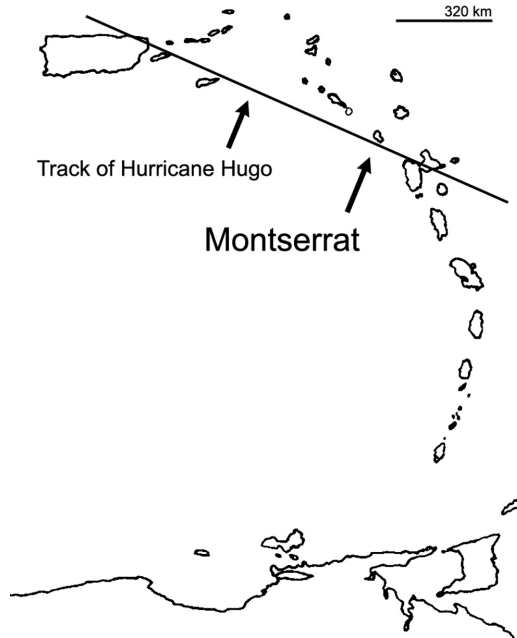


Figure 11.1. Map of the Lesser Antilles showing the position of Montserrat ($16^{\circ}45'N$, $62^{\circ}10'W$).

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.

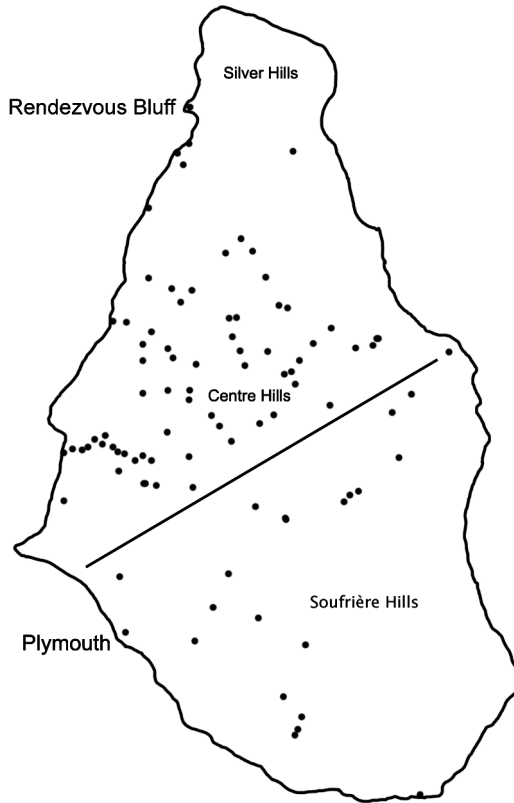


Figure 11.2. Map of Montserrat indicating the three volcanic massifs and all collection localities visited from 1978 to 2006. The region south of the line has been badly damaged if not destroyed by volcanic activity since 1995.

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.

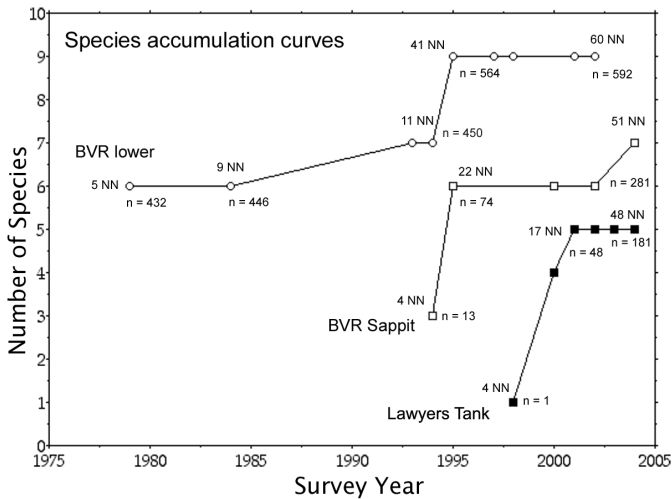


Figure 11.3. Species accumulation curves for three typical netting localities on Montserrat, 1978–2004. Vertical axis is number of species, and horizontal axis is survey year. n = individual bats captured; NN = net-nights.

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

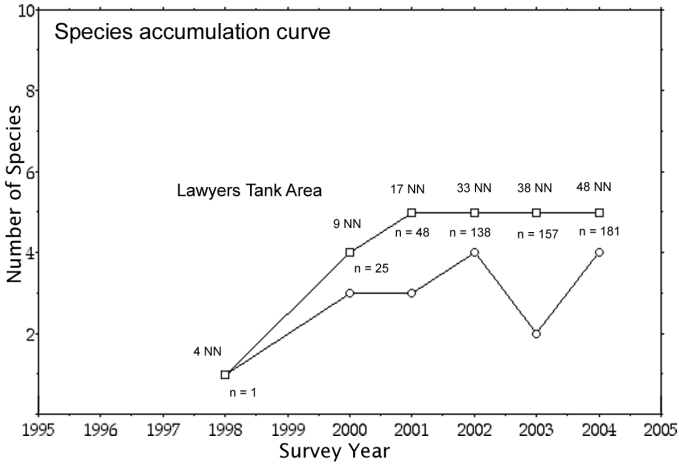


Figure 11.4. Species accumulation curve and species tally for the Lawyers Tank site, 1978–2004 (from fig. 11.3). Vertical axis is number of species, and horizontal axis is survey year. Note that the yearly species tally falls short of the known species inventory at this site. *n* = individual bats captured;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

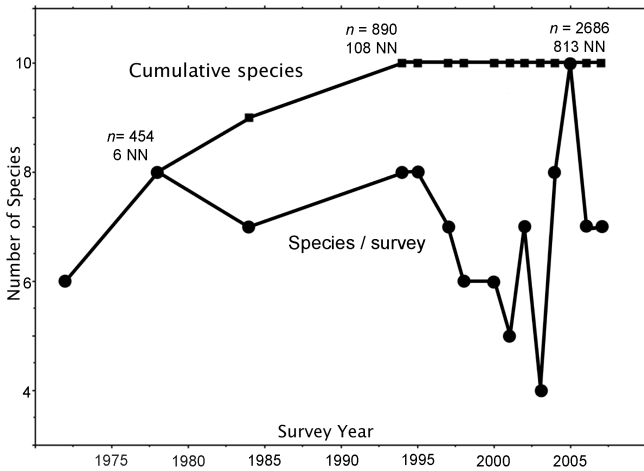


Figure 11.5. Species accumulation curve and species tally for the entire island of Montserrat, 1978–2004. Vertical axis is number of species, and horizontal axis is survey year. Note that the yearly species tally falls short of the known species inventory of the island. *n* = individual bats captured;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

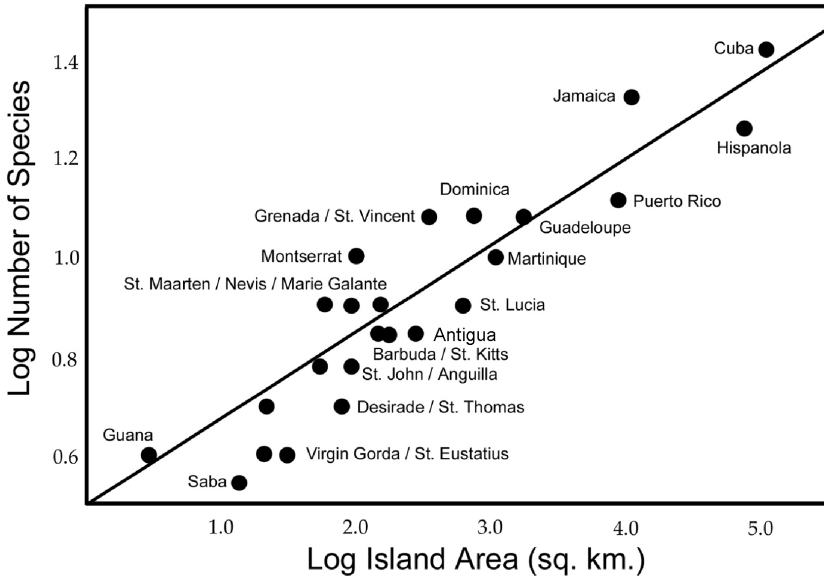


Figure 11.6. Species-area curve (Pedersen et al. 2005 after Genoways et al. 2001). Linear regression of log-transformed data: $y = 0.17x + 0.49$ ($R^2 = 0.81$).

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).

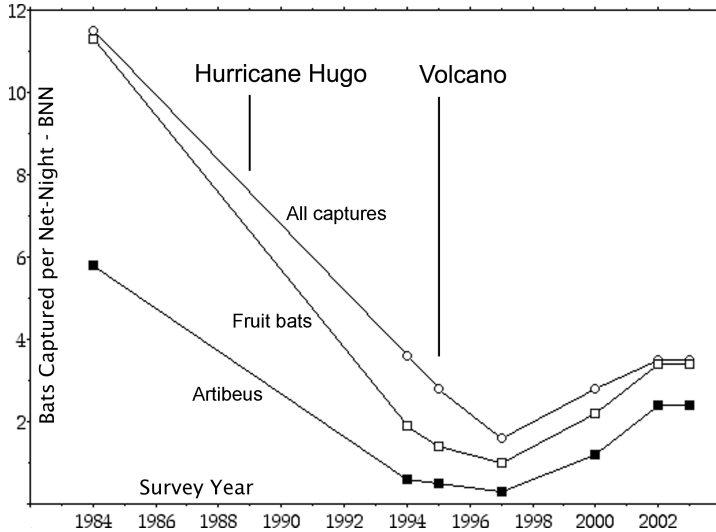


Figure 11.7. Average capture rates. Open circles, all taxa per net-night; open squares, all fruit bat captures per net-night; closed squares, *Artibeus jamaicensis* captures per net-night.

Table 11.3. Relative abundance (% of all fruit bat captures) of four fruit bats estimated from mist-net captures at foraging/commuting sites on five islands in the northern Lesser Antilles

Island	Ajam (%)	Anic (%)	Mple (%)	Bcav (%)	Fruit bat captures	NN	Survey years
Islands in the northern Lesser Antilles							
Saba	41	5	9	45	37	26	2002, 2003
St. Maarten	83	3	1	13	72	78	2002–2004
St. Kitts	45	49	3	2	97	66	1999, 2001
Nevis	55	39	2	4	49	34	2001
Montserrat	65	8	12	15	1757	576	1978–2004
Details for Montserrat							
1978	90	5	0	4	222	5	
1984	52	3	41	5	192	17	
1993–1994	32	5	17	45	142	73	
1995	37	8	28	26	102	72	
1997–1998	31	18	9	42	67	67	
2000–2001	56	9	9	26	252	115	
2002	70	5	16	9	350	102	
2003–2004	70	5	13	11	430	125	

Note: Ajam = *Artibeus jamaicensis*; Anic = *Ardops nicholli*; Mple = *Monophyllus plethodon*; Bcav = *Brachyphylla cavernarum*; NN = net nights.

Five years after Hugo, *B. cavernarum* dominated the frugivore guild (45% of all fruit bat captures). This relative increase in *B. cavernarum* captures was dramatic (from 4% to 45% of fruit bat captures; table 11.3) and may be explained by two aspects of this species' natural history: (1) *B. cavernarum* is omnivorous (Pedersen et al. 1996) and apparently was able to subsist on abundant insects, hardy fruits, and young legumes during the period immediately after the hurricane; (2) *B. cavernarum* lives in caves and rock shelters, which are more hurricane-proof than are the tree roosts typically used by *A. jamaicensis* and *A. nichollsi* on Montserrat (*M. plethodon* could be included here as a de facto "tree bat, as it has been observed in a cave [Happy Hill] on only one occasion, 1993–2006). With respect to the first point, omnivory has clearly been a successful strategy for other vertebrates living in the hurricane belt. For example, substantial population declines in nectivorous and frugivorous birds were noted on St. John, U.S. Virgin Islands, after Hugo (Askins and Ewert 1991), whereas omnivorous and insectivorous bird populations were relatively unaffected in the aftermath of Hugo on Puerto Rico (Waide 1991).

A. jamaicensis and *A. nichollsi* are both stenodermatine frugivores that occur together on many islands of the Lesser Antilles. Typically, *A. jamaicensis* is more abundant than *A. nichollsi*, but this situation was not the case on Nevis and St. Kitts, where the abundance of *A. nichollsi* approached, and in some cases exceeded, that of *A. jamaicensis* (table 11.3); as such, the frugivore guild on Nevis and St. Kitts could bear further study. However, as on other nearby islands (St. Maarten, Saba), *A. nichollsi* is not common on Montserrat (3–18% of all frugivore captures; combined years average 8%) and is often encountered less frequently than either *B. cavernarum* or *M. plethodon* (table 11.3, fig. 11.8). Therefore, it is difficult to discern any real trends in their population with regards to the affects of either Hurricane Hugo or the volcanic crisis on Montserrat.

On Puerto Rico, populations of *Stenoderma rufum* (a close relative of *Ardops*) decreased immediately after Hugo. Whereas the *A. jamaicensis* population rebounded after two years, the *S. rufum* population did not (Gannon and Willig 1994). With respect to *A. jamaicensis*, this rebound may be due more to the ability of bats to disperse across the larger landmass of Puerto Rico into unaffected regions temporarily, rather than due to some unique aspect of their reproductive physiology or ecology per se. This transient relocation from damaged forests was not an option available to bats on the smaller island of Montserrat. It would have been very interesting to monitor and compare the recovery of these matched frugivores on two islands that differed greatly in size and degree of habitat destruction; however, eruptions of the Soufrière Hills volcano on Montserrat in 1995 terminated/complicated any subsequent comparisons. That being said, *A. jamaicensis* seems to be the most capable of rapid recovery on both islands, an observation that will be discussed below.

Although we have single captures of both *Chiroderma improvisum* and *Stur-nira thomasi* on Montserrat in 2005, *C. improvisum* had not been netted on Mont-

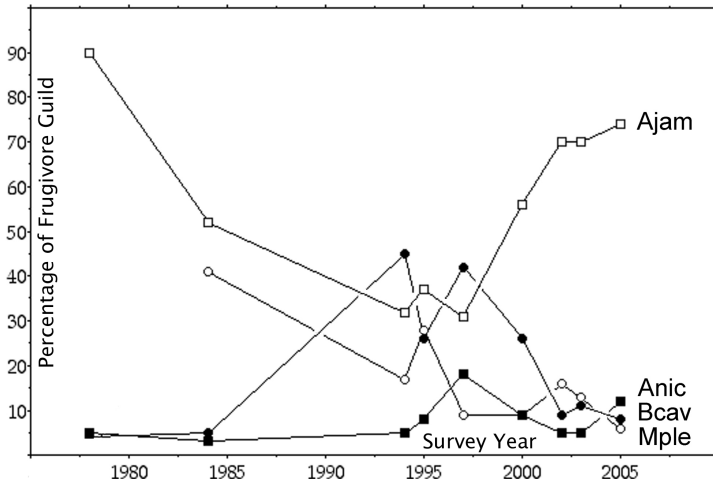


Figure 11.8. Frugivore guild composition. *Ajam*, *Artibeus jamaicensis*; *Anic*, *Ardops nichollsi*; *Bcav*, *Brachyphylla cavernarum*; *Mple*, *Monophyllus plethodon*.

serrat since 1984, and we had only the single record of *S. thomasi* from 1994. In the intervening years, 1994–2004, we caught neither taxon and entertained the idea that perhaps both *C. improvisum* and *S. thomasi* had been extirpated by volcanic activity. In retrospect, these musings were naïve, and it is most likely that these two species had simply become so rare as to have become “invisible” to our mist-netting efforts (R. J. Larsen et al. 2005; R. J. Larsen et al. 2007).

Fenton et al. (1992) demonstrated that phyllostomid bats are useful indicators of habitat disruption; they observed a 21% decrease (from 4.20 to 3.29 BNN) in phyllostomid capture rates in a comparison between undisturbed with disturbed habitats in Akumal, Mexico. Although a comparison of Neotropical logging and hurricane damage may not be entirely appropriate, island populations of fruit bats would appear more susceptible to habitat disruption than are mainland populations (Barlow et al. 2000). Indeed, if similar contrasts between pre- and post-Hugo surveys are made using comparable data collected on Montserrat, it would appear that capture rates on an island may decrease by as much as 66% after a natural disaster (table 11.1).

Hurricane Hugo and the Insectivore Guild

The chiropteran fauna of Montserrat includes three insectivores (*Natalus stramineus*, *Tadarida brasiliensis*, *Molossus molossus*), and one insectivore/carnivore (*Noctilio leporinus*). Of these, *T. brasiliensis* and *N. stramineus* are known primarily from cave surveys (Morton and Fawcett 1996; Pedersen 1998). Neither species was recorded during the two pre-Hugo surveys, but this is not too surprising given that no *N. stramineus* has ever been mist-netted on Montserrat

in over 2,600 captures. *T. brasiliensis* are far more abundant than mist-netting data would suggest, as they typically forage above the canopy (based on visual observations and unpublished acoustic data collected by MNM and SCP). *M. molossus* is an abundant commensal species that is commonly netted over pools and streams (30–40% of all captures 1993–1995). *M. molossus* quite probably benefited from Hugo given the abrupt increase in standing water and insects and a wealth of newly evacuated/ruined houses that could be used as roosts.

Numerous fishing bats (*Noctilio leporinus*) were commonly netted over the Belham River in 1978, 1994, and 1995, but one individual was netted in a deep protected ravine in 1984 (Hope Springs, 900 m elevation). The fact that the Hope Springs site was 1.5 km distant from the nearest foraging area suggests that there was a *N. leporinus* roost site somewhere in that ravine. *N. leporinus* was commonly observed taking prey from the surface of the pools along the Belham River and from the surf line along the Old Towne Beach in 1994. Although readily netted, these bats have never been captured in large numbers on Montserrat—the highest observed activity of these bats was recorded in 1994–1995 (post-Hugo, prevolcano) along the Belham River.

Eruptions of the Soufrière Hills Volcano and Its Effects

The most recent period of tectonic activity on Montserrat began in 1994, and although these early quakes did little more than release gas and steam, one of us (SCP) experienced one of the largest preeruption earthquakes in June 1994. One year later, steam and ash venting intensified, and the first large eruption that delivered ash across the lower portion of the island occurred in August 1995. Subsequent eruptions exhibited a cyclic pattern of dome growth and collapse attended by pyroclastic flows. Pyroclastic flows are fast-moving clouds of superheated gas, ash, and rock (tephra) that travel at a wide range of speeds of up to 150 km/h, gas temperatures range from 100°C to 800°C, and probes have recorded temperatures of 300°C at a subsurface depth of 15–20 cm three to four days after a large flow (Montserrat Volcanic Observatory staff, pers. comm.; Cole et al. 1998). There have been several eruptive phases (1995–1998, 1998–1999, and 1999–present), and a few individual events deserve mention.

On June 25, 1997, huge pyroclastic flows surged down Mosquito ghaat on the northeastern flank of the volcano, devastating the villages of Harris, Bramble, Bethel, and Farms and leaving 19 people dead. In all likelihood, this massive flow also destroyed the rock shelter used as a roost by *B. cavernarum* and presumably *M. plethodon* at the head of Mosquito ghaat in an old volcanic vent (Morton and Fawcett 1996). Throughout 1997 major pyroclastic flows spread down the western and eastern flanks of the volcano, burning the airport on the east coast and causing significant damage in the capital of Plymouth on the west coast of the island. Two of the authors (GGK, SCP) and their colleague Karen Hadley experienced 8 to 9 hours of ash fall during the major dome collapse of July 29, 2001. Approximately 45 million cubic meters of the

dome (150 m of elevation) was removed by this blast, and strong winds blew this ash up to Puerto Rico and the Virgin Islands some 400 km to the northwest. Environmental damage to our remaining survey sites (5 to 15 cm of ash) for that season led us to evacuate the island. On July 12, 2003, one of the largest dome collapses occurred (120+ million cubic meters), with vertical explosions that pushed ash up to an altitude of 15 km. Numerous eruptions of varying sizes have occurred since then, and our field crew experienced ash fall during the small-to-moderate event of July 18, 2005, which spread ash across the lower two-thirds of the island.

Direct Effects of Volcanic Ash

Volcanic ash fall has several affects on forest ecosystems. The dry volcanic ash itself is easily blown off plants, but if it becomes wet or lands as a mud rain, the sheer weight of ash easily crushes small to mid-sized plants and can break limbs off larger plants. Sulfur dioxide gas is emitted during large explosive eruptions and is easily converted to sulfuric acid (H_2SO_4) that condenses rapidly into acid rain, which causes extensive leaf perforation and necrosis and contaminates water sources (McGee et al. 1997). This damage to the forests has dramatically altered the breeding dynamics of the endangered Montserrat oriole (*Icterus oberi*), which nests in *Heliconia* and banana plants, with both types of plant being quite vulnerable to ash fall (Hilton et al. 2003). Chronic effects of ash on animals include ash-related conjunctivitis (Hayward et al. 1982) and blindness in birds (Martin 1913, quoted in Pyke 1984). Volcanic ash also causes respiratory problems in cattle and horses (Kwiecinski et al. 2005; Rees 1979), and hair loss/swollen eyes in small mammals (Andersen and McMahon 1986; Pyke 1984). Volcanic ash also is harmful to insects, as it blocks their spiracles and causes abrasion and excessive dehydration (Edwards and Schwartz 1981). Due to their position in the food chain, insects and their mortality rates may effect changes in the populations of insectivorous bats, birds, and other animals (Foster and Myers 1982).

Apart from having habitat destroyed by pyroclastic flows, the bats of Montserrat have also endured near misses by hurricanes Luis (1995), Georges (1998), Jose, and Lenny (1999), and two drought years (2000, 2001). As a result, the 1995–2005 data are confounded by the cumulative effects of several different natural disasters that make it difficult if not impossible to identify the specific impact of any one disaster on the bat populations. However, we have some data that provide clues as to specific effects, and we can start the discussion with three issues: reduction in land area, destruction of foraging habitat, and destruction of roost sites.

Effective Reduction in Land Area

In comparison to many islands in the northern Lesser Antilles, Montserrat is already quite small (100 km²). Before the onset of volcanic activity in 1995, the whole island was covered with some form of vegetation, ranging from xeric

scrub in the upper windward quadrant of the island to dry evergreen/secondary rain forest (Beard 1949) in the deeper ravines and protected valleys. Abandoned agricultural lands were typically covered with thorny shrub woodland. From the perspective of a fruit bat, however, we estimate that no more than 70% of the island supported forested areas that would provide protection from the wind for foraging or commuting bats. Pyroclastic flows eventually sterilized the eastern and western flanks of the volcano by burning or burying all but the largest trees, while ash fall and mudflows severely damaged the dry forest on the northern flank of the volcano. As a result, fruit bats were displaced into the relatively undisturbed habitats located in the midnorthern portion of the island (Centre Hills)—approximately 50% of their original range.

Initial competition for food and roost sites (especially tree roosts) is thought to have been intense through the earlier eruptions of 1997–1998, which resulted in a great deal of stress on the bats. The success of *Brachyphylla cavernarum* after Hurricane Hugo and perhaps very early on during the volcanic crisis (fig. 11.8) is probably related to this omnivore's aggressive nature and its ability to monopolize and defend ephemeral and potentially limited food resources. Indeed, *B. cavernarum* is a robust, aggressive species, and large feeding mobs of *B. cavernarum* displace other bats (e.g., *Artibeus jamaicensis*) from feeding trees (Morrison 1979; Nellis and Ehle 1977; pers. obs. by authors).

Destruction of Foraging Sites

By 1998 pyroclastic and mudflows from the Soufrière Hills volcano had incinerated the hamlets of Molyneux and Dyers at the upper end of the Belham valley, and mudflows had also begun to bury the river and golf course at the lower end of the Belham valley under 6 to 7 m of pumice and volcanic debris (the loss of the delightfully quirky 13-hole golf course was clearly a setback for the Montserratian golfing community). The lower portions of the Belham River had been prime foraging habitat for fishing bats (*Noctilio leporinus*), but we did not capture any *N. leporinus* between July 1997 and June 2004 despite directed netting and spotlighting efforts across the island, leaving us to wonder if this species had been extirpated. However, during the 2004 and 2005 surveys, we netted them again in small numbers 2 km from the ocean in a deep ravine that holds the Sappit River, a tributary of the Belham.

In 1993–1994 one of us (SCP) spent a great deal of time in the Paradise Estate, which is located on the windward flank of the volcano and was partitioned into sections by three deep ravines (Mosquito, Tuitt, and White ghauts) each containing a small seasonal stream. Mosquito ghaut was the largest of these and was netted frequently in 1994. This ghaut was filled with dry evergreen/deciduous rain forest, natural and cultivated fruit trees, and many large fern trees. *Chiroderma improvisum* and *Sturnira thomasi* were both captured at this unique site, and at least five species of bats (50% of the species on the island) were commonly netted there in late 1994. This location has since been mostly

obliterated by several large pyroclastic flows that have come down Mosquito, Tuitt, and White ghauts over the last ten years.

Vegetation is likely to regenerate on the less heavily damaged areas fairly quickly once volcanic activity has ceased. Indeed, some areas covered by shallow pyroclastic flows are beginning to support sparse vegetation on the northern flanks of the volcano, but we surmise that these outcrops are derived from rootstock that was not destroyed by previous eruptions. (Note: Krakatau erupted in 1883, and the remnant islands [Rakata, Sertung, and Panjang] now exhibit a species-poor mixed forest—see Shilton and Whittaker, chapter 7, this volume; Thornton et al. 1996.) It seems likely that the pyroclastic flows on Montserrat may be revegetated in a shorter period of time than on Krakatau as there is vegetation nearby, and bats and birds are available on Montserrat to readily transport seeds into the damaged areas. In areas that have received airborne ash deposits, the recovery of the forest understory was apparent as early as summer 2000.

Destruction of Known Roost Sites

One can imagine that the loss of roosting sites on a small island such as Montserrat could dramatically effect changes in the bat population; however, given our incomplete data and the multifactorial nature of this drawn-out natural disaster we will limit our discussion to the destruction of known roosts on the island.

The *Brachyphylla cavernarum* population on Montserrat consists of a single large colony (Morton and Fawcett 1996; Pedersen et al. 1996). *B. cavernarum* populations are vulnerable to catastrophic loss and/or predation due to their use of large cave roosts; indeed, this large colony probably served as a food source for early Amerindians on Montserrat (ca. 200 AD; Steadman et al. 1984a; Steadman et al. 1984b; Wheeler 1988). Presence/absence data collected throughout 1993–1995 strongly suggest that the colony of *B. cavernarum* on Montserrat alternated between a large rock shelter in Mosquito ghaut (above the Paradise Estate) on the northeastern flank of the volcano and the Rendezvous Bluff cave complex at the north end of the island (Pedersen et al. 1996). For several weeks at a time, each location served as a regional shelter from which the colony would visit fruiting trees in the vicinity. We do not have data from 1996, but the Mosquito ghaut roost was probably destroyed by pyroclastic flows in 1997 (and was probably abandoned much earlier due to earthquakes and acid rainfall), leaving Rendezvous Bluff as the only roost site for this large colony of 5,000+ bats. As such, Rendezvous Bluff has been occupied continually since 1997 (pers. comm. with dive operators Wolf Krebs and Bryan Cunningham, who visit the island on a weekly basis; observations by several of the authors), suggesting that no other roost sites for this colony exist on the island.

This Rendezvous Bluff cave system consists of three separate cavities, of which only two have been observed being occupied by *B. cavernarum*. We

have noted that this colony subdivides seasonally in response to the presence/absence of pregnant females and pups in the larger of the two occupied caves, wherein the males relocate to a smaller adjacent cave to the north. We have observed mixed and bachelor roosts of *B. cavernarum* on both Nevis and St. Christopher (Kitts) (Pedersen et al. 2003; Pedersen et al. 2005), but we do not have roost-shifting data for those two islands.

Throughout the Lesser Antilles, early human colonists excavated volcanic sands to be used as aggregate for making concrete for their estate houses and mill operations. These crude mines (tarrish pits) are frequently associated with estate ruins and are often occupied by bats (typically *B. cavernarum*, *Artibeus jamaicensis*, *Monophyllus plethodon*, and *Natalus stramineus*; Genoways et al. 2007b; Pedersen et al. 2003; Pedersen et al. 2005; Pedersen et al. 2006). In 1995 one of us (MNM) discovered two medium-sized tarrish pits situated north of the Belham River in Aymers ghaut and observed a half-dozen *N. stramineus* in these artificial caves. Since then (1995–2005), the number of *N. stramineus* in these neighboring chambers has varied considerably (from 0 to 15), and despite extensive efforts to find *N. stramineus* roosts elsewhere on the island, this site remains the only one on record for Montserrat at present. During surveys performed in 1995–2002, one could easily walk upright into either of these large living-room-sized chambers without hitting one's head on the ceiling. In 2004, both cavities began filling with volcanic ash washed into the caves by heavy rains. The northernmost cavity was half full of sediment in 2005 and will be filled-in over the next few years if this rate of sedimentation continues.

The only known colony (maternity) of *Tadarida brasiliensis* was located in a basalt cliff on the southern coast of the island (Shoe Rock); however, this roost subsequently collapsed, presumably due to seismic activity sometime after 1995, and no animals were observed during a brief search of this outcrop in June 1998.

Volcanic Activity and the Frugivore Guild

Given that bat populations had already been depressed by Hurricane Hugo, it is difficult to gauge the independent effects of volcanic activity. However, bat diversity (fig. 11.5) and bat abundance (fig. 11.7) decreased early in the volcanic crisis (1995–1998) due to the direct or indirect destruction of foraging habitat and roost sites by pyroclastic flows, acid rain, and ash fallout (table 11.3). Yearly species tallies fall short of the known species inventory at individual sites (fig. 11.4) and across the entire island (fig. 11.5), but the decrease in perceived bat diversity across the entire island coincided with the advent of volcanic activity in 1995 (fig. 11.5; low point: 4 species netted in 2003). The species were there, but they had just become so rare that they did not register in our mist-netting efforts. It was during this period that bats began to exhibit several nonlethal, stress-related pathologies—hair-loss (alopecia) and excessive tooth wear (dental attrition). From the low point in 1997 (fruit bats: 1.0 BNN; all

captures: 1.46 BNN), overall capture rates had rebounded somewhat following a very wet spring in 2000, but this was followed by a bad drought in 2001 (as reported by two climatologists on Montserrat: R. Aspin and E. Duberry), which may have suppressed fruit/flower production that year. Regardless, the July 2002 survey met with a great abundance of fruiting trees—several varieties of fig trees that had not been observed to produce a significant fruit set since 1995 were heavily laden with fruit that summer following a very wet spring and a brief cessation in volcanic activity. Fruit bat netting data at stations that have been repeatedly sampled since 1993 indicated that capture rates were 3.4 times greater in 2002 (3.43 BNN) than those during the early eruption phases (1997–1998, 1.00 BNN) and 2.14 times greater than the previous census in 2001 (1.6 BNN). This rather dramatic fluctuation in fruit bat populations is due almost entirely to an increase in both the absolute and relative numbers of *A. jamaicensis* and *M. plethodon* captured (0.09 vs. 0.56 *M. plethodon* captures per net per night; 0.31 vs. 2.39 *A. jamaicensis* per net per night; table 11.3, fig. 11.8).

Guild dynamics throughout this 25-year period are interesting (table 11.3, fig. 11.8): *B. cavernarum* would appear to be a hurricane survivor (which is curious in that it is not broadly distributed throughout the Caribbean: Genoways et al. 2005) but has not done well during volcanic activity; *M. plethodon* and *A. nichollsi* have not been major components of the frugivore guild on Montserrat during these surveys (fig. 11.8). However, these interpretations must be tempered by awareness of sampling artifacts associated with overall low capture rates during the period 1997–2000 (figs. 11.5, 11.7) and the great increase in the *A. jamaicensis* population.

Although there appears to be a four- to five-year lag between disaster and population increase, *A. jamaicensis* would seem to thrive on disturbance, but this may be due simply to their ability to outreproduce their immediate competition when an opportunity presents itself. *A. nichollsi* and *B. cavernarum* are monestrus, producing a single pup per year, and very little is known of the reproductive cycle and reproductive potential in *M. plethodon* (Homan and Jones 1975; Jones and Genoways 1973; Swanepoel and Genoways 1978, 1983). However, *A. jamaicensis* is polyestrus, and females usually undergo two pregnancies per year (Gardner et al. 1991; Handley et al. 1991; Wilson et al. 1991). *A. jamaicensis* is also capable of producing three young per year (not counting twins) if there is no delay in the reproductive cycle (Kwiecinski and Pedersen 2002). Given this higher reproductive potential, populations of *A. jamaicensis* are clearly capable of, and perhaps predisposed to, rapid recovery following large-scale disturbances such as those noted on Montserrat.

In 2002 we noted for the first time serious wounds to the head and neck of a half-dozen lactating female *A. jamaicensis*. We had not observed wounds of this magnitude before 2002 and only rarely in 2004. These wounds included damaged and/or missing ears and eyes, and grossly infected, puss-filled masses about the face and neck. In light of the dramatic increase in *A. jamaicensis*

activity that year, we surmise these wounds were most probably the result of intraspecific squabbles and speculate that animals were fighting over limited resources at roosts and/or foraging sites. Since that time, the *A. jamaicensis* population seems to have leveled off (figs. 11.7, 11.8), and we have not observed damaged *A. jamaicensis* in either of our 2005 and 2006 surveys.

Volcanic Activity and the Insectivore Guild

Molossid bats remain abundant on Montserrat although they typically forage above the forest canopy and are therefore underrepresented in our mist-netting surveys (~0.8 BNN). *Molossus molossus* is a common human-commensal species that is commonly found in human residences throughout the region and that probably benefited from both Hugo and the volcanic activity by moving into recently abandoned/damaged homes and buildings across the island. For example, we have observed small groups of *M. molossus* on numerous occasions in both occupied and unoccupied homes and ruins across the island during our roost searches. We also located a maternity colony of *Tadarida brasiliensis* ($n = 1,000+$) in an abandoned concrete-block (unfinished) home in the village of Lee's in 2005. Previously, the only known colony of *T. brasiliensis* was located in deep cavities in a basalt cliff on the southern coast of the island (Shoe Rock, 1995 survey).

With regards to the fishing bat, *Noctilio leporinus*, we netted one in 2004 and two in 2005 above pools along the lower portions of the Sappit River, a tributary of the Belham. We radio-tagged and tracked both bats in 2005 in an unsuccessful attempt to locate a *N. leporinus* roost in that drainage. Much of that area was severely damaged in 2006 by large mudflows, leaving the status of *N. leporinus* very much in doubt at the present time.

Sublethal Pathology Associated with Volcanic Activity

We have documented dramatic increases in sublethal pathologies coincident with the onset of volcanic activity on Montserrat, including alopecia, increased ectoparasite loads, and abnormal tooth wear in adult *Brachyphylla cavernarum*, *Artibeus jamaicensis*, and *Ardops nichollsi*. We will publish a full accounting of these various pathological conditions at a later date.

Alopecia

Generally, hair loss in mammals is a multifactorial phenomenon, with mineral deficiencies, plant toxins, external parasites, lactation, and general stress working alone or in concert as likely causal agents (Noxon 1995). Hair loss in phyllostomid bats is not uncommon, and we have noted that lactating females often display small bald patches about the head and abdomen during our work throughout the Lesser Antilles. However, hair loss was not observed in any of the approximately 1,000 bats captured on Montserrat before 1997.

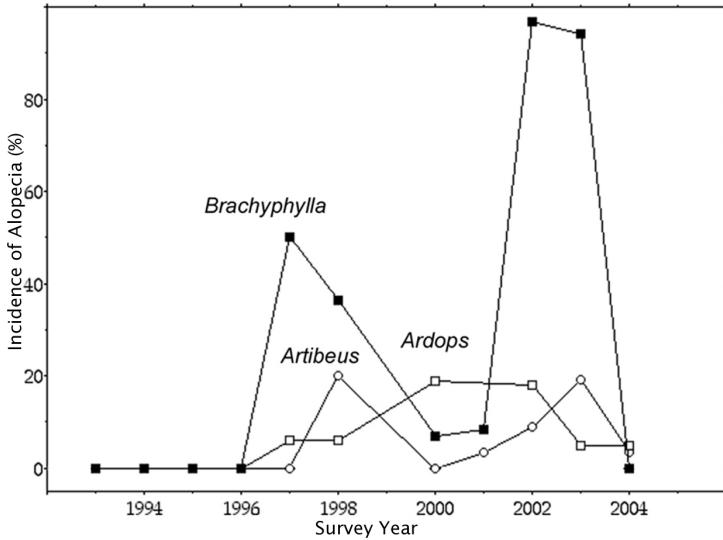


Figure 11.9. Incidence of alopecia, 1994–2004.

In the first survey performed after the eruptions began (1997), *A. nichollsi* and *B. cavernarum* showed varying degrees of hair loss, ranging from small bare patches on the neck and shoulders to complete depilation, and by 1998, almost all male and female *B. cavernarum*, *A. jamaicensis*, and *A. nichollsi* exhibited some degree of hair loss (fig. 11.9; Adams and Pedersen 1999; Morton and Fawcett 1996; Pedersen et al. 1996; Pedersen et al. 2003; Pedersen et al. 2005).

The incidence of hair loss has varied most dramatically over the years in *B. cavernarum* (fig. 11.9), with peak occurrences coinciding with two periods of great stress: 1997–1998 during the initial eruptions, and 2002–2003 coincident with both the great increase in the *A. jamaicensis* population in 2002 and the large eruption of July 2003, when at least 75% of the *B. cavernarum* roosting in Rendezvous Bluff cave were nearly or totally bald. Hair loss also has been observed, but to a lesser extent, in tree/foilage-roosting bats, *A. jamaicensis* and *A. nichollsi*. Hair loss has not been observed in rats, domestic livestock, the nectarivorous bat *M. plethodon*, or any of the animalivorous bats on Montserrat (*N. leporinus*, *N. stramineus*, *T. brasiliensis*, and *M. molossus*), suggesting that alopecia is related to ash ingestion by dedicated frugivores.

Whether ash is ingested during feeding and grooming, or aspirated during foraging and roosting, fruit bats cannot help but introduce large amounts of volcanic ash into their respiratory and digestive systems. The mineral content of the ash on Montserrat has been shown to contain silicon dioxide with aluminum, iron, and calcium oxides (Wilson et al. 2000). Iron and calcium oxides are known to compete with dietary zinc in the intestinal wall (Noxon

1995) and may have triggered zinc-deficiency-related alopecia in these affected animals. Antigua, Nevis, and St. Kitts have received wind-blown ash from Montserrat during many of the larger eruptive events (1997–2004), and we might expect to see zinc-deficiency alopecia in those populations as well. We have observed that a small number (5–10%) of *B. cavernarum* on Nevis and St. Kitts exhibited varying degrees of hair loss in 1999 (Pedersen et al. 2003; Pedersen et al. 2005), but many of the females were lactating or pregnant. Several years later, in 2001, no *B. cavernarum* (lactating or not) exhibited hair loss on either Nevis or St. Kitts (Pedersen 2001; Pedersen et al. 2003; Pedersen et al. 2005). We cannot rule out zinc deficiency as the primary causal agent, but this would be a simple matter to test in a controlled situation. There may be some threshold effect with respect to how stress and ash ingestion interact and subsequently influence the incidence and duration of alopecia.

On the adjacent island of Nevis, we observed transitory hair loss in *B. cavernarum* following Hurricane Georges in 1998. There was extensive defoliation following that hurricane, and one of the first trees to recover was the false tamarind (*Leucaena leucocephala*), a shrubby legume with pink/yellow puffball flowers that produces a natural depilatory toxin (mimosine), which is known to cause hair loss in livestock when consumed in large quantities (Brewbaker 1987). During periods of drought, posthurricane damage, or heavy ash fall, *B. cavernarum* will resort to alternate forage such as legume seedpods and citrus fruits (Pedersen et al. 1996; Pedersen et al. 2005), but it is unknown if *B. cavernarum* forages upon false tamarind during times of stress when preferred foods have been destroyed or are unavailable. This mimosine-ingestion hypothesis is something that could be easily studied in a controlled situation to either support or to rule out this interesting possibility.

External Parasites

The permanent occupancy of the Rendezvous Bluff cave complex by *B. cavernarum* since 1997 has resulted in levels of external parasites that are significantly higher than any recorded previously (Jones and Baker 1979; Morton and Fawcett 1996; Pedersen et al. 1996). Indeed, the ectoparasite load on *B. cavernarum* has gone from negligible in 1993–1994 (Pedersen pers. obs.) to what can only be described as “heavily infested,” with *all* mist-netted bats and bats taken from the cave walls themselves being covered with as many as 15–20 streblid flies, 2–3 nycterbiids, and several dozen ticks and mites. The walls of this cave have been literally covered with insects and insect larvae during each survey since 1997. In comparison, the large *B. cavernarum* colony in Bats Cave on the neighboring island of Antigua are also parasitized, but exhibited neither the extreme parasite loads (<10 streblid flies, *Trichobius*; <5 wing mites on each bat) nor the extensive hair loss noted in *B. cavernarum* on Montserrat during this same period (Pedersen et al. 2006). One plausible explanation for the alterna-

tion between roost sites on Montserrat before 1995 may have had more to do with escaping heavily parasitized roosts than tracking food resources across the island. Given that both male and female *B. cavernarum* on Montserrat exhibit alopecia, it is quite possible that hair loss is due to excessive grooming in response to high ectoparasite loads, as much as to any other physiological stress associated with ingestion of volcanic ash or lactation.

Abnormal Tooth Wear in Fruit Bats

Tooth-wear patterns may reflect differences in craniodental specializations, chewing patterns, and simple wear due to age (Freeman 1988). Since the onset of volcanic activity in 1995, however, we have examined the dentitions of 1,482 bats, of which 1,299 were fruit bats, and have recorded the acute onset of abnormal damage to the teeth in 330+ fruit bats (~25%) coincident with the ingestion of ash-laden food or the incidental ingestion of ash during grooming. To put this in perspective, only 3 of 641 (<1%) fruit bats examined by Pedersen in 1993 and 1994 exhibited tooth damage, and these three *Artibeus jamaicensis* were obviously very old, heavily scarred bats whose worn teeth were much like what we have encountered in other old bats netted throughout the region.

The degree of tooth wear varies among fruit-eating bats but may reflect minor differences in food selection (e.g., fruit stickiness or ash-carrying capacity), food-handling ability, and/or grooming behavior. Certainly, taxa vary with respect to the degree of bodily contact with ash-contaminated surfaces during feeding. For example, *Monophyllus plethodon* employs hovering flight while drinking nectar, and has very limited contact with fruit as it has a habit of biting into small fruits and allowing the weight of its body to carry the fruit away from the stem. In addition, one of the favored fruits of *M. plethodon* on Montserrat (and elsewhere in the region) is *Piper* sp., whose vertical fruits do not seem to accumulate much ash (SCP pers. obs.). Regardless, actual contact with ash-covered surfaces is minimal, which may explain why none of the 108 *M. plethodon* captured between 1995 and 2006 exhibited abnormal tooth wear. Furthermore, we have not observed abnormal tooth wear in any of the animalivorous bats due to their limited amount of contact with ash-covered surfaces.

In contrast, *A. jamaicensis*, *A. nichollsi*, and *B. cavernarum* often fly directly onto the ash-laden crowns of trees, thus putting themselves in direct contact with ash as they forage among ash-laden fruit, leaves, and flowers (Gannon et al. 2005; Kunz and Diaz 1995). *A. jamaicensis*, *A. nichollsi*, and *B. cavernarum* also consume papaya and mango fruits, which cover these bats with sticky fruit juice that accumulates volcanic ash and must be subsequently groomed off the pelage. In each instance, these bats undoubtedly ingest large amounts of ash, and it is in these taxa that we observed the greatest amount of damage to the teeth (fig. 11.10; full data to be published elsewhere).

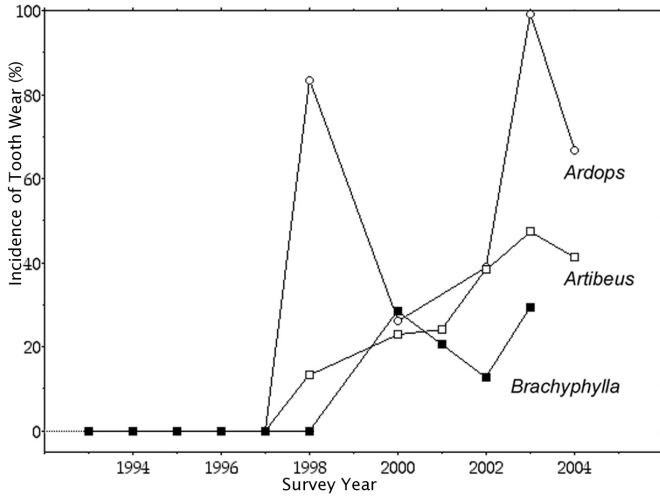


Figure 11.10. Average incidence (%) of dental wear, 1994–2004.

Since 1997 the incidence of dental attrition has varied considerably. The erratic incidence of abnormal tooth wear in *A. nichollsi* and *B. cavernarum* (fig. 11.10) may be a sampling artifact related to their relatively small contribution to the fauna; however, we do have sufficient capture data to make comments on the incidence of abnormal tooth wear in *A. jamaicensis*. That is, 222 of 902 *A. jamaicensis* collected during the period 1997–2006 exhibited abnormal tooth wear (average ~25%; peak of 45% in 2003). We have recorded a steady increase in the percentage of affected *A. jamaicensis* since 1998, presumably influenced by the retention of older animals in the population that lived through heavy ash-fall years (fig. 11.10). However, coincident with the recruitment of young animals into the population and the great population increase of 2002–2003, there was a slight decrease in 2004 in the overall severity of tooth wear (41%; fig. 11.11). The degree of abnormal tooth wear is negatively correlated ($R^2 = -0.368$) with proximity to the volcano suggesting a “dosage effect”—animals that live in heavily ash-polluted environments are the most affected (fig. 11.12).

The observed damage to the dentition ranges from moderate blunting of all teeth in a uniform manner (scale values 1–2; fig. 11.11) to the ablation of entire enamel crowns with the subsequent infection and abscess of the underlying pulp cavities (scale values 6–8). Under high magnification (fig. 11.13) the occlusal surfaces of the teeth do not exhibit gouges, pits, or cracks, but rather, they appear highly burnished. These wear patterns are not consistent with thagosis (self-sharpening); ablation of these teeth is due to the abrasive insult of fine volcanic ash that is taken into the mouth during feeding and grooming activities.

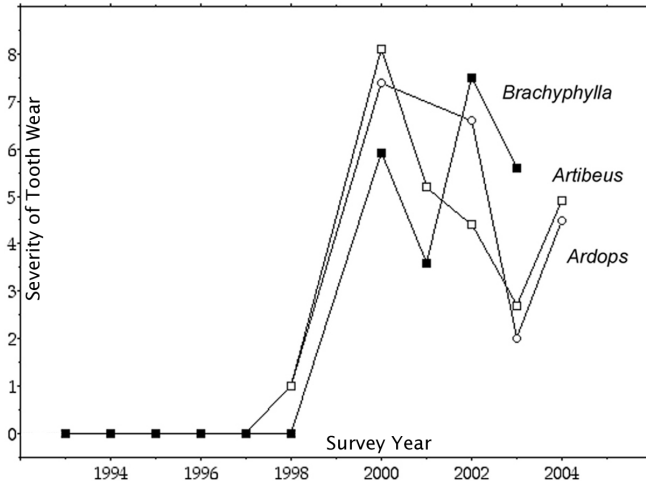


Figure 11.11. Average severity of tooth wear, 1994–2004. Y-axis increments are demonstrated photographically in fig. 11.13.

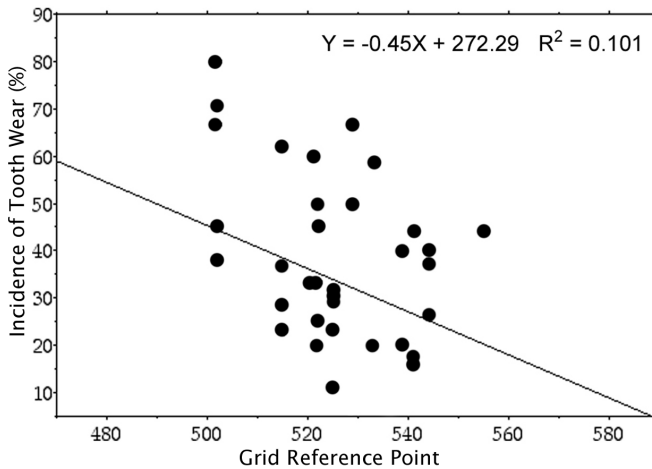


Figure 11.12. Tooth wear in *Artibeus jamaicensis* as a function of distance from the volcano, 1997–2004. The x-axis corresponds to the 1 km grid-reference system utilized on the 1989 British Ordinance Survey map of Montserrat. The Soufrière Hills volcano is located at grid 470 at the far left side of the figure—increasing values on the x-axis indicate greater distance from the volcano (i.e., grid 570 = 10 km distant from volcano). The y-axis reflects the incidence (%) of captured *A. jamaicensis* that exhibited abnormal tooth wear (see fig. 11.10). The y-axis scale is represented photographically (albeit in *Brachyphylla cavernarum*) in figure 11.13.

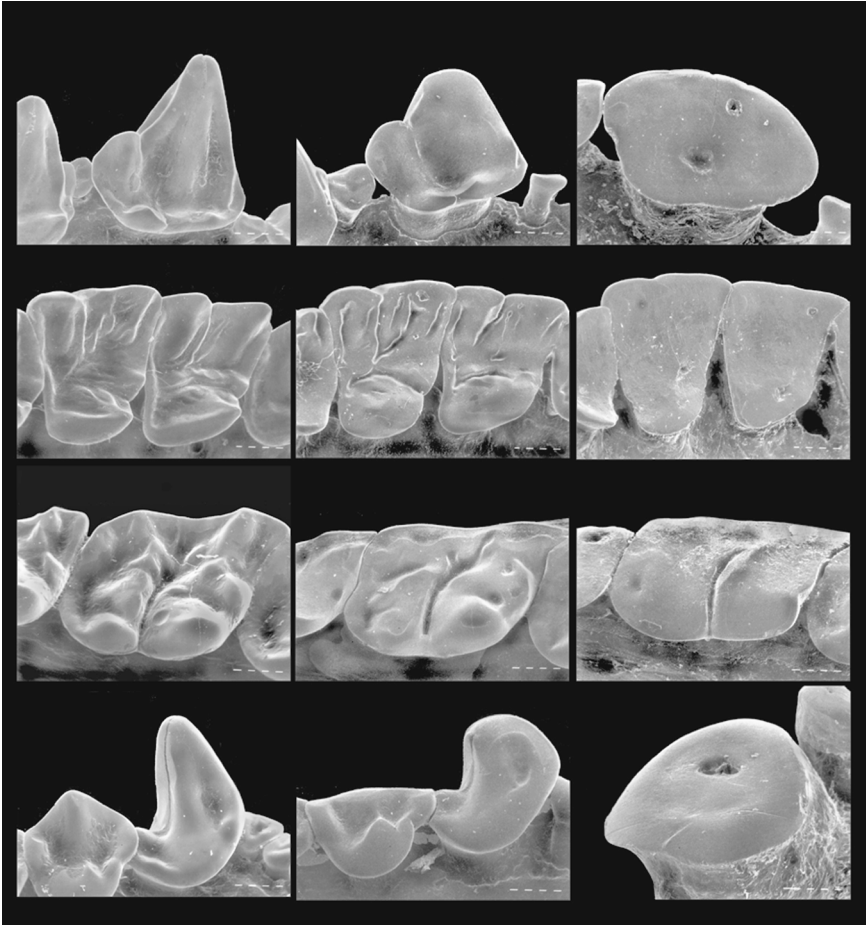


Figure 11.13. Representative scanning-electron micrographs of abnormal tooth wear in *Brachyphylla cavernarum* on Montserrat. *Left*, negligible wear (y-axis values of 1–2 in fig. 11.11). *Middle*, moderate wear (y-axis values of 3–5 in fig. 11.1). *Right*, heavy wear (y-axis values of 6–8 in fig. 11.11); teeth are worn down to or below the gum line, often with perforation into the pulp cavity. *Top row*, upper right canine; *second row*, upper right molar; *third row*, lower right molar; *bottom row*, lower right canine. Each frame is approximately 5 mm across.

Discussion

Understanding the ecological and evolutionary mechanisms responsible for patterns of faunal distribution among island archipelagos is a long-standing goal of biogeographic research. Certainly, the severity and frequency of environmental disturbance has considerable influence on biodiversity. The intermediate disturbance hypothesis (Connell 1978) proposed that biodiversity is

highest when disturbance is neither too rare nor too frequent. At intermediate disturbance levels, environmental heterogeneity is maintained, thereby maximizing opportunities for the coexistence of potentially competing species. In the eastern Caribbean, however, disturbance is very much a part of the evolutionary fabric—what appears to the human eye and to human interests as a natural disaster may be perceived by the biota on any one of these hurricane-dominated volcanic islands as perfectly “normal,” evolutionarily speaking. Indeed, one of our most interesting findings is that, despite great fluctuations in bat abundance, none of the ten species of bats known from Montserrat has been lost despite the impact of over ten years of volcanic activity and several recent hurricanes. Should we interpret this to mean that the concerted efforts of these two natural disasters are insufficient to impact biodiversity on Montserrat? Is there a disturbance frequency/severity threshold for bats, and if so, how does it relate to our interpretation of species-area curves (fig. 11.6)?

On one hand, Montserrat’s environment may be more resilient to these natural disasters than other islands in the northern Lesser Antilles, as it is one of the least developed islands in the region. As a result, recent human impact on the environment is much less than has been observed on other islands. Whereas sugarcane fields have stripped the native vegetation at low to moderate elevations on many of the other islands, agricultural development during the last 50 years has been limited to small farms and gardens on Montserrat. In recent years, uncontrolled housing and tourist development have removed native vegetation and lowered the water table to the extent that streams no longer flow on islands such as St. Barts and St. Martin/St. Maarten. Fortunately for the biota on Montserrat, tourist development has been limited to a few small hotels and guesthouses.

On the other hand, are we looking in the wrong place for answers? Rodríguez-Durán and Kunz (2001) indicated that the diversity and availability of various resources underpinned the patterns of biodiversity that they observed. Cave roosts are clearly an important resource on small islands, a fact that is underlined by the observation that extinction events throughout the Antilles are most prevalent among obligate cave-dwelling bats (Morgan 2001). We do not have a fossil record of bats on Montserrat; however, Steadman et al. (1984a) reported three species of cavernicolous bats in the fossil record on the neighboring island of Antigua that no longer occur on that island—*Pteronotus parnellii*, *Mormoops blainvillei*, and *Phyllonycteris major* (4300 to 2560 BP)—all of which have occupied broader geographic ranges in the past than now (see discussion in Pedersen et al. 2006). Caves may greatly benefit their inhabitants because they provide a robust shelter against storms (Pedersen et al. 1996); conversely, they may doom their inhabitants if the cave is destroyed suddenly (e.g., by earthquake or pyroclastic flow; Genoways et al. 2007b; Genoways et al. 2007c). On the positive side, cave-dwelling bat populations on Puerto Rico

rebounded two years after Hurricane Hugo, whereas tree-roosting species took at least three years to recover (Gannon and Willig 1994). This cave bias may be misleading, as only portions of Puerto Rico were damaged by Hugo and the differential migration of bats out of damaged areas played an important role in the subsequent recovery of that island, something that was not available to the bats on the much smaller island of Montserrat. Despite its volcanic nature, we have not found lava tubes on Montserrat and there are no historical records of caves on the island—this dearth of caves on Montserrat makes any cave a very important resource. Of the four caves and rock-shelter roosts known on Montserrat, only two remain—one is an artificial cavity (tar-rish pit; *Natalus stramineus*) and the other is a sea cave on the leeward side of the island, occupied solely by *Brachyphylla cavernarum*. The other two roosts were both destroyed sometime before 1998 by pyroclastic flows or seismic activity (Mosquito ghaut and Shoe Rock). The cave-dwelling *B. cavernarum* has shown itself to be a hurricane survivor on Montserrat, but how do the other species of bats survive hurricanes? Deep sheltered ravines on this mountainous island must provide sufficient refuge during large storms, and perhaps deep ravines and caves should be viewed as ecological equivalents from both evolutionary and animal conservation perspectives.

Are bats in the Lesser Antilles disturbance adapted? There are very few endemic genera in this archipelago, but unlike their mainland congeners these animals and their reproductive strategies have evolved in a region dominated by natural disasters. The low reproductive rates of most chiropteran taxa (“*K*-selected” organisms) lack an “*r*-selected” reproductive strategy that would be more suited for responding rapidly to disturbance in these complex, inherently unstable, tropical communities. Interestingly, *Artibeus jamaicensis* would seem to be capable of alternating between *K*- and *r*-selection regimes (Kwiecinski and Pedersen 2002), whereas other fruit bats are not. If this holds true, this phenomenon should be easy to test—we would expect populations of *A. jamaicensis* to recover quickly and become numerically dominant on other small islands that have recently experienced an ecological disaster or have been recently visited by hurricanes. Of note, *A. jamaicensis* is the dominant species of fruit bat on six of the nine islands with which we are very familiar (Montserrat, St. Martin, Nevis, Saba, St. Eustatius, and arguably St. Kitts), whereas the very dry islands of Barbuda, Antigua, and St. Barts are each dominated by a nectarivore or omnivore (*Monophyllus plethodon* or *B. cavernarum*). This is an interesting question that would bear further investigation: To what extent does reproductive strategy account for the contemporary community structure of bats throughout the Lesser Antilles?

Dispersal of bats throughout the Lesser Antilles is influenced by regional storm patterns, species vagility, and distances among islands. Yet despite our wealth of survey data from the region, actual movements of bats throughout

the Lesser Antilles are poorly known. They have been thought to be limited because interisland distances present formidable barriers to dispersal and gene flow among islands (Carstens et al. 2004; Genoways 1998; Koopman 1976), and perhaps these barriers are insurmountable given the navigational abilities of bats. Nevertheless, bat populations throughout the northern Lesser Antilles might arguably be considered a metapopulation (population of populations), and the local extirpation of a species from a severely damaged island may not matter, as bats may readily recolonize the island from adjacent islands. However, one looming question remains unanswered: Can the contemporary distribution of bats in the Lesser Antilles be accounted for by spontaneous movements among islands or is the movement and distribution of bats driven predominately by the impact of tropical storms and hurricanes?

If we compare the effects that hurricanes and volcanoes have on bat populations, hurricanes have a more immediate impact. Due to their size, hurricanes and large tropical storms can devastate an entire island the size of Montserrat in just a few hours, whereas pyroclastic activity on the scale we have observed on Montserrat usually impacts only small portions of an island, albeit repeatedly. This temporal difference in habitat disruption may allow bats to adapt over time by simply shifting their distribution to avoid ash-contaminated areas. Conversely, small islands such as Montserrat may take three to five years to recover from a hurricane, but it will take decades for forested habitat to be restored in areas hit by the volcano. So when do we perform a species inventory/biodiversity survey on one of these troubled islands?

Despite the recent attention to rapid biodiversity assessments and their potential benefit as being a pragmatic initial effort (UNEP 2006; U.S. EPA 2006), perhaps we need to reevaluate our survey protocols and understand that there should be nothing rapid about an accurate biodiversity assessment for bats. Short-duration and single-season surveys would have seriously underestimated bat biodiversity on Montserrat during the years 1994–2004, reporting only five to eight species, not the ten that have been recorded (fig. 11.5). For Montserrat, our species accumulation curve peaked in the vicinity of 1,000 captures and 100 net-nights—values that are similar for many islands in the immediate region. The capture of very rare species requires a significantly greater investment of time and effort. For example, given our cumulative efforts on Montserrat, which include 780 net-nights and 2,602 total captures, we have capture records for only three *Chiroderma improvisum* and two *Sturnira thomasi*. We conclude that without long-duration, multi-year survey efforts, biodiversity estimates can only be *approximations* at best and quite probably grossly underestimate the true faunal diversity of an island, thus providing a poor foundation for any subsequent conservation guidelines.

Conclusion

None of the species of bats occurring in the northern Lesser Antilles is endemic to that region, suggesting considerable dispersal among islands. However, movement patterns of bats in the Lesser Antilles are poorly known and thought to be limited because interisland distances present barriers to dispersal for most species. Genetic data imply restricted dispersal among the islands for the cave-roosting *B. cavernarum*, whereas *A. jamaicensis* apparently moves among the islands more freely (Carstens et al. 2004). Nevertheless, we do not believe that Antillean bats strike out on their own on a regular basis to move over water from one island to another. It is our conclusion, based on the available data, that stochastic tropical storms and hurricanes moving primarily from southeast to northwest effect dispersal and gene flow for bat populations living in the Lesser Antilles.

Strong hurricanes and volcanic activity are powerful agents of ecological and evolutionary change throughout this archipelago. However, despite the great fluctuations in bat abundance on Montserrat over the last 30 years, none of the species of bats has been extirpated as a result of the dramatic impact of volcanic devastation and a category 5 hurricane. Were these disasters simply insufficient to impact bat biodiversity on Montserrat? Is there a disturbance frequency and severity threshold for bat extirpation, or could it be that we are observing the resilience of a metapopulation in the northern Lesser Antilles?

We are left with a great many questions. None is more important than, when do we perform a species inventory on disaster-prone islands? Evolutionarily speaking, is there ever a point in time that one of these islands could be considered "normal," or at equilibrium? If our data from Montserrat are any indication, short-duration and/or single-season biodiversity surveys can only provide crude approximations of faunal diversity and unreliable data for subsequent conservation guidelines.

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