ARTICLES

Herpetological Review, 2011, 42(2), 160–165.

Ecological Consequences of Continual Volcanic Activity on the Lizard, *Anolis lividus*, from Montserrat

Understanding the effects of environmental disasters on ecosystems and mechanisms of ecological recovery is a central pursuit in biology. Acute episodes, such as tsunamis or volcanic eruptions, can decimate entire ecosystems, but research has shown that recovery from single devastating events can prove to be rapid. For example, following the destructive eruption of the Krakatau islands in Indonesia in 1883, which left its land and associated waters completely sterilized, both the terrestrial and marine life rebounded quickly (Barber et al. 2002; Dammerman 1929; Thornton 1996). Furthermore, under certain conditions ecosystems can prove to be resilient to environmental devastation. For example, corals growing on hard substrate, such as rock, were largely unaffected by the tidal waves of the tsunami in Aceh, Indonesia in 2005, whereas corals growing on rubble and sand, and their associated communities, were devastated (Baird et al. 2005).

Many contemporary environmental disasters occur continually, and require that ecosystems respond to recurrent assault. Beginning in 1995 the island of Montserrat in the West Indies has suffered acute and persistent volcanic activity from the Soufrière Hills Volcano (Robertson et al. 2000). The most devastating volcanic events are pyroclastic flows, or high-speed currents of rocks and gas resulting from dome collapse, and periodic ash clouds composed of volcanic gases and particulate matter (Montserrat Volcano Observatory Team 1997; Fig. 1). There are also periodic landslides termed lahars that deposit meters of pyroclastic material into the river valleys, and acid rain that affects the areas closest to the volcano. These events occur regularly and are undoubtedly traumatic to the Montserratian ecosystem, particularly in communities in the southern half of the island, where volcanic impact is more severe and continual. Knowledge of how persistent volcanic activity affects the island's endemic flora and fauna can inform efficient conservation efforts, but little is currently known.

Fig. 1. View of Plymouth, the defunct capital, where *Anolis lividus* was once quite abundant, as seen from the sea following the January 2010 dome collapse.

Research has shown that the long-term effects of the volcano on local wildlife can be severe. For example, despite intense sampling, many endemic coleopteran species have not been captured since volcanic activity began (Marske et al. 2007). Furthermore, the rare endemic oriole, *Icterus oberi*, is in imminent threat of extinction (Lovette et al. 1999). More than half of the oriole's habitat has been destroyed due to eruptions from the Soufrière Hills (Hilton et al. 2003), while periodic ash episodes further deplete populations and nesting sites (Dalsgaard et. al. 2007). The endemic galliwasp, *Diploglossus montiserrati*, was commonly found before the eruption of 1995, but only a handful of individuals have been captured since, despite extensive sampling by the Department of Agriculture (G. A. L. Gray, pers. comm.). And while efforts are focused on the northern half of Montserrat, even

MARTHA M. MUÑOZ
Department of Organismic and Evolutionary Biology
26 Oxford Street, Harvard University
Cambridge, Massachusetts 02138, USA
e-mail: mmunoz@oeb.harvard.edu
JAMES HEWLETT
Department of Science and Technology
3325 Marvin Sands Drive, Finger Lakes Community College
Canandaigua, New York 14424, USA
e-mail: hewletja@flcc.edu

less is known about populations in close proximity to the volcano, especially in the permanent exclusion zone of the island, where human traffic is prohibited.

Beginning in 2009 we have been monitoring populations of the endemic anole, *Anolis lividus* (Fig. 2), both in the safe zone (northern Montserrat) and in the permanent exclusion zone (southern Montserrat). In comparison to many other reptiles and amphibians on the island, much is known about the biology of *A. lividus*, such as its natural history (Lazell 1972; Schwartz and Henderson 1991; Underwood 1959; Williams 1962), malarial parasites (Staats and Schall 1996), and evolutionary relationships (Losos and Thorpe 2004; Schneider et al. 2001; Thorpe and Malhotra 1996). Despite more general knowledge of the species, there has been no assessment of how populations have been affected by volcanic activity until now. We present the first field observations of lizard habitat conditions from six sites within the permanent exclusion zone in southwestern Montserrat. The extent of environmental damage due to ash, gas venting, and acid rain varies in the exclusion zone, but some areas appear qualitatively similar to sites in northern Montserrat, which are comparatively less affected by volcanic activity. Despite the availability of apparently suitable habitat, we captured only a single adult male lizard in the permanent exclusion zone, suggesting that volcanic activity in this area may have a dramatic impact on lizard abundance.

Additionally, we compared body size among populations of *A. lividus* across the island, and compared current average body size to those of ethanol-preserved specimens in the Museum of Comparative Zoology collections at Harvard University, which were collected before the major volcanic eruption. We find that average body size (snout–vent length) is lower in recently-sampled populations, which may indicate that persistent volcanic episodes periodically deplete populations, making it rare for males to attain larger body sizes. Interestingly, however, the sole male found in the exclusion zone was also the largest collected to date, suggesting that large body size may facilitate colonization or persistence in this highly disturbed area. Because lizard abundance in the exclusion zone is extremely low, it is possible that volcanic activity may cause local extinction and may also delay or hamper recolonization.

Materials and Methods.—Because of the periodic fluctuations in volcanic activity, Montserrat is subdivided into zones that vary according to risk, which the Montserrat Volcano Observatory (MVO) monitors and updates according to current conditions (Fig. 3). While most of the north is permanently open, areas south of Salem in the west and Jack Boy Hill in the east are restricted, especially when volcanic activity increases. Even when the volcano is relatively calm, these areas are more affected by acid rain, ash, and pyroclastic activity than the northern half of the island. Travel into the permanent exclusion zone is prohibited, but the MVO granted our team special permission to enter the northwestern fringe of the exclusion zone for one day (29 June 2009) to survey *Anolis*

Fig. 2. Adult male *Anolis lividus* captured in Jack Boy Hill, in northeastern Montserrat.

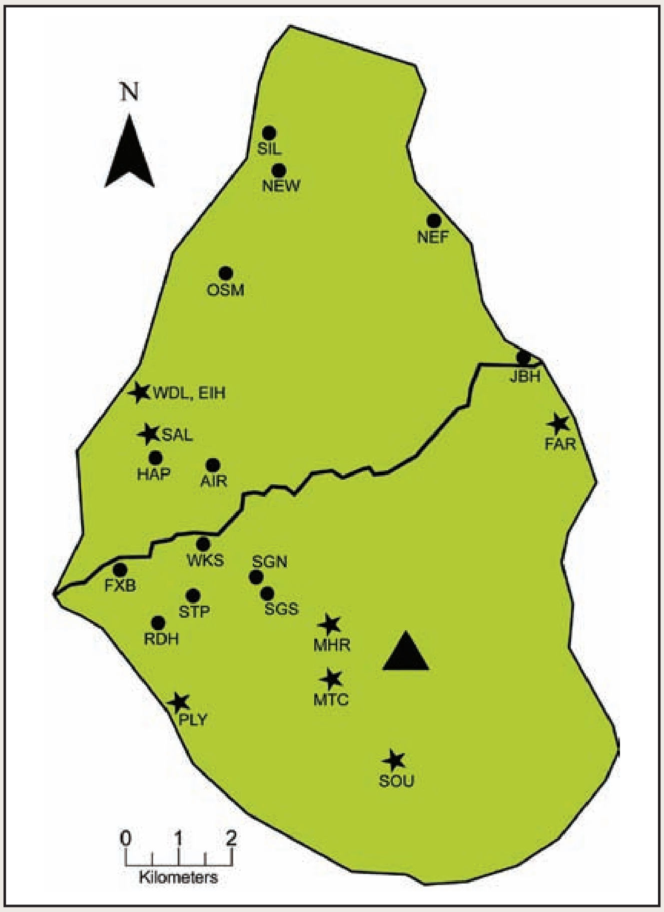

Fig. 3. Map of Montserrat showing our sampling strategy. Black dots denote localities sampled in 2009 and 2010 and stars denote localities sampled before the eruption (museum specimens). The black line shows the permanent exclusion zone boundary, and the triangle shows the location of the Soufrière Hills volcano.

COLOR REPRODUCTION SUPPORTED BY THE THOMAS BEAUVAIS FUND

TABLE 1. Data for body size and habitat conditions collected from wild-caught and museum specimens. Sites visited in the exclusion zone are denoted with an asterisk (*).

Locality	Abbreviation	Coordinates (lat, long)	Individuals	Min SVL (mm)	Max SVL (mm)	Ash Impact	Sulfur Odor	Acid Rain Impact
Summer Sampling (June 2009)								
Air Studios	AIR	16.74, -62.22	13	43.3	60.4	Low	Absent	Absent
Jack Boy Hill	JBH	16.76, -62.16	5	41.8	60.7	Low	Absent	Absent
Northeast Field	NEF	16.78, -62.18	13	47.2	64.5	Low	Absent	Absent
Sturge's Park*	STP	16.72, -62.22	0	-	-	High	Present	Absent
Richmond Hill*	RDH	16.71, -62.22	0	-	-	High	Present	Absent
Weeke's*	WKS	16.73, -62.22	1	-	67.9	Low	Absent	Absent
Fox's Bay*	FXB	16.72, -62.23	0	-	-	Low	Present	Absent
St. George's Hill - N*	SGN	16.72, -62.21	0	-	-	High	Present	Present
St. George's Hill - S*	SGS	16.72, -62.21	0	-	-	High	Present	Present
Winter Sampling (January 2009, 2010)								
Silver Hills - Rendezvous Bay	SIL	16.81, -62.20	11	44.7	63.9	Low	Absent	Absent
New Town	NEW	16.80, -62.20	13	48.6	63.5	Low	Absent	Absent
Old Sugar Mill	OSM	16.78, -62.21	7	41.3	58.2	Low	Absent	Absent
Happy Hill	HAP	16.74, -62.22	10	44.7	64.5	Low	Absent	Absent
Summer Sampling Museum Specimens								
Emerald Isle Hotel	EIH	-	5	56.3	68.4	-	-	-
Farmer's Estate	FAR	-	7	48.2	70.8	-	-	-
Monkey Hill River	MHR	-	2	55.5	62.0	-	-	-
Mount Chance	MTC	-	2	50.8	58.9	-	-	-
Plymouth	PLY	-	14	50.0	64.7	-	-	-
Salem	SAL	-	2	48.9	50.0	-	-	-
South Souffriere	SOU	-	1	-	55.4	-	-	-
Woodlands	WDL	-	7	51.5	62.8	-	-	-
Unknown	UNK	-	1	-	64.8	-	-	-

lividus, providing a first glimpse into lizard habitat conditions in this area.

In the exclusion zone we visited six sites of varying degrees of volcanic impact and seven sites outside of the zone (Table 1, Fig. 3). Because our time was limited in the exclusion zone, we qualitatively assessed each site we visited for relative ash, sulfur, and acid rain impact as compared to sites we visited in the safe zone. Ash impact referred to abundance of standing ash. We considered a site to have low ash impact if only a light coat of ash was present, no more than a few centimeters deep, and high impact when large quantities of standing ash were present, often at least half a meter high. Two observers confirmed the odor of sulfur and the presence of trees denuded of leaves with blanched trunks and branches were considered strong evidence of acid rain damage.

We captured adult male lizards with a standard noose and using digital calipers we measured body length (snout–vent length; SVL), which is the distance from the tip of the snout to the cloaca. We captured and measured individuals from populations outside of the exclusion zone in the winters of 2009 and 2010 (N = 43) and in the summer of 2009 (N = 30). We kept summer and winter individuals separate for statistical analyses because population body size can vary by season in lizards.

We also measured SVL for 41 ethanol-preserved specimens of adult male *A. lividus* from the Museum of Comparative Zoology at Harvard University, all of which were captured before the 1995 eruption (Table 1). While there was no minimum body size for inclusion in our analyses, we only considered samples captured in summer because of low sample size for museum specimens captured in winter. Because exact coordinates are unavailable for these animals we provide approximate localities based upon the available information of capture site. We performed all analyses on log-transformed data using SPSS ver. 16.0 statistical software (SPSS Inc., Chicago, Illinois; http://www.spss.com). We conducted

FIG. 4. Image of several trees and a satellite dish damaged by acid rain in St. George's Hill (SGS), in the exclusion zone. The damaged trees are defoliated with blanched trunks and branches.

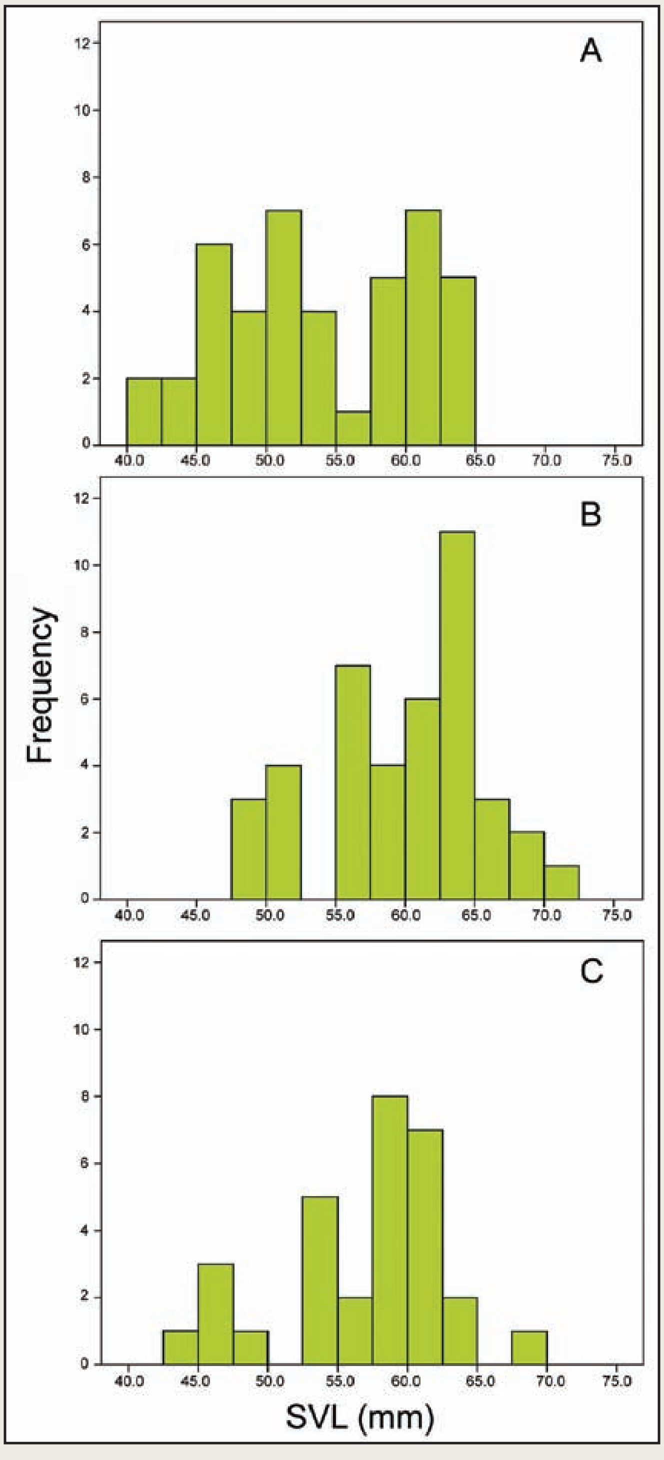

FIG. 5. Histograms depicting distributions of body length (SVL) for (a) lizards captured in winter 2009/2010, (b) museum specimens captured in summer before the eruption of 1995 (c) lizards captured in summer 2009.

a one-way ANOVA on mean body length to determine if SVL of ethanol-preserved specimens differed from that of the animals we captured in summer and in winter. We performed post-hoc tests (Tukey) to identify populations that differed from each other.

Results.—While sites in the north are qualitatively quite similar to each other, there are pronounced environmental differences between the sites visited in the exclusion zone (Table 1). Ash impact in Fox's Bay and Weeke's was low and comparable to sites outside of the exclusion zone (Air Studios, Northeast Field, Jack Boy Hill), but the remaining sites had considerably more ash present. Acid rain damage was noticeable only in St. George's Hill, although it may affect other sites to a lesser extent (Fig. 4). We noticed a distinct sulfurous odor in the air in all exclusion zone sites except Weeke's, and it was not appreciable anywhere outside of the exclusion zone. While the sites within the exclusion zone differed from each other environmentally, they were similar in that lizard abundance was very low. While lizards were abundant in the sites sampled outside of the exclusion zone, we observed only two animals (a mating pair) in a day of surveying, both of which were perching on the same tree in Weeke's.

We divided our data into three groups: winter 2009/2010, summer 2009, and summer-collected museum specimens. Histograms (Fig. 5) show the distributions of body size for the summer 2009 (N = 30, mean = 56.9 mm, SD = 5.7), winter 2009/2010 (N = 43, mean = 53.9 mm, SD = 6.8), and museum collection lizards (N = 41, mean = 59.9 mm, SD = 5.8). The male we caught in the exclusion zone (SVL = 67.9 mm) is also the largest lizard we have sampled to date across all seasons. However, several lizards from the museum collections were larger than this male, and the largest lizard sampled on Montserrat is 70.8 mm in body length. An analysis of variance (ANOVA) revealed that mean SVL differed significantly between groups sampled ($F = 9.785$, df=2, $p < 0.001$), and a post-hoc test (Tukey) showed that only the winter samples and the museum specimens were significantly different from each other ($p < 0.001$).

Discussion.—Our field observations revealed that habitats within the exclusion zone differed qualitatively in their degree of volcanic impact. Most importantly, the sites closest to the boundary of the exclusion zone, Fox's Bay and Weeke's, appeared very similar to our sampling sites outside the zone, except that a sulfurous odor was appreciable in Fox's Bay. Despite being qualitatively more similar to the northern portion of Montserrat, all sites within the exclusion were alike in that *Anolis lividus* was uniformly scarce. We sampled as close to Plymouth as we could safely get (Richmond Hill), where *A. lividus* was considered ubiquitous before the eruption and now appears absent or nearly so (Lazell 1972). The only two lizards that we found in the exclusion zone were a mating pair in Weeke's, the site that is physically closest to the exclusion boundary and also qualitatively most similar to the north. Furthermore, this male was the largest lizard by more than 3 mm that we have sampled to date (although it is also 3 mm smaller than the largest museum specimen).

Mean body size in winter-caught lizards was significantly smaller than the summer-caught museum population, which is not unexpected because body size increases from winter into the breeding season. However, if seasonal effects alone could account for the difference in body size between museum and winter-caught specimens, then the winter specimens should also be significantly smaller than our summer-caught specimens, but this is not the case. Although not significant, there is a trend towards larger average body size in the museum specimens than in the summer 2009 samples. This may reflect a collection bias towards larger animals in the museum collections, but cannot explain why we have not caught larger animals. The largest museum specimen (SVL = 70.8 mm) is much larger than the biggest (SVL = 67.9 mm) and second largest (SVL = 64.5 mm) specimen, collected at Weeke's and Happy Hill, respectively. Our collection technique is completely agnostic; we capture any adult males we see and given that larger males should be more conspicuous it appears that larger males are potentially less abundant..

Population size in anoles can be quite large, especially in the West Indies, and is fairly constant between years (Andrews 1979; Losos 2009; Schoener 1985, but see Schoener and Schoener 1978). The scarcity of anoles in the exclusion zone, an area where *A. lividus* once abounded, suggests that populations within the exclusion zone potentially go locally extinct more often, and that more persistent environmental assaults in that area may retard recolonization efforts as compared to sites further north. Although recolonization by canopy insect populations is quite rapid (Marske et al. 2007), it would likely take more time for lizards, which have a longer generation time and take longer to disperse than flying insects. Furthermore, dispersal from the north into more suitable parts of the exclusion zone may be hampered by the Belham River valley, a wide mudflat straddling the exclusion boundary, as this barren riverbed is periodically covered in ash and pyroclastic material. However, long-term ecological surveys are needed to tease apart the patterns affecting local abundance and extinction. As we sample populations at a single point in time we lack detailed data regarding the ecological fluctuations a given region has undergone due to volcanic activity that can affect local extinction and recolonization.

If periodic episodes deplete populations closer to the exclusion zone more often, then it would be rare for males to live long enough to grow very large in that area, but the largest male we sampled in our trip came from Weeke's, in the exclusion zone. It is possible that larger animals are more resilient to periodic environmental fluctuations, such as crashes in insect populations. Larger lizards are socially dominant over smaller males, and have better territories, which may be more important in areas that are periodically food-limited by crashes in insect populations (Rand 1967; Stamps and Krishnan 1994; Stuart-Smith et al. 2007; Trivers 1976). Again, more sampling in the permanent exclusion zone is needed to determine if the male we caught was rare, or if there is greater size spread in populations close to the volcano. Further investigation of *Anolis lividus* both within and outside the permanent exclusion zone will provide insights into the ecological processes influencing response to continual volcanic activity.

Material Examined.—All samples are from the Herpetology collections at the Museum of Comparative Zoology (MCZ) at Harvard University. Specimen numbers and corresponding localities are provided. MCZ 18318 (Plymouth), MCZ 38379 (Plymouth), MCZ 57785 (Plymouth), MCZ 57786 (Plymouth), MCZ 57787 (Plymouth), MCZ 65333 (Plymouth), MCZ 65335 (Plymouth), MCZ 82022 (Plymouth), MCZ 82023 (Plymouth), MCZ 82024 (Plymouth), MCZ 82025 (Plymouth), MCZ 82026 (Plymouth), MCZ 82027 (Plymouth), MCZ 82028 (Plymouth), MCZ 82032 (Woodlands), MCZ 82033 (Woodlands), MCZ 82034 (Woodlands), MCZ 82035 (Woodlands), MCZ 82036 (Woodlands), MCZ 82037 (Woodlands), MCZ 82038 (Woodlands), MCZ 82044 (Farm Estate), MCZ 82045 (Farm Estate), MCZ 82046 (Farm Estate), MCZ 82047 (Farm Estate), MCZ 82048 (Farm Estate), MCZ 82049 (Farm Estate), MCZ 82050 (Farm Estate). Collected by Julian Boos in 1970: MCZ 125465 (Salem), MCZ 125466 (Salem), MCZ 125468 (Monkey Hill River), MCZ 125469 (Monkey Hill River), MCZ 125470 (Emerald Isle Hotel), MCZ 125472 (Emerald Isle Hotel), MCZ 125473 (Emerald Isle Hotel), MCZ 125474 (Emerald Isle Hotel), MCZ 125475 (Emerald Isle Hotel), MCZ 65331 (South Soufrière), MCZ 82042 (Mount Chance), MCZ 82043 (Mount Chance), MCZ 55837 (Unknown).

Acknowledgments.—Our research was supported by National Science Foundation grants to J. H. (DEB-0816515) and our collaborator, Bruce Jackson (award number DEB-0511791). We thank R. Stewart and the Montserrat Volcano Observatory for granting permission to visit the permanent exclusion zone, R. Malin for allowing us to join his surveying team, and G. A. L. Gray and the Montserrat Department of Agriculture for expediting our requests to conduct research on *Anolis lividus*. We acknowledge the work of our field assistants and local contacts, D. Campbell, T. Campbell, J. Fergus, D. Harenda, S. Mosher, K. Parker-Johnson, E. Snyder, and S. Stuck. We thank J. Lazell, J. Boos, A. Algar, B. A. S. Bhullar, Y. Stuart, D. L. Mahler, and

J. Losos for helpful comments during the preparation of this manuscript.

LITERATURE CITED

ANDREWS, R. M. 1979. Evolution of life histories: A comparison of *Anolis* lizards from matched island and mainland habitats. Breviora 454:1–51.

BAIRD, A. H., S. J. CAMPBELL, A. W. ANGGORO, R. L. ARDIWIJAYA, N. FADLI, Y. HERDIANA, T. KARTAWIJAYA, D. MAHYIDDIN, A. MUKMININ, S. T. PARDEDE, M. S. PRATCHETT, E. RUDI, AND A. M. SIREGAR. 2005. Acehnese reefs in the wake of the Asian tsunami. Curr. Biol. 15:1926–1930.

BARBER, P. H., M. K. MOOSA, AND S. R. PALUMBI. 2002. Rapid recovery of genetic diversity of stomatopod populations on Krakatau: Temporal and spatial scales of marine larval dispersal. Proc. R. Soc. London, Ser. B 269:1591–1597.

DALSGAARD, B., G. M. HILSTON, G. A. L. GRAY, L. AYMER, J. BOATSWAIN, J. DALEY, C. FENTON, J. MARTIN, L. MARTIN, P. MURRAIN, W. J. ARENDT, D. W. GIBBONS, AND J. M. OLESEN. 2007. Impacts of a volcanic eruption on the forest bird community of Montserrat, Lesser Antilles. Ibis 149:298–312.

DAMMERMAN, K. W. 1929. Krakatau's new fauna. *In* Proceedings of the Fourth Pacific Science Congress, Batavia, pp. 83–118.

DAY, M. 1996. *Diploglossus montiserrati. In* IUCN 2009. IUCN Red List of Threatened Species. Version 2009.2.

HILTON, G. M., P. W. ATKINSON, G. A. L. GRAY, W. J. ARENDT, AND D. W. GIBBONS. 2003. Rapid decline of the volcanically threatened Montserrat oriole. Biol. Cons. 111:79–89.

LAZELL, J. D., JR. 1972. The anoles (Sauria: Iguanidae) of the Lesser Antilles. Bull. Mus. Comp. Zool. 143:1–115.

LOSOS, J. B. 2009. Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles. University of California Press, Berkeley, California. 508 pp.

———, AND R. S. THORPE. 2004. Evolutionary diversification of Caribbean *Anolis* lizards: Introduction. *In* U. Dieckmann, M. Doebeli, J. A. J. Metz, and D. Tautz (eds.), Adaptive Speciation, pp. 343–344. Cambridge University Press, Cambridge, UK.

LOVETTE, I. J., E. BERMINGHAM, AND R. E. RICKLEFS. 1999. Mitochondrial DNA phylogeography and the conservation of endangered Lesser Antillean *Icterus* orioles. Conserv. Biol. 12:1088–1096.

MARSKE, K. A., M. A. IVIE, AND G. M. HILTON. 2007. Effects of volcanic ash on the forest canopy insects of Montserrat, West Indies. Environ. Entomol. 36:817–825.

MONTSERRAT VOLCANO OBSERVATORY TEAM. 1997. The ongoing eruption in Montserrat. Science 276:371–372.

OGRODOWCZYK, A., P. MURRAIN, L. MARTIN, AND R. P. YOUNG. 2007. Recent observations of the Montserrat galliwasp (*Diploglossus montisserratti*). Herpetol. Bull. 98:9–11.

RAND, A. S. 1967. Ecology and social organization in the iguanid lizard *Anolis lineatopus*. Proc. U.S. Nat. Mus. 122:1–79.

ROBERSTON, R. E. A., W. P. ASPINALL, R. A. HERD, G. E. NORTON, R. S. J. SPARKS, AND S. R. YOUNG. 2000. The 1995–1998 eruption of the Soufrière Hills volcano, Montserrat, WI. Philos. Trans. R. Soc. London, Ser. A 358:1619–1637.

SCHNEIDER, C. J., J. B. LOSOS, AND K. DE QUEIROZ. 2001. Evolutionary relationships of the *Anolis bimaculatus* group from the northern Lesser Antilles. J. Herpetol. 35:1–12.

SCHOENER, T. W. 1985. Are lizard population sizes unusually constant through time? Am. Nat. 126:633–641.

———, AND A. SCHOENER. 1978. Estimating and interpreting body-size growth in some *Anolis* lizards. Copeia 1978:390–405.

SCHWARTZ, A., AND R. W. HENDERSON. 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History. University of Florida Press, Gainesville, Florida. 720 pp.

STAATS, C. M., AND J. J. SCHALL. 1996. Malarial parasites (Plasmodium) of *Anolis* lizards: Biogeography in the Lesser Antilles. Biotropica 29:388–393.

STAMPS, J. A. AND V. V. KRISHNAN. 1994. Territory acquisition in lizards: I. First encounters. Anim. Behav. 47:1375-1385.

STUART-SMITH, J., R. SWAIN, AND E. WAPSTRA. 2007. The role of body size in competition and mate choice in an agamid with female-biased size dimorphism. Behaviour 144:1087-1102.

THORNTON, I. 1996. Krakatau. Harvard University Press, Cambridge, Massachusetts. 346 pp.

THORPE, R. S., AND A. MALHOTRA. 1996. Molecular and morphological evolution within small islands. Philos. Trans. R. Soc. London, Ser. B 351:815–822.

TRIVERS, R. L. 1976. Sexual selection and resource-accruing abilities in *Anolis garmani*. Evolution 30:253–269.

UNDERWOOD, G. 1959. The anoles of the eastern Caribbean, Part III. Revisionary notes. Bull. Mus. Comp. Zool. 121:191–226.

WILLIAMS, E. E. 1962. The anoles of the northern Leewards, Anguilla to Montserrat: new data and a new species. Bull. Mus. Comp. Zool. 127:453–465.