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SCOTT C. PEDERSEN,* TRACY E. POPOWICS, GARY G. KWIECINSKI, AND DAVID E. B. KNUDSEN

Department of Biology and Microbiology, South Dakota State University, Brookings, SD 57007, USA (SCP)

Department of Oral Biology, University of Washington, Seattle, WA 98195, USA (TEP)

Department of Biology, University of Scranton, Dalton, PA 18510, USA (GGK)

Department of Veterinary Science, South Dakota State University, Brookings, SD 57007, USA (DEBK)



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Department of Biology, University of Scranton, Dalton, PA 18510, USA (GGK)

Department of Veterinary Science, South Dakota State University, Brookings, SD 57007, USA (DEBK)

* Correspondent: scott.pedersen@sdstate.edu

The small Caribbean island of Montserrat has been battered by several hurricanes, and beginning in 1995, pyroclastic eruptions from the Soufriere Hills Volcano have destroyed the southern portion of the island. In addition to being incinerated by pyroclastic flows (300+°C), the bats of Montserrat also have had to contend with acid rain and the deposition of volcanic ash on leaves, fruits, and flowers and its subsequent ingestion by the bats. We document a dramatic decrease in the bat population and increases in several sublethal pathologies associated with the accumulation of ash across the island coincident with the onset of volcanic activity. Before 1995, less than 1% of the fruit bats exhibited evidence of unusual tooth wear. Since 1995, fruit bats have exhibited abnormal tooth wear advanced by the ingestion of volcanic ash while feeding and grooming. Damage to the teeth often includes ablation of the entire enamel crown and the exposure of the pulp cavity. Idiopathic hair loss was practically nonexistent before 1997 but alopecia has been frequently recorded since that time in adult frugivorous bats that live within the most damaged habitats on the island. This baldness is most likely related to physiological stress, high ectoparasite loads, or possible mineral deficiencies associated with the ingestion of ash. Furthermore, we have found evidence for respiratory pathologies in *Artibeus jamaicensis* resulting from the inhalation of volcanic dust and ash.

Key words: Chiroptera, hurricane, Montserrat, pathology, volcano

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The British Crown Colony of Montserrat is a small, 100-km² island located in the northern Lesser Antilles. Located in the middle of the “hurricane belt,” this small island has undergone dramatic ecological changes resulting from 2 very different types of natural disasters during the last 20 years: hurricanes Hugo (1989) and Louis (1995), and sporadic eruptions of the Soufriere Hills Volcano since 1995. As such, Montserrat provides a dynamic setting and a unique opportunity to monitor a natural experiment in island biogeography and bat biodiversity.

The bat fauna of Montserrat has received a great deal of attention from bat biologists over the last 35 years. Seventeen surveys (current study; J. Eger and D. Nagorsen, pers. comm.; Jones and Baker 1979; Morton and Fawcett 1996; Pedersen et al. 1996; Pierson et al. 1986) have produced a substantial database including 3,154 captures from 50+ locations of 10 species of bats, including 6 frugivores (*Monophyllus plethodon*, *Sturnira thomasi*, *Chiroderma improvisum*, *Artibeus jamaicensis*, *Ardops nichollsi*, and *Brachyphylla cavernarum*),

3 insectivores (*Natalus stramineus*, *Tadarida brasiliensis*, and *Molossus molossus*), and 1 piscivore (*Noctilio leporinus*).

Montserrat is one of many volcanic islands in the archipelago created by the subduction of the Atlantic tectonic plate beneath the Caribbean plate (Iturralde-Vinent and MacPhee 1999). Most of these islands are dominated by conical andesitic stratovolcanoes that are composed of alternating layers of volcanic debris resulting from explosive eruptions and pyroclastic activity. There are 3 volcanic massifs on Montserrat and small earthquakes are not uncommon. Although quiet since 1934 (Perret 1939), the southernmost massif (Soufriere Hills Volcano) renewed seismic activity in 1995, and pyroclastic eruptions have progressively reduced the eastern and western flanks of the volcano to what can only be described as an ecological wasteland.



These eruptions of superheated rock and volcanic tephra (300–500°C) incinerate and bury everything in their paths, including the island’s capital of Plymouth. Heavy rains convert unconsolidated pyroclastic material into massive lahars that have systematically filled entire valleys. Dry volcanic ash is easily blown off of plants, but if it becomes wet or lands as a mud rain, its weight crushes small to mid-sized plants and can break limbs off of larger plants. Sulfur-dioxide gas is emitted during large explosive eruptions and is converted to sulfuric acid (H₂SO₄) that then falls as acid rain. This rain subsequently affects aquatic life in the rivers and streams (transitory pH of 2–3 in many streams) and causes extensive leaf perforation and necrosis in plants (McGee et al. 1997).

Chronic effects of ash on animals include ash-related blistering of the skin in amphibians and conjunctivitis and blindness in birds (Hayward et al. 1982; Martin 1913 [not seen, cited in Pyke 1984]), respiratory problems in cattle and horses (Rees 1979), and hair loss and swollen eyes in small mammals (Andersen and MacMahon 1986; Pyke 1984). Volcanic ash also is harmful to insects because it blocks their spiracles and causes abrasion and excessive dehydration (Edwards and Schwartz 1981; Marske et al. 2007). Because of the position of insects in the food chain, their mortality rates may effect changes in populations of insectivorous bats, birds, and other animals (Askins and Ewert 1991; Foster and Myers 1982; Hilton et al. 2003; Waide 1991).

Here, we describe how fluctuation in the numbers and composition of the fruit bat population on Montserrat has reflected the environmental damage caused by both hurricanes and volcanic activity. We also report on the acute increase in several sublethal pathologies in bats associated with volcanic eruptions on Montserrat.

MATERIALS AND METHODS

Seventeen mistnetting surveys were conducted on Montserrat typically during the months of June and July 1975–2009. These efforts have produced a substantial database including 3,154 captures from 50+ locations of 10 species of bats. Survey methods and the selection of netting localities were consistent throughout these studies. Two of the authors (SCP and GGK) performed 13 of the 17 most-recent surveys, and those efforts were specifically designed to complement the 3 prehurricane surveys (J. Eger and D. Nagorsen, 1975, pers. comm.; Jones and Baker 1979; Pierson et al. 1986; Table 1). The posthurricane survey conducted by Morton and Fawcett (1996) followed a protocol readily comparable to that used in the present study. Five netting sites were common to each of the 17 surveys and no site was sampled more than once in any one field season.

Survey effort varied considerably among years (average net-nights per survey = 53 ± SE 42; Table 1) depending on weather, ashfall, available staff (1–4), and trip duration (2–4 weeks). Typically, 5–8 mist nets of varying lengths (6 and 8 m) were erected diagonally across roads, gullies, or streams at 40- to 60-m intervals. Nets were monitored for 4–6 h depending on bat activity and weather. After the nets were closed, bats were examined and measured (body mass, forearm length, reproductive status, tooth wear, condition of the fur, presence of scars, and external parasites). Two natural roosts were commonly surveyed, the large cave in the base of Rendezvous Cliff and a small mine (tarrish pit) at Happy Hill. Field notes or capture records (R. Baker, Texas Tech University; J. Eger, Royal Ontario Museum; M. Morton, Durrell Wildlife; and E. Pierson, University of California Berkeley; pers. comm.) were searched for notations concerning the incidence of mange, hair loss, and tooth wear in fruit bats.

TABLE 1.—Summary of survey effort, hair loss, and dental wear in fruit bats on Montserrat, 1975–2009.

	1975	1978	1984	1994	1995	1997	1998	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
All captures	66	432	181	256	206	41	60	194	80	359	73	145	273	185	191	101	159
Fruit bat captures	28	221	175	137	115	21	47	125	79	350	73	129	236	177	149	95	101
Net-nights	12	5	17	60	63	16	36	74	41	98	23	46	157	50	45	31	30
Bats/net-night	5.5	86.4	10.6	4.3	3.3	2.6	1.7	2.6	2.0	3.7	3.2	3.2	1.7	3.7	4.2	3.3	5.3
Fruit bats/net-night	2.3	44.2	10.3	2.3	1.8	1.3	1.3	1.7	1.9	3.6	3.2	2.8	1.5	3.5	3.3	3.1	3.4
<i>Monophyllus plethodon</i>																	
Captures	0	0	78	24	29	3	1	18	5	57	1	3	13	5	3	5	2
Hair loss %	—	—	—	—	—	—	—	—	—	12.3	—	—	—	—	—	—	—
Tooth wear %	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ardops nichollsi</i>																	
Captures	0	12	4	7	8	6	7	19	4	18	5	3	29	9	7	4	21
Hair loss %	—	—	—	—	—	—	—	—	—	5.6	20.0	—	—	—	—	—	—
Tooth wear %	—	—	—	—	—	—	71.4	26.3	—	38.9	100.0	66.7	20.7	22.2	42.9	25.0	14.3
<i>Artibeus jamaicensis</i>																	
Captures	21	200	84	46	52	6	15	83	58	244	57	115	180	144	129	81	65
Hair loss %	—	—	—	—	—	—	20.0	—	3.4	2.5	15.8	1.7	1.1	6.3	2.3	—	35.4
Tooth wear %	—	—	—	—	—	—	13.3	22.9	25.9	38.1	45.6	41.7	23.9	18.1	45.0	23.5	20.0
<i>Brachyphylla cavernarum</i>																	
Captures	7	9	9	60	26	6	24	5	12	31	10	8	14	19	10	5	13
Hair loss %	—	—	—	—	—	50.0	33.3	7.3	8.3	12.9	81.3	—	—	36.8	9.1	40.0	—
Tooth wear %	—	—	—	—	—	—	—	29.3	20.8	9.7	37.5	—	—	10.5	9.1	20.0	15.4

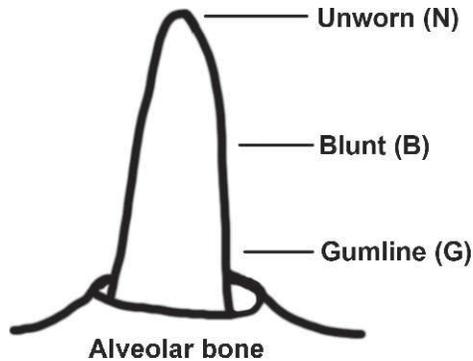


FIG. 1.—Different degrees of tooth wear and their coding scheme: unworn sharp teeth (N), at least half of the crown is lost (B), and crown is lost down to the level of the gingiva (G).

All protocols involving live bats followed guidelines of the American Society of Mammalogists published by the Ad Hoc Committee on Acceptable Field Methods in Mammalogy (1987) and were consistent with guidelines published more recently by Sikes et al. (2011). The collection of histological samples by GGK in June 2004 was approved by the Institutional Animal Care and Use Committee at the University of Scranton (IACUC protocol 8-03).

We estimated relative population size and species dominance directly from the numbers of bats captured per mist net per night (Table 1). We did not observe any health problems with the animalivorous bats on Montserrat, therefore, our discussion will only concern fruit bats. However, *C. improvisum* and *S. thomasi* are rare on Montserrat and these fruit bats were excluded from this analysis (Larsen et al. 2007).

After 1997, it became necessary to represent the degree of hair loss in 4 stages: 25–33%: small patches of hair missing, often about head and venter; 50%: medium patches of hair lost from head, neck, and venter; 75%: large patches of fur lost from head, neck, venter, and dorsum; and 100%: completely denuded or remaining only in small tufts between the shoulder blades or top of the head.

We developed a simple alphanumeric tooth-wear code based on 3 stages of tooth damage: N = intact sharp crowns, B = half of crown lost, and G = loss of entire crown (Fig. 1); followed by the number of pulp cavities that had been perforated and stained dark brown–black. A young bat with undamaged teeth would be coded N-0; an animal coded B-4 would exhibit blunt canines and premolars and have 4 blackened teeth; an animal coded G-8 would exhibit a mouth where more than half of the teeth had been worn down to the gum line and 8 teeth would be blackened. In practice, no bat exceeded G-18 and those were effectively edentulous.

The skulls of 3 *B. cavernarum* (University of Nebraska State Museum [UNSM] 20061, UNSM 20924, and UNSM 27686) were cleaned and carbon sputter-coated (Hummer IV; Technics, Union City, California) for viewing with a scanning electron microscope (Super IIIA; International Scientific Instruments, Pleasanton, California). These specimens were



FIG. 2.—Upper jaw of *Brachyphylla cavernarum*. In this composite image, the left side of the photograph shows the right upper jaw of a young adult male that exhibits only minor tooth wear. The right side of the photograph shows the left upper jaw of an adult male where most of teeth are worn to the gum line. At the time of capture, the unaffected young adult was coded N-0, and the damaged adult was coded G-10.

selected to represent the observed range of dental attrition (Figs. 2 and 3).

In each of the 4 species of fruit bat on Montserrat, we expected that dental attrition would increase with proximity to the volcano. However, because of unequal sample sizes among years, we restricted the regression analysis to a sample of 244 *A. jamaicensis* mistnetted during the 2002 field season.

For histological examination, lungs and kidneys were harvested in June 2004 from 6 *A. jamaicensis*, 2 *B. cavernarum*, 1 *M. plethodon*, and 2 *A. nicholli*. Tissues were placed in separate vials containing 10% neutral buffered formalin for 48 h before washing, transferred to 70% ethanol for storage, and transported to the University of Scranton. Tissues were subsequently trimmed, dehydrated in a graded series of ethanol, and embedded in paraffin. Paraffin-embedded tissue was sectioned at 7–10 μm with a rotary microtome (AO 80; American Optical Co., Southbridge, Massachusetts), and sections were mounted on glass slides. Slides were stained with periodic acid Schiff and hematoxylin, hematoxylin and eosin, or Mallory's trichrome (Bancroft and Stevens 1977; Presnell and Schreiber 1997). Stained sections were examined using a light microscope (BH-2 Olympus; Olympus, London, United Kingdom) and selected fields were photomicrographed and digitized (Spot RTKE; Diagnostic Instruments, Sterling Heights, Michigan).

RESULTS

Population dynamics.—Population size fluctuated throughout this study (1975–2009) reflecting the significant habitat disturbance by both hurricanes and eruptions of the Soufriere Hills Volcano. Netting data from stations that had

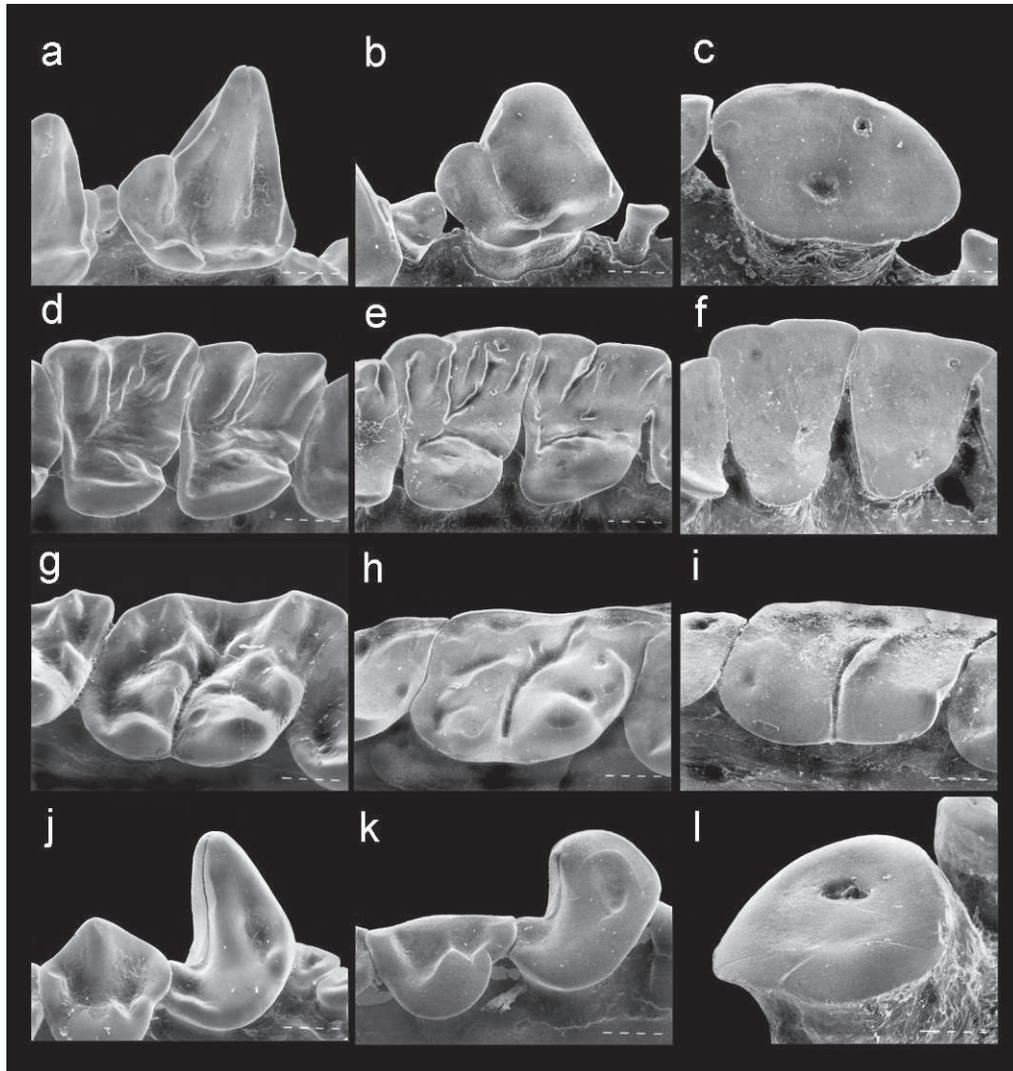


FIG. 3.—Scanning electron micrographs of the dentition of 3 *Brachyphylla cavernarum* collected on Montserrat—left to right: UNSM 20061, male, 6 November 1993; UNSM 27686, female, 18 July 2000; and UNSM 20924, female, 27 July 1997. Left to right: 3 different functional states: low wear, moderate wear, and extreme wear. Top to bottom: a–c) upper canine, C1; d–f) upper molars, M2 and M3; g–i) lower 2nd molar, m2; and j–l) lower canine, c1.

been repeatedly sampled since 1993 indicated that fruit bat capture rates increased from a low in 1998 (1.3 bats per net-night for fruit bats and 1.7 bats per net-night for all captures) to a high point in July 2002 (3.6 bats per net-night for fruit bats and 3.7 for all captures; Table 1). The 2002 peak in bats per net-night followed a very wet spring wherein several varieties of fig tree that had not set fruit since 1995 were heavily laden in 2002 (R. Aspin and E. Duberry, Montserrat Utilities, Ltd., pers. comm.). This dramatic increase in capture rate was due almost entirely to an increase in both the absolute and relative numbers of *A. jamaicensis* captured per net per night (2.5 bats per net-night; Table 1; Figs. 4 and 5). Juvenile *A. jamaicensis* are frequently mistnetted (2–6%), but the relative number of juveniles that were mistnetted dramatically increased from 2001 to 2004 (13.8–16.4% juveniles; pers. obs.).

Monophyllus plethodon luciae.—These small (12–17 g), cave-dwelling bats are relatively common throughout the

Lesser Antilles, although usually restricted to moist ravines at elevations above 800 m on Montserrat. *M. plethodon* hovers to take nectar from flowers, eats small native fruits, and has been observed hawking insects during periods of drought. Tooth damage in *M. plethodon* was limited to the occasional broken or missing canine (~1/100). Only 7 of the 247 *M. plethodon* captured during this study exhibited hair loss and those were all lactating females captured in 2002 (Figs. 6 and 7).

Ardops nichollsi montserratensis.—These tree-dwelling, medium-sized (15–33 g) fruit bats are found only in the northern Lesser Antilles and rarely in great numbers (Lindsay et al. 2010; Pedersen et al. 2005, 2006). They are usually restricted to moist ravines at elevations above 800 m on Montserrat. Thirty-eight of the 163 *A. nichollsi* examined in this study exhibited tooth wear or hair loss, or both (Figs. 7 and 8). Tooth wear (often severe) was 1st noted in 1998, and hair loss was noted in a small number of animals in 2002 and 2003.

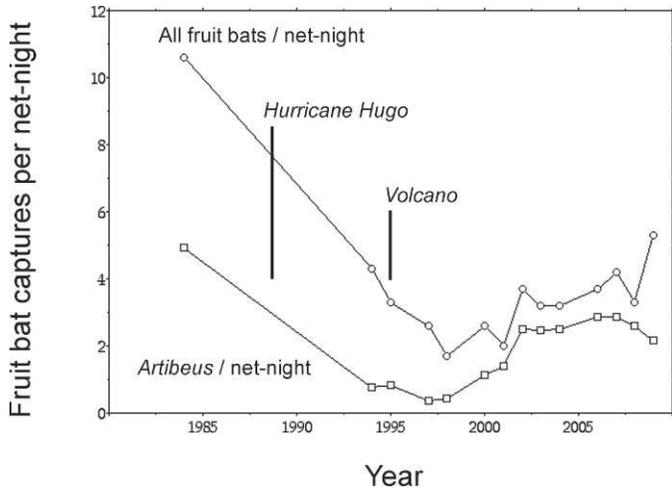


FIG. 4.—Fruit bat captures per net-night. The upper line shows all fruit bat captures including *Artibeus jamaicensis* and the lower line shows captures of *A. jamaicensis* alone.

Artibeus jamaicensis jamaicensis.—These medium-sized (31–49 g) fruit bats are distributed widely throughout the Antilles and have catholic roosting (caves, trees, and human structures) and foraging preferences. Of the 1,580 *A. jamaicensis* examined, 434 exhibited tooth wear or hair loss, or both, during this period. Except for a single lactating female whose remaining tufts of hair were gray and the majority of whose teeth were missing (April 1994), no evidence of any sort of pathology was observed in the population of netted bats before 1997. Since that time, the incidence of hair loss and tooth damage has fluctuated dramatically in this species (Figs. 7–9). Neither mange mites (demodicosis) nor inflammation of the integument have been observed in *A. jamaicensis*.

Brachyphylla cavernarum cavernarum.—These medium-sized (34–55 g) omnivorous bats are common throughout the Lesser Antilles and are typically found in large cave colonies and only occasionally in human structures. These bats will readily eat hard-skinned fruits and hard-shelled beetles, and they supplement their protein intake with immature legumes (Pedersen et al. 1996). Of the 268 *B. cavernarum* that were mistnetted during this study, 67 exhibited hair loss or tooth wear, or both. However, the degree of hair loss and tooth wear in this species has varied considerably during the survey (Figs. 7 and 8). No evidence of mange mites (demodicosis) or skin infection was observed in a series of these bats collected and tested in 1998.

Incidence and severity of alopecia.—Female bats often display small bald patches about the head and abdomen due to lactational stress (Kwiecinski et al. 1987; Pedersen et al. 1996, 2003, 2005, 2006, 2007). However, hair loss was not observed in any of the ~1,000 bats captured on Montserrat before 1997. Alopecia was 1st recorded on Montserrat in *A. jamaicensis* and *B. cavernarum*. The incidence of hair loss varied most dramatically in *B. cavernarum*, with peak occurrences coinciding with the initial volcanic eruptions (1997–1998), and the large eruption in July 2003. We observed hair loss, but

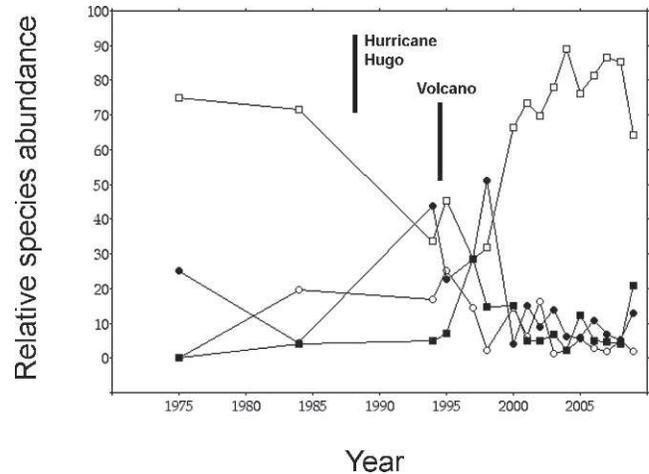


FIG. 5.—Relative species abundance of 4 species of fruit bat mistnetted on Montserrat 1975–2009 (open squares: *Artibeus jamaicensis*; closed squares: *Ardops nichollsi*; open circles: *Mono-phyllus plethodon*; closed circles: *Brachyphylla cavernarum*).

to a lesser extent, in tree- and foliage-roosting fruit bats, *A. jamaicensis* and *A. nichollsi*, as well as lactation-associated hair loss in *M. plethodon*. We found no evidence of hair loss in the animalivores (*Noctilio*, *Natalus*, *Tadarida*, or *Molossus*—Morton and Fawcett 1996; Pedersen et al. 2009), that is, alopecia is apparently limited to the fruit bats on Montserrat.

Incidence of ectoparasites.—The ectoparasite load on *B. cavernarum* went from negligible in 1993–1994 to what can only be described as “heavily infested,” with bats being covered with as many as 20 streblid flies, 2 or 3 nycterbiids, and several dozen ticks or mites. Whether due to stress or excessive grooming due to these parasite loads, 75% of the *B. cavernarum* roosting in Rendezvous Cave were essentially hairless in July 2003. In comparison, the large colony of *B. cavernarum* on the neighboring island of Antigua also has shown evidence of parasites, but those animals exhibited neither the extreme parasite loads, nor the extensive hair loss noted in *B. cavernarum* on Montserrat during this same period (Pedersen et al. 2006). External parasites were found only rarely on *A. jamaicensis*, *A. nichollsi*, and *M. plethodon*.

Incidence and severity of tooth wear.—Before 1998, the incidence of tooth damage in the bats on Montserrat was limited to that observed in 2 heavily scarred *A. jamaicensis* whose teeth were blunted or broken, or both. Since the onset of volcanic activity in 1995, damage to bat dentition has fluctuated from the moderate blunting of a few teeth in a uniform manner to the ablation of entire enamel crowns with subsequent staining or abscess of the underlying pulp cavities. Thegosis, as defined by Phillips and Steinberg (1976), is a characteristic of normal wear within the dentition that contributes to the sharpening of dental edges. However, the extreme wear described in this paper is notable for the ablation of cusps and the rounding of edges associated with simple abrasion, rather than a sharpening of edges as predicted by thegosis. In addition, enamel perforations are located where abrasion, rather than bacterial accumulation, is indicated.

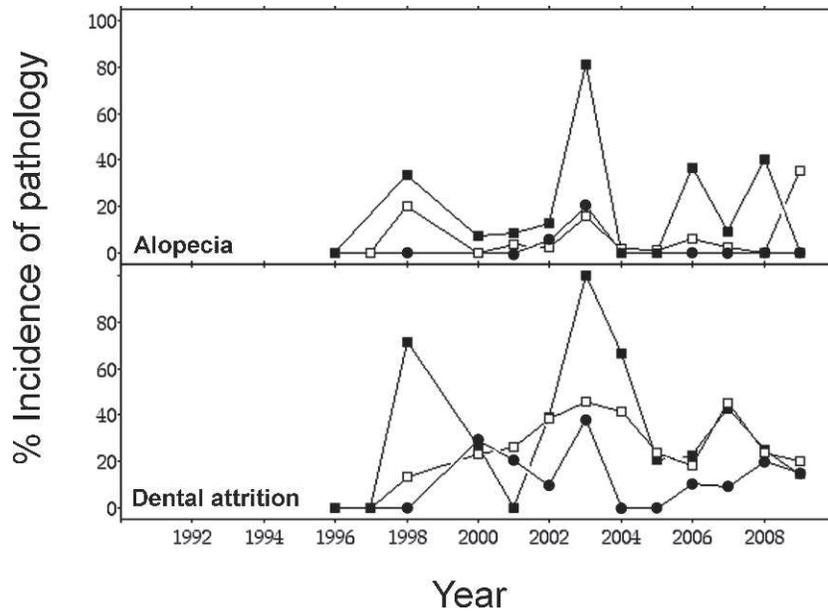


FIG. 6.—Incidence of 2 sublethal pathologies in fruit bats on Montserrat. Upper panel displays percentage of mistnetted bats that exhibited alopecia and the lower panel displays percentage of netted bats that exhibited unusual tooth wear 1997–2009 (open squares: *Artibeus jamaicensis*; closed squares: *Ardops nichollsi*; closed circles: *Brachyphylla cavernarum*).

Staining of dentin and enamel is related to normal carie formation, albeit accelerated here by the ablation the protective enamel crown (Phillips and Jones 1970).

The degree of tooth wear varies among taxa: *B. cavernarum*, N0-G18; *A. nichollsi*, N0-G16; and *A. jamaicensis*, N0-G18 (Fig. 8). During the 2002 survey, we documented a weak

dosage relationship between the distance from the source (volcano) and the incidence of tooth wear in *A. jamaicensis* ($R^2 = 0.368$, $P = 0.083$). Specifically, 60% of the *A. jamaicensis* exhibited damage to the dentition at 3 km distant from the crater but only 30% of the *A. jamaicensis* exhibited damage at 7 km (Fig. 9).

Tooth wear in B. cavernarum.—Molar cusp homologies for *B. cavernarum* vary among authors (Griffiths 1985; Koopman and MacIntyre 1980; Miller 1907; Slaughter 1970); however, we follow those of Koopman and MacIntyre (1980) and Miller (1907). Under high magnification, the worn occlusal surfaces of the teeth in this sample of *B. cavernarum* do not exhibit gouges, pits, or cracks. Rather, they appear highly burnished under the abrasive insult of fine volcanic ash (Figs. 2 and 3). In all cases, enamel edges do not appear sharp or sharpened, rather they are polished and exhibit rounded contours.

Minor wear to the canine teeth reduces the cusp height and rounds the high-relief edges (Fig. 3a). With intermediate tooth wear, the secondary cusps on the premolar-directed edge show rounding, and the cuspules at the lingual margin have been flattened to a narrow loph (Fig. 3b). Extreme wear has reduced the canine to a dentin stub with a central abscess (Fig. 3c). With relatively low wear, the paracone and metacone on an upper molar retain a high-relief buccal ridge that slopes lingually to a concavity (Fig. 3d). Intermediate crown wear is immediately apparent from the burnished appearance of the tooth's surfaces (Fig. 3e). Extensive wear has flattened the major cusps and exposed dentin at cusp tips, and loss of enamel in the central basin has removed the central conules. The concave curvature of the tooth is diminished by the reduction in buccal and lingual cusp height. In fact, buccal cusp identities are no longer distinguishable and are united in a single loph of

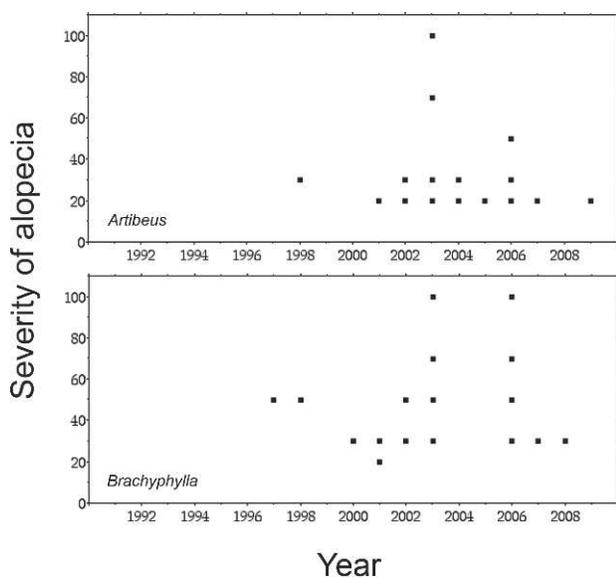


FIG. 7.—Severity of alopecia in *Artibeus jamaicensis* (upper panel) and *Brachyphylla cavernarum* (lower panel): 25–33%—small patches of hair missing, often about head and venter; 50%—medium patches of hair lost from head, neck, and venter; 75%—large patches of fur lost from head, neck, venter, and dorsum; 100%—the only hair remaining on the animal was in small tufts typically located between the shoulder blades or top of the head.

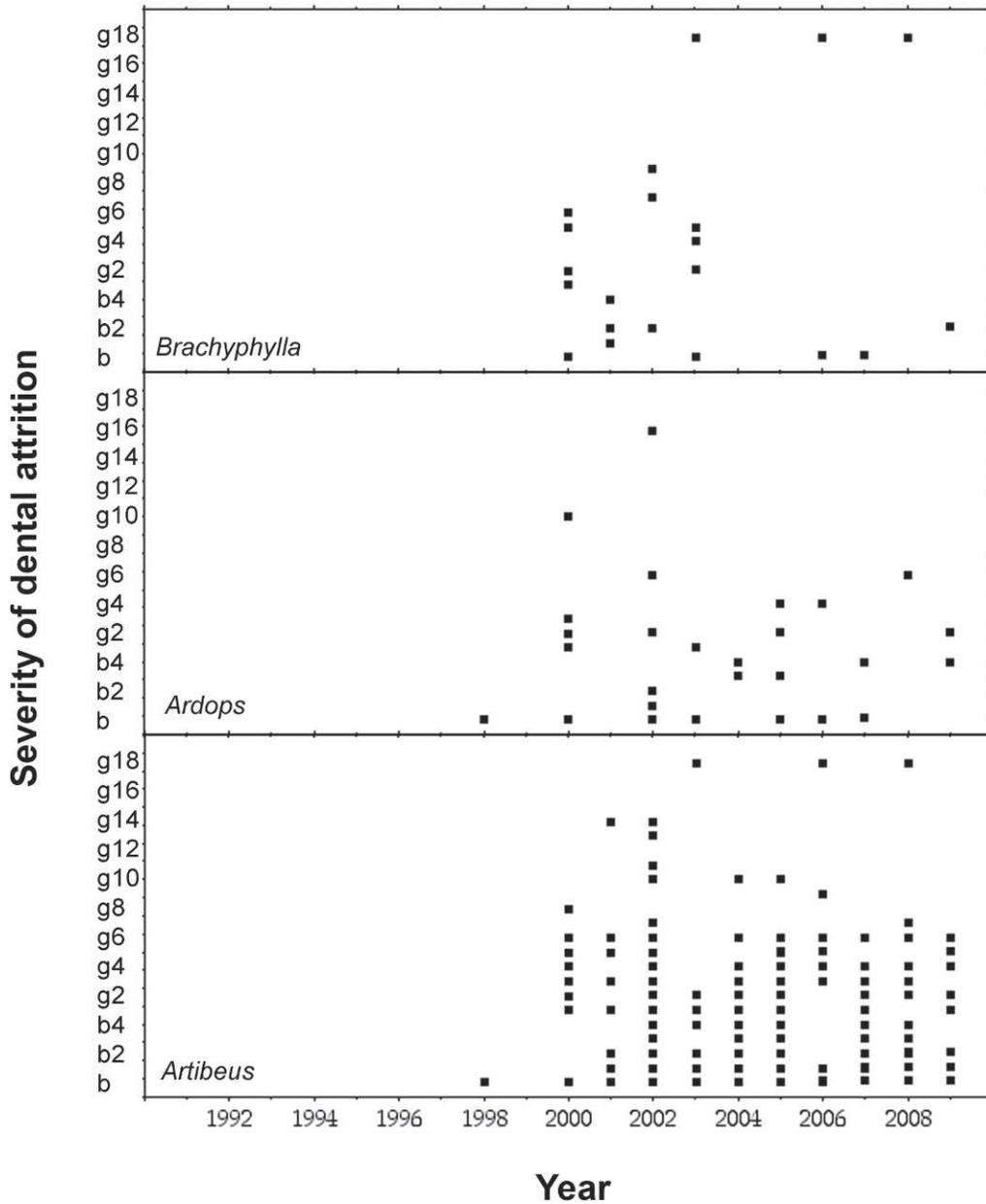


FIG. 8.—Severity of dental attrition in *Brachyphylla cavernarum* (upper panel), *Ardops nichollsi* (middle panel), and *Artibeus jamaicensis* (lower panel). Alphanumeric tooth-wear code is based on 3 stages of tooth damage (N, B, and G; Fig. 1) and a count of the number of pulp cavities that had been perforated and stained dark brown–black. The scale is discontinuous; see text for explanation.

dentin surrounded by an elongated ring of enamel. Cuspules within the central basin and the single lingual cusp have been obliterated as well. Thus, the enamel crown has been completely worn away, leaving enamel only on the crown margins and the slope of the buccal loph.

The lower dentition (Figs. 3g–l) exhibits a similar degree of dental ablation as that noted on the upper jaw. Minor wear on the lower cheek teeth leaves them highly polished and rounds both the major and minor features, but the cusps and cuspules maintain their identities (Fig. 3g). More extensively worn crowns show flattening of the major cusps and absence of the accessory cusps (Fig. 3h) wherein the protoconid and

hypoconid cusps have been reduced to a ridge of exposed dentine and enamel has been lost from the site of the hypoconid. With extreme wear (Fig. 3i), there is absolute destruction of the buccal cusps. The exposed dentin extends to the cervical margin of the teeth. The lower canine normally appears as a daggerlike main cusp with a small protuberance on the posterior base. After exposure to volcanic ash, this tooth has taken on the burnished appearance of other parts of the dentition and shows blunting of the cusp tip and rounding of the crown surface (Figs. 3j and 3k). As with the upper canine, extreme wear reduced the crown to its dentin base and exposed an abscess in the pulp cavity (Fig. 3l).

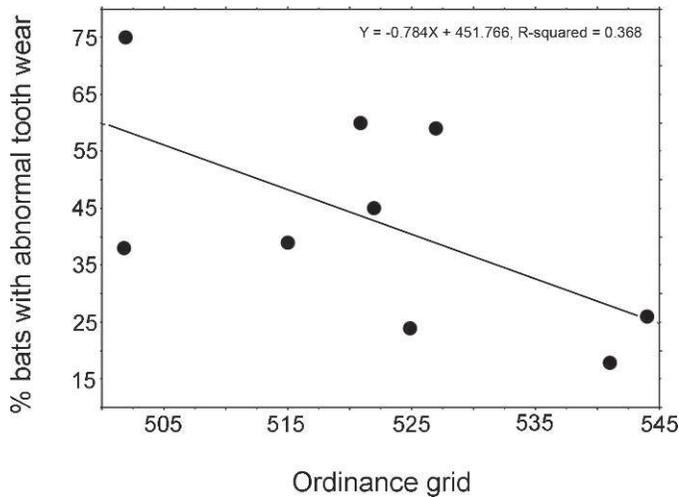


FIG. 9.—Negative relationship ($R^2 = 0.368$, $P = 0.083$) between the percentage of *Artibeus jamaicensis* that exhibited abnormal tooth wear during the 2002 survey and their capture distance from the source of volcanic ash. The x-axis is drawn from the Ordinance grid map for Montserrat (British Government Ministry of Overseas Development, 1983). The grid extends 590–420 north to south and the Soufriere Hills Volcano is located at grid line 470 in the southern one-half of the island.

Histological data.—All bats examined exhibited evidence of minor pathology. The predominant lesion in kidneys was minimal to mild multifocal tubulointerstitial nephritis in some animals (not shown). Most lungs examined were essentially normal, with multiple bronchiole-associated lymphoid aggregates apparent in all animals (Fig. 10a). Some animals had varying degrees of interstitial congestion, fibrosis, and inflammation, which often surrounded small vessels (Fig. 10b). This chronic interstitial response may have resulted in a reduction of lung compliance, leading to observed alveolar emphysema and deposition of acellular, eosinophilic periodic acid Schiff–positive material that was suggestive of alveolar silicoproteinosis (Fig. 10d). Occasional cross-sectional profiles of an arthropod parasite were noted in airways (Fig. 10c); host response to these parasites was not detected using our sampling methods. Based on anatomy and location, these are likely to be mesostigmatid mites (possibly *Pneumonyssoides* or *Mortelmansia*), which can be found in the respiratory tract of New World primates.

DISCUSSION

Hurricanes and volcanic activity differ fundamentally in both their immediate and long-term impacts on ecosystems—both types of natural disaster impose significant stress on bats as they adjust to altered roosting and foraging parameters. The

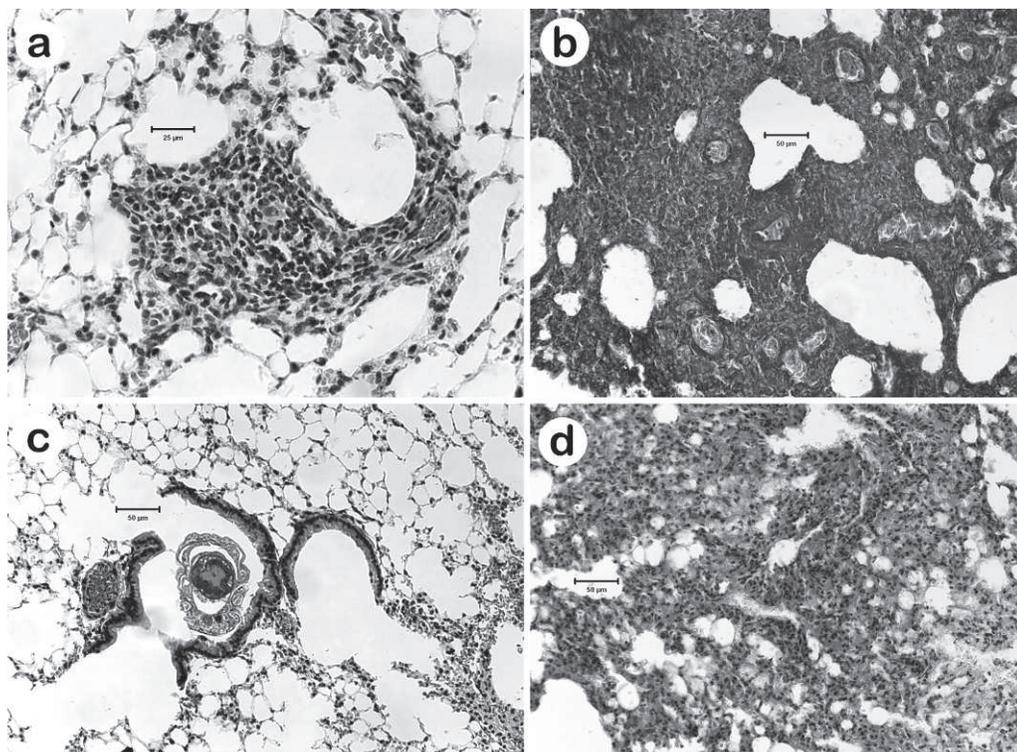


FIG. 10.—Sections of lung from bats collected on Montserrat in 2004: a) *Artibeus jamaicensis*, stained with hematoxylin and eosin, 572 \times , scale bar is 25 μ m; b) *Monophyllus plethodon*, stained with Mallory's trichrome, 286 \times , scale bar is 50 μ m; c) *Artibeus jamaicensis*, stained with hematoxylin and eosin, 286 \times , scale bar is 50 μ m (note parasitic arthropod in respiratory bronchiole; see text for discussion); d) *Artibeus jamaicensis*, stained with periodic acid Schiff (PAS) and hematoxylin, 286 \times , scale bar is 50 μ m. See text for discussion of each image.

effects of hurricanes on bat communities have been well summarized elsewhere (Barlow et al. 2000; Fleming and Murray 2009; Gannon and Willig 1994, 2009; Jones et al. 2001; Pedersen et al. 1996, 2009; Rodríguez-Durán and Vázquez 2001).

Early in the volcanic crisis (1995–1998), fruit bat diversity and relative abundance decreased on Montserrat. This was associated with the destruction of much of the island's forested habitat by pyroclastic flows, acid rain, and ash fallout. Remaining fruit bats were displaced and compressed into less-disturbed habitats located in the Centre Hills in the northern portion of the island—approximately one-third of their original range. Population numbers decreased during this volcanic period to such an extent that our yearly species inventory often fell short of the 10 species recorded from Montserrat, that is, a minimum of 3 species were “missing” during each of the 1997–2003 surveys (Pedersen et al. 2009). The species were not extirpated, but their population numbers had decreased to the point that they no longer appeared in our mist nets (Larsen et al. 2007).

Examination of our data indicates that before 1995, the fruit bat guild was dominated by *A. jamaicensis*. Surveys conducted early in the volcanic period (1995–2000) showed that the seemingly depauperate fruit bat guild structure was in turmoil (Fig. 5). However, *A. jamaicensis* reemerged as the dominant fruit bat on Montserrat in 2000. Juvenile *A. jamaicensis* are often mistnetted (5–6%) but the relative number of juveniles that were mistnetted (proxy for breeding success) dramatically increased through the period 2001 through 2004 (13.8–16.4%—Larsen et al. 2007; pers. obs.). In comparison, juvenile capture rates of the 3 other species of fruit bats on Montserrat are typically <5%. Indeed, the relative numbers of captures of *B. cavernarum*, *M. plethodon*, and *A. nichollsi* did not fluctuate dramatically and variation in guild structure was driven almost entirely by the boom–bust population dynamics of *A. jamaicensis* on Montserrat (Fig. 5). *A. jamaicensis* is clearly a disturbance-adapted species and its ability to recover after natural disasters would seem related as much to its catholic diet and flexible roost selection as to its reproductive capacity.

Given the previous statements, our pathology data are confounded by sampling bias, the considerable reproductive potential of *A. jamaicensis*, and the cumulative effects of 2 different kinds of natural disaster (Soufriere Hills Volcano and several hurricanes: Hugo in 1989, Luis in 1995, Georges in 1998, and Jose and Lenny in 1999). Nevertheless, the nadir in bat diversity on Montserrat (1995–2002) coincided with the appearance of several nonlethal, stress-related pathologies.

Abnormal hair loss in fruit bats.—Generally, hair loss in mammals is a multifactorial phenomenon, with plant toxins, external parasites, lactation, and general stress working alone or in concert as likely causal agents (Hargis and Ginn 2007). Dietary protein deficiency is probably one of the more common causes of alopecia in mammals, occurring in many species including primates (Harkness and Wagner 1995; Mundy et al. 1998). Other causes of alopecia in mammals include micronutrient deficiencies, compromised immune systems,

renal disease, excessive grooming behavior (e.g., high ectoparasite loads), crowded roosting conditions, and bacterial infections (Fowler and Miller 1999; Harkness and Wagner 1995; Kleiman et al. 1996; Lollar and Schmidt-French 1998). Fruit bats on Montserrat have suffered under many, if not all, of these stressors at some point during the volcanic period.

Hair loss due to mineral deficiencies.—Whether ingested during feeding or 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). Calcium oxides are known to compete with dietary zinc in the intestinal wall (Hargis and Ginn 2007) and may trigger zinc-deficiency-related alopecia in affected animals; however, hair loss has not been reported in pets or livestock on Montserrat. The adjacent islands of Antigua, Nevis, and St. Christopher (St. Kitts) have received wind-blown ash from Montserrat during many of the larger eruptive events (1997–2005) and we might expect to see alopecia in those populations as well. We observed that nearly 10% of *B. cavernarum* on Nevis and St. Christopher (lactating females) exhibited varying degrees of hair loss in 1999 but no *B. cavernarum* (lactating or otherwise) exhibited hair loss on either Nevis or St. Kitts in 2001 (Pedersen et al. 2003, 2005). There may be some threshold effect with respect to how dietary stress and ash ingestion interact and subsequently influence the incidence and duration of alopecia. Therefore, we cannot rule out zinc deficiency as the primary causal agent, and this could be tested in a controlled situation.

Hair loss due to plant toxins.—On the adjacent island of Nevis, transitory hair loss was observed in *B. cavernarum* following Hurricane Georges in 1998 (Pedersen et al. 2003). There was extensive defoliation during that hurricane—one of the 1st trees to recover was the false tamarind (*Leucaena leucocephala*), a shrubby legume that not only thrives under such conditions but produces a natural depilatory toxin, mimosine. Mimosine is a nonprotein amino acid found in leaves, pods, and seeds of tropical legumes of the genus *Leucaena*. When consumption of *Leucaena* exceeds about 30% of a nonruminant animal's diet, mimosine toxicity results in reduced weight gain, hair loss, goiter, and abortion (Brewbaker 1987; Maberley 1987; Windholz et al. 1983). During periods of drought, posthurricane damage, or heavy ashfall, *B. cavernarum* resorts to alternate forage such as pigeon pea seedpods (Pedersen et al. 1996, 2005), and possibly the flowers, leaves, and young pods of the only tree available, the false tamarind. It is unknown to what extent the stochastic affects of habitat destruction and use of substandard forage have impacted other fruit bat populations on Montserrat during this period, but this mimosine-ingestion hypothesis also could be studied in a controlled situation.

Hair loss due to external parasites and excessive grooming.—The population of *B. cavernarum* on Montserrat consists of a single large colony, as it does on many islands in the region (Morton and Fawcett 1996; Pedersen et al. 1996,

2003, 2005, 2006, 2007) and populations of *B. cavernarum* are therefore vulnerable to catastrophic loss or predation, or both, especially because they are obligate cave or crevice dwellers (Steadman et al. 1984a, 1984b; Wheeler 1988). Presence–absence data collected throughout 1993–1995 indicate that the colony of *B. cavernarum* on Montserrat alternated between a large rock shelter in Mosquito Ghaut on the northeastern flank of the Soufriere Hills 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 bivouac from which the colony would visit fruiting trees in the vicinity. The Mosquito Ghaut roost was destroyed by pyroclastic flows in 1997 (probably abandoned before that due to earthquakes and acid rainfall), leaving Rendezvous Bluff as the only roost site for this large colony, the population of approximately 5,000 bats has remained remarkably constant since 2000. The permanent occupancy of this cave complex by *B. cavernarum* since 1997 has resulted in extreme levels of external parasites that are significantly higher than recorded previously on Montserrat or on any other island in the region (Jones and Baker 1979; Morton and Fawcett 1996; Pedersen et al. 1996, 2003, 2005, 2006, 2007). Indeed, the ectoparasite load on *B. cavernarum* went from negligible in 1993–1994 to what can only be described as “heavily infested,” with mistnetted bats and all bats taken from the cave walls themselves being covered with as many as 20 streblid flies, 2 or 3 nycterbiids, and several dozen ticks or mites. Whether due to stress or excessive grooming imposed by the heavy infestation by parasites, 75% of the *B. cavernarum* roosting in Rendezvous Cave were nearly or totally bald in July 2003. As a comparison, the large colony of *B. cavernarum* in the much larger Bats Cave on the neighboring island of Antigua also is parasitized. However, those animals exhibited neither the extreme parasite loads, nor the extensive hair loss noted in *B. cavernarum* on Montserrat during surveys performed on Antigua during this same period (Pedersen et al. 2006). One plausible explanation for the alternation 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 (Bartonicka and Gaisler 2007). Given that both male and female *B. cavernarum* on Montserrat have exhibited alopecia, it is probable that hair loss was due initially to excessive grooming in response to high ectoparasite loads as much as a response to any other physiological stress associated with ingestion of volcanic ash or lactation.

Hair loss due to general stress and competition.—Early in the volcanic crisis, fruit bats on Montserrat had to contend with deposition of volcanic ash on leaves, fruits, and flowers and destruction of tree roosts. At that time, fruit bats were compressed into approximately one-third of their previous range. Predictably, competition for food was presumably quite intense, a circumstance for which *B. cavernarum* is well adapted, being an aggressive species that has been observed displacing other bats from feeding sites (Nellis and Ehle 1977). In 2002, we observed serious wounds to the head and neck of 6 lactating female *A. jamaicensis*, which included damaged or

missing ears and eyes and grossly infected abscesses about the face. These wounds may have been the result of interspecific resource guarding, but given the dramatic increase in activity of *A. jamaicensis* that same year, we surmise these wounds were most probably the result of intraspecific squabbles over limited resources at roosts or foraging sites. We have not observed such wounding in *A. jamaicensis* since that time.

Abnormal tooth wear in fruit bats.—Tooth-wear patterns in bats reflect differences in craniodental specializations, chewing patterns, and simple wear due to age or behavior (Clark 1976; Dumont 1999; Freeman 1988; Khan et al. 1998; Sluiter 1961; Ungar et al. 1995). However, we have recorded the acute onset of abnormal damage to the teeth in 3 species of fruit bats (*A. jamaicensis*, *B. cavernarum*, and *A. nichollsi*) coincident with the ingestion of ash-laden food or the incidental ingestion of ash during grooming. The degree of tooth wear varies among these species and may reflect minor differences in food selection (e.g., fruit stickiness or ash-carrying capacity), food-handling ability, or grooming behavior. It is unlikely that any animal with tooth wear above G-18 would be able to process anything but the softest, ripest or most rotten of fruit pulp. Animals with such extreme levels of tooth wear were not always emaciated as one might expect, rather, many are otherwise healthy, pregnant, and even lactating.

Certainly, taxa vary with respect to the degree of bodily contact with ash-contaminated surfaces during feeding. For example, *M. plethodon* can hover above flowers while drinking nectar, or will have only limited contact with a contaminated surface because it has a habit of biting into small fruits and allowing the weight of the bat's body to carry the fruit away from the stem. In addition, one of the favored fruits of *M. plethodon* is *Piper*, whose vertical fruits do not accumulate ash. As such, none of the *M. plethodon* captured between 1995 and 2009 exhibited abnormal tooth wear. Neither have we observed abnormal tooth wear in any of the animalivorous bats (*M. molossus*, *T. brasiliensis*, *N. stramineus*, and *N. leporinus*) because of their limited contact with ash-covered prey items and roosting surfaces.

Conversely, *A. jamaicensis*, *A. nichollsi*, and *B. cavernarum* often fly directly into the ash-laden crowns of trees, putting themselves in direct contact with ash-laden fruit, leaves, and flowers. When feeding on fruits such as papaya and mango, the bats become covered with fruit juice and fruit pulp, which in turn accumulates considerable volcanic ash that must be subsequently groomed off of the pelage. In each instance, these fruit bats undoubtedly ingest large amounts of ash, and it is in these taxa that we observe the greatest amount of damage to the teeth.

Since 1997, the incidence of dental attrition has varied considerably. The erratic incidence of abnormal tooth wear in *A. nichollsi* and *B. cavernarum* is most likely a sampling artifact related to their relatively small contribution to the fauna (Fig. 8). However, the incidence of abnormal tooth wear in *A. jamaicensis* steadily increased from 1998 through 2003, influenced by proximity to the volcano (dosage affect) and retention of affected animals in the population during years of heavy ashfall (Figs. 6, 8, and 9). Since its peak in 2003,

incidence of tooth wear in *A. jamaicensis* has oscillated (18–45%) but has not been associated with volcanic activity in any obvious manner. Rather, this oscillation may reflect sampling artifacts of the reproductive cycle (Wilson et al. 1991), differential survival of older bats during numerous tropical storms that hit Montserrat, and increase in the numbers of juvenile *A. jamaicensis* mistnetted in 2004 (16.4%, normal range 2–6%).

Lung damage due to respiration of ash.—Volcanic ash and pyroclastic flows on Montserrat have been more than just a nuisance to human and bat populations. There have been multiple studies that claim volcanic ash to be pathogenic in human populations, with volcanic ash being reported to be the cause of physical and pathologic problems in human populations on Montserrat in particular (Forbes et al. 2003; Martin et al. 1986). The volcanic ash generated by the long-lived eruption of the Soufriere Hills Volcano has been shown to contain respirable particles smaller than 4 μm (Horwell et al. 2003), as well as cristobalite, a crystalline silica polymorph (Baxter et al. 1999) that has been implicated to lead to silicosis, pneumoconiosis (Fujimura 2000; Mossman and Churg 1998), and alveolar silicoproteinosis (Honma et al. 1997; Weill et al. 1994). Previous studies in rats challenged with up to 3 doses of cristobalite and examined at various times up to 49 weeks demonstrated lymph node granuloma, lung inflammation, and mild lipoproteinosis; there was no evidence of lung fibrogenic response in these studies, and it was concluded that there was very little biological activity following short-term exposure (Housley et al. 2002; Lee and Richards 2004). The pulmonary lesions of bats from Montserrat in this study were of varying pathologic degrees. The most abnormal lungs or severe form of lesions were characterized by alveolar emphysema, mild interstitial inflammation and fibrosis, and alveolar silicoproteinosis resembling that of silicosis (Fujimura 2000; Heppleston 1994; Katabami et al. 2000; Mossman and Churg 1998; Weill et al. 1994). Our results differed from that of previous rat studies in that our samples were from randomly selected plant-visiting bats that were exposed to environmental ash their entire life. The most severe lesions were most likely in older animals that had been chronically breathing dust from the irregular eruptions and environmental persistence of volcanic ash. Because we have no way of aging bats once they reach reproductive maturity, it is reasonable to conclude that less-developed lesions were found in younger animals.

We are anxious to further investigate the direct effects of ingested and aspirated ash on the tissues of the respiratory and digestive systems in these animals. We will continue our monitoring efforts over the next decade, because Montserrat provides a unique opportunity to study a natural experiment concerning island biogeography, biodiversity, and how wildlife is affected and subsequently responds to natural disasters on small islands.

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