Seasonal Shifts in Relative Density of the Lizard *Anolis polylepis* (Squamata, Dactyloidae) in Forest and Riparian Habitats

Seasonal Shifts in Relative Density of the Lizard *Anolis polylepis* (Squamata, Dactyloidae) in Forest and Riparian Habitats

Mason J. Ryan[1] and Steven Poe

Department of Biology and Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico 87131-0001 USA

Abstract.—Seasonal abundance is known to fluctuate in many reptile species, but comparative studies of proximal macrohabitats across seasons are rare. We surveyed for differences in abundance in a common lowland Central American forest anole, *Anolis polylepis*, across proximal forest and riparian habitats during the wet and dry seasons in southwest Costa Rica. We found that dry-season decreases in population abundance of *A. polylepis* in a forest habitat are mirrored by simultaneous increases in abundance in an adjacent riparian area. This result is compatible with seasonal movements between forest and riparian macrohabitats in *A. polylepis*. Likely causal factors for this macrohabitat shift include increased risk of desiccation and decreased prey abundance in the forest habitat during dry periods. We briefly discuss potential conservation implications of habitat shifts to suitable microhabitats on this tropical lizard.

Habitat use is a fundamental concept in ecology and refers to the physical location of animals in the environment (Whitaker et al., 1973; Chase and Leibold, 2003). *Anolis* lizards (anoles) have been model organisms in the study of habitat use, especially three-dimensional microhabitat use including perch height and diameter (Schoener and Schoener, 1971; Williams, 1972). The study of microhabitat use in anoles led to the concept of the ecomorph and increased the understanding of how species partition resources and niche space (Collette, 1961; Rand and Williams, 1969). Less studied in anoles are shifts in habitat use on a larger, macrohabitat scale such as forest interior, forest edge, or along riparian corridors. Changes in the use of macrohabitat by lizards include, for example, shifts between vegetation types (e.g., forest interior to forest edge) or between vegetated and rocky areas (Morris, 1987; Bishop and Echternacht, 2004; Schlaepfer, 2006).

Habitat use at both micro- and macroscales may vary seasonally as populations respond to differential pulses of resource distribution and availability (Spiller et al., 2010) or physiological stresses (Huey, 1991). Seasonality plays an important role in microhabitat shifts, abundance, and breeding cycles in *Anolis*. Anoles in seasonal tropical environments have been found to occupy lower perches in the dry season and higher perches in the wet season in response to prey and moisture availability (Andrews, 1971; Fleming and Hooker, 1975; Lister and Aguayo, 1992), exhibit seasonal variation in abundance (Scott, 1976; Guyer, 1990), and timing of breeding cycles (Andrews, 1971; Guyer, 1988). Seasonal resource pulses can enhance local *Anolis* densities, as in the congregation of lizards in subsidized plots in the Bahamas (Spiller et al., 2010). At the macrohabitat level, Schlaepfer and Gavin (2001) found *Anolis polylepis* and *Anolis woodi* were more abundant at the forest edge during the dry season and became more abundant in the forest interior during the wet season. The seasonal shift in lizard abundance between exposed forest edge and shaded forest interior may be driven by reduced parasitism (Schlaepfer, 2006) or insect prey abundance (Schlaepfer and Gavin, 2001).

Patterns of macrohabitat use in anoles are generally considered rigid, with the vast majority of anoles occupying strictly terrestrial/arboreal habitats with only a few species occupying stream habitats (Losos, 2009). The semi-aquatic anole lifestyle is considered a habitat specialization similar to the ecomorph classifications of terrestrial anoles (Leal et al., 2002). Although semi-aquatic anoles are not known to venture more than 4 m from riparian habitats (Eifler and Eifler, 2010), terrestrial forest anoles are known to occasionally occupy riparian habitats. Observations of streamside habitat occupancy have been noted for the forest and pasture species *Anolis pulchellus* and *Anolis cristatellus* in Puerto Rico (Heatwole et al., 1962), but the seasonality and frequency of this behavior has not been addressed.

Seasonal shifts in macrohabitat use may be detected by comparing relative abundances in different macrohabitats over time (Morris, 1987; Huey, 1991). Here, we compare seasonal density patterns of a common forest anole, *A. polylepis,* in forest and adjacent streamside macrohabitats in central southwestern Costa Rica. *Anolis polylepis* is a very abundant anole (densities up to 300 individuals/ha) that breeds throughout the year, but with a lull in the dry season, and exhibits seasonal population fluctuations (Andrews, 1971; Scott, 1976). This species is found within forested environments perched on vegetation from 0.75– 3 m during the day (Andrews, 1971) or sleeping on leaves and twigs up to 4.5 m at night (unpubl. data). We document prolonged use of streamside habitat and shifts in seasonal densities of *A. polylepis* in forest and streamside macrohabitats.

Materials and Methods

Study Site and Seasonality.—We studied seasonal habitat use in *A. polylepis* at the Tropical Forestry Initiative (T.F.I.), Tres Piedras, Puntarenas Province, Costa Rica (Decimal Degrees datum WGS84: 9.325 N; −83.8666 W; 95 m elev.). T.F.I. is located in the Golfo Dulce Region within the Pacific Lowland Tropical Moist Forest life zone (McDiarmid and Savage, 2005). Mean annual rainfall is 4730.1 ± 884.8 (SD) mm over a 53-yr period (1960–2011; no data for 1982 and 2009, unpubl. data). We follow McDiarmid and Savage (2005) in considering months with less than 200 mm of precipitation to be dry season and under this criterion January, February, and March are considered dry season months. However, during our survey period, April was abnormally dry (Fig. 1) but the 53-year monthly rainfall mean for April is 269.98 ± 132.9 mm. All surveys were conducted by MJR.

Field Methods.—Surveys were conducted in January, February, March, April, May, and June 2001, and February 2002, covering the entire dry season and first three months of the wet season. We did not survey later into the wet season because the study stream
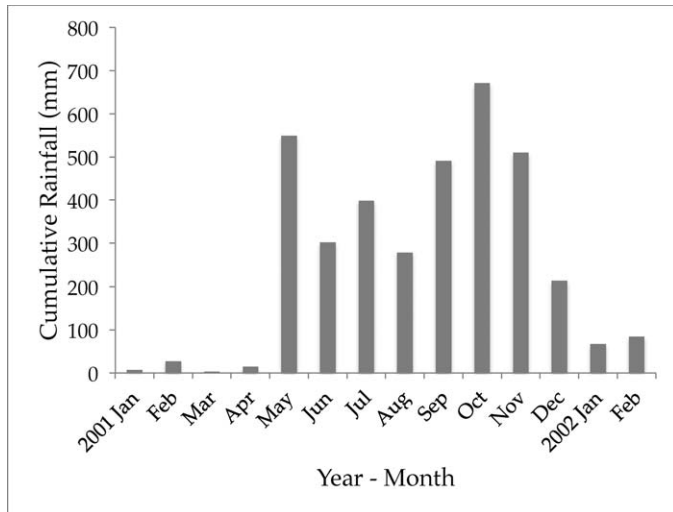
FIG. 1. Cumulative monthly rainfall during our study. Note that April is a wet season month according to the 53-yr mean monthly average, but in 2001, April rainfall was well below this average.

water level was high and unpredictable and was deemed unsafe for survey. We used a standard time-constrained transect design to estimate lizard densities in the forest and along the stream (Fisher and Foster, 2012). We established two 200-m transects in a primary forest remnant and one 300-m transect along a stream within the forest patch. The stream and forest transects were separated by approximately 275 m and the forest transects were separated by 400 m. We were limited in stream site selection because 1) it was the only stream within approximately 900 m of the study area; and 2) the ends of our 300 m stream transect were bounded by a steep waterfall and the boundary of the T.F.I. property.

Transects were surveyed at night between 1930 h and 2330 h by slowly walking and scanning the vegetation for sleeping lizards. This method is standard for detecting nocturnal amphibians and is ideal for surveying understory anoles. *Anolis polylepis* are easier to detect during nighttime surveys as opposed to traditional daytime surveys because 1) at night *A. polylepis* sleeps on exposed leaf-tops, branches, and twigs (Savage, 2002); and 2) during the day *A. polylepis* may be more difficult to observe because they may move out of sight in response to a surveyor. We counted only those lizards observed within 2 m on either side of the transect to calculate relative density. Using this method, we assume that all lizards are equally likely to be encountered in each habitat, each individual is encountered once per survey, and the surveyor (MJR) is proficient at observing lizards (i.e., Guyer and Donnelly, 2012). We recognize the limitations of this method because, on subsequent surveys, we were likely counting some of the same individuals observed in previous surveys. For this reason, we make no inference of absolute population density or size and,

instead, rely on the metric of relative density per survey to assess anole seasonal macrohabitat use between the forest and stream transects (Rodda, 2012). By repeatedly sampling the same transects, we were able to account for nightly and seasonal variation that compensates for the lack of replication or number of transects (Fisher and Foster, 2012).

Analysis.—We calculated lizard relative density as the number of lizards observed per meter for each survey and considered each survey to be a data point. Surveys of both forest transects in the same evening were combined as single data points. We recognize that the incorporation of detection probability (e.g., Mazerolle et al., 2007) would allow us to estimate absolute density of *A. polylepis*, but instead we are interested in relative density to detect seasonal habitat use. However, our comparison of relative density between sites is unlikely to be affected by the inclusion of detection probabilities unless detection probabilities are different between sites. For the reasons discussed above, we find this possibility unlikely.

We used a Kruskal–Wallis test to compare lizard densities between the dry (January through March) and wet (April through June) seasons for the forest and stream transects. We made four comparisons: forest dry versus forest wet, stream dry versus stream wet, forest dry versus stream dry, forest wet versus stream wet.

Our experimental design of surveying the same transects multiple times has advantages for consistency of habitat type and, thus, behavioral response but may lead to problems of nonindependence if surveys are spaced too close in time. In four cases, we surveyed transects within 24–48 h. To test whether these instances improperly affected our results, we performed analyses both with and without the data from the second night of consecutive surveys.

RESULTS

We conducted 41 surveys between January 2001 and February 2002, counted 239 *A. polylepis* and used these data to calculate relative density (Table 1, Fig 2). Below, we present results as P-values for two classes of analyses (consecutive surveys included, P_{CSI}; consecutive surveys excluded, P_{CSE}).

Relative density did not differ between the two forest transects within each season (dry season: $P = 0.415$, $Z = 0.761$, $\chi^2 = 0.665$; wet season: $P = 0.882$, $Z = 0.000$, $\chi^2 = 0.022$; Kruskal–Wallis test comparing between transects within dry season, wet season, respectively). There were significant seasonal (dry vs. wet) differences in relative densities within the forest transects ($P_{CSI} < 0.001$, $Z = 4.178$, $\chi^2 = 17.696$; P_{CSE} $P = 0.001$, $Z = 3.215$, $\chi^2 = 10.538$) and the stream transect ($P_{CSI} = 0.001$, $Z = -3.363$, $\chi^2 = 11.672$; P_{CSE} $P = 0.018$, $Z = -2.285$, $\chi^2 = 5.562$).

Dry season relative densities were significantly greater along the stream transect than along forest transects (Stream: $x = 0.043 \pm 0.027$/m, $N = 10$; Forest: $x = 0.013 \pm 0.011$/m, $N = 17$; $P_{CSI} <$

TABLE 1. Survey effort and lizard density summaries for the three study transects. Density was calculated as number of observations per meter of transect. See text for transect lengths. Means are presented with $\pm$ 1 SE; total observations in parentheses.

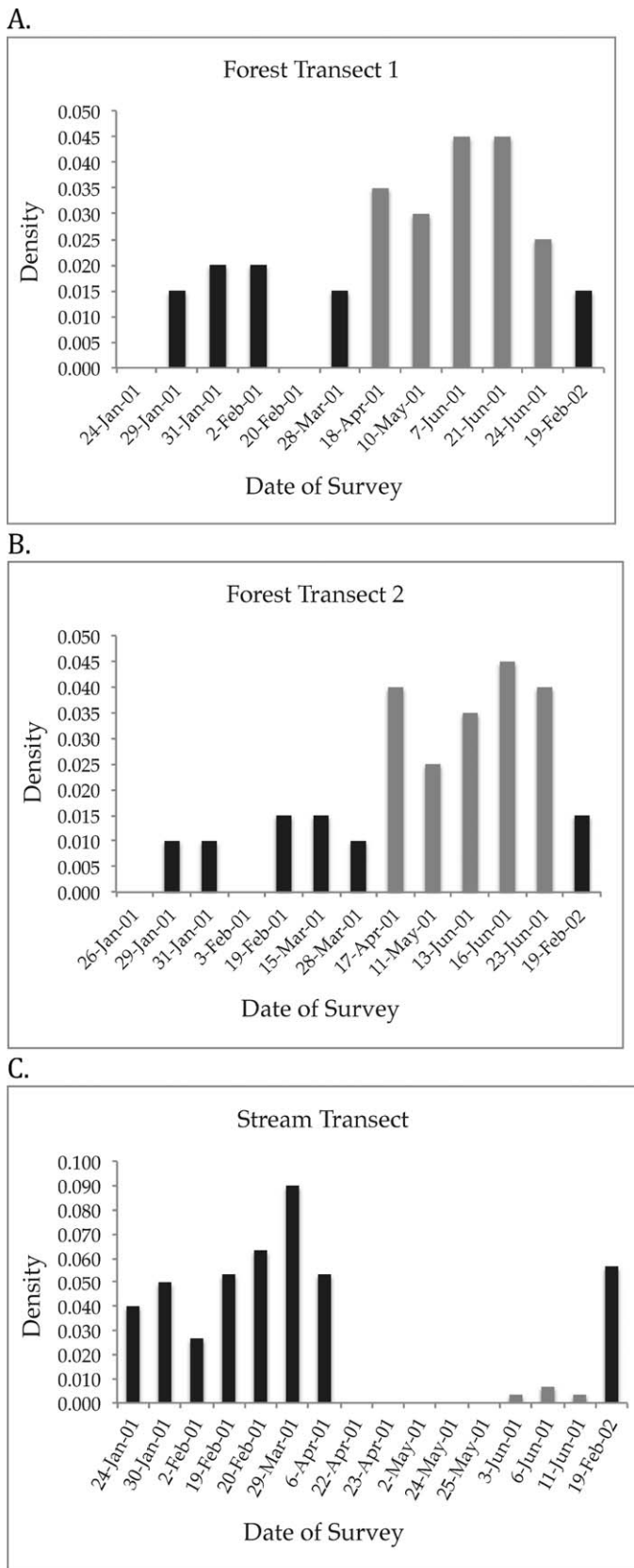| Transect	Dry season surveys	Mean dry season density	Dry season density range	Wet season surveys	Mean wet season density	Wet season density range
Forest 1	6	0.010 ± 0.008 (13)	0.00–0.020	5	0.036 ± 0.008 (36)	0.025–0.045
Forest 2	8	0.009 ± 0.006 (15)	0.00–0.015	5	0.037 ± 0.007 (37)	0.025–0.045
Forest transects combined	14	0.010 ± 0.007 (28)	0.00–0.020	10	0.036 ± 0.007 (73)	0.025–0.045
Stream	7	0.052 ± 0.019 (111)	0.02–0.09	6	0.002 ± 0.002 (4)	0.000–0.006

A.

B.

C.

FIG. 2. *Anolis polylepis* densities (individuals/meter) during sampling periods along A) Forest Transect 1; B) Forest Transect 2; and C) Stream Transect at T.F.I. Forest transects were 200 m, and the stream transect was 300 m in length. Black bars represent dry season surveys and gray bars represent wet season surveys.

0.001, $Z = 3.890$, $\chi^2 = 15.388$; $P_{CSE} = 0.004$, $Z = 2.845$, $\chi^2 = 8.274$). Wet season relative densities were significantly greater along the forest transects than were the stream transect (Stream: $x = 0.002 \pm 0.002/m$, $N = 6$, Forest: $x = 0.036 \pm 0.008/m$; $Z = 0.002$, $\chi^2 = 9.816$, $P_{CSI} < 0.001$, $Z = -3.562$, $\chi^2 = 13.007$; $P_{CSE} = 0.003$, $Z = -2.882$, $\chi^2 = 8.874$). Additional analyses with April treated as wet season (to allow for alternative views of wet/dry seasonality) obtained the same results for significance shown above.

DISCUSSION

Our study documented two novel patterns of habitat use in *A. polylepis*. First, sustained use of streamside habitat has not been noted previously for this common forest species (Andrews, 1971; Savage, 2002), even though occasional stream use of forest anoles has been noted. Although many studies on *A. polylepis* have occurred in floodplain forests or adjacent to streams, they have not quantified habitat use or density in these riparian habitats (Andrews, 1971; Perry, 1996; R. M. Andrews, pers. com.). We observed *A. polylepis* sleeping on streamside vegetation both overhanging the running water and on the stream bank. During sporadic daytime visits to the stream, we observed *A. polylepis* active on trunks, branches, and herbaceous vegetation along the banks as well as boulder islands within the stream. Our limited daytime observations suggest this species makes use of the available perches and microhabitats within the streambed. We suspect that streamside habitat use by forest anoles is far more common than has been reported. Most anole studies occur within upland forest areas (Losos, 2009) and not along streams; thus, streamside behavior cannot be observed. During our study we recorded *Anolis biporcatus*, *Anolis limifrons*, *Anolis marsupialis*, and *Anolis cupreus* along streamside habitat during the dry season. Because of the duration (3 months) and high number of streamside observations of *A. polylepis* during the dry season (Fig. 2), we believe that these observations are not isolated or accidental but represent a general aspect of this species' ecology.

Second, we document reciprocal seasonal changes in density between forest and streamside macrohabitats similar to the forest edge–forest interior density shifts seen at Las Cruces Biological Station, Costa Rica (Schlaepfer and Gavin, 2001). Dry and wet seasonal patterns are important drivers of habitat use and population fluctuations in reptiles (Bock et al., 1985; Andrews, 1991; Lister and Aguayo, 1992; Madsen and Shine, 1996). We found that densities of *A. polylepis* were higher along the stream transect during the dry season compared to adjacent forest transects, with a reciprocal macrohabitat density change during the wet season (Fig. 2). Schlaepfer and Gavin (2001) postulated that higher dry season forest edge densities were related to ectoparasite loads, which were lower in the dry, warm edge compared to the moist, cooler forest interior (Schlaepfer, 2006). In our system, the forest transects and stream were both under a forest canopy, and relative humidity was higher along the stream during the dry season compared to the forest.

Multiple nonindependent explanations exist for the seasonal differences in population density between forest and streamside habitats in *A. polylepis*. For example, *A. polylepis* may be altering its sleeping behavior seasonally such that it is more visible along streams during the dry season and in forest during the wet season. Daytime, mark–recapture surveys would be helpful in assessing this and other hypotheses related to behavioral shifts or issues of detectability but were beyond the scope of this

project. Seasonal sedentary behavior has been observed in the Mexican anole *A. nebulosus* and is hypothesized to be attributable to a combination of high predation pressures, competition, and water stress during the dry season (Lister and Aguayo, 1992).

Another possible explanation for our observed patterns is that populations of *A. polylepis* are responding to differing seasonal predation pressures from their primary predators, snakes, in the forest versus the stream (Lister and Aguayo, 1992; Brown et al., 2002). However, if predator density and predation pressures were to vary seasonally, streamside lizard densities would be expected to be lower in the dry season when snakes are more common in riparian habitats (Henderson and Hoevers, 1977; Brown and Shine, 2002; Sasa et al., 2009). In fact, we observed the opposite pattern with densities of lizards higher at streamside during the dry season.

We tentatively suggest that migration, possibly in response to decreased local resources, may be a principle driver of the observed patterns (Reagan, 1974; Spiller et al., 2010). The symmetry and timing of changes in density—the decrease in density in one habitat coincides with a comparable increase in the other habitat (Fig. 2)—is expected under the migration hypothesis, and seasonal movements have been documented for other *Anolis* (Jenssen, 2002; Bishop and Echternacht, 2004). Higher densities of invertebrate prey are likely near streams, especially in the dry season, and this hypothesized migration may be in response to depressed insect prey availability in the forest (e.g., Schlaepfer and Gavin, 2001; Levings and Windsor, 1996; Vasconcelos and Luizão, 2004). Alternatively, *A. polylepis* could migrate to the humid streambed during the dry season to avoid desiccation stress (Ruibal, 1961; Schoener and Schoener, 1971; Fleming and Hooker, 1975) or use more suitable egg-laying sites (Socci et al., 2005).

We note that these explanations of desiccation avoidance, prey availability, predation, and competition are not independent. For example, water stress can lead to a decrease in foraging efficiency, which may be further exacerbated by lower prey availability and higher predation rates in forest in the dry season. Teasing apart these interconnected factors is likely to be challenging.

Finally, there are conservation implications to these results. Under the current threat of climate change and altered rainfall patterns, the ability of anoles to use streams as seasonal refuges could have important consequences for the persistence of local populations (Dawson et al., 2011). Climate change is altering seasonal rainfall patterns and moisture levels, potentially leading to harsher dry seasons and overall drying in the lowlands and montane environments (Pounds et al., 1999; Karmalkar et al., 2008). Under harsher climatic conditions the ability of tropical lizards to shift habitat use to suitable local microhabitats such as stream corridors may increase their ability to cope with changing conditions (Dawson et al., 2011). We have shown that *A. polylepis* moves seasonally and that the movements may be an important factor in local population dynamics. Maintaining habitat corridors to streams may help anoles, as well as other reptile and amphibian species, survive in a changing world.

LITERATURE CITED

ANDREWS, R. M. 1971. Food Resource Utilization in Some Tropical Lizards. Unpubl. PhD diss., University of Kansas, Lawrence.
———. 1991. Population stability of a tropical lizard. Ecology 72:1204–1217.
BISHOP, D. C., AND A. C. ECHTERNACHT. 2004. Emergence behavior and movements of winter-aggregated green anoles (*Anolis carolinensis*) and the thermal characteristics of their crevices in Tennessee. Herpetologica 60:168–177.
BOCK, B. C., A. S. RAND, AND G. M. BURGHARDT. 1985. Seasonal migration and nesting site fidelity in the green iguana. Contributions in Marine Science 27:435–443.
BROWN, G. P., AND R. SHINE. 2002. Influence of weather conditions on activity of tropical snakes. Austral Ecology 27:596–605.
BROWN, G. P., R. SHINE, AND T. MADSEN. 2002. Responses of three sympatric snake species to tropical seasonality in northern Australia. Journal of Tropical Ecology 18:549–568.
CHASE, J. M., AND M. A. LEIBOLD. 2001. Ecological Niches: Linking Classical and Contemporary Approaches. University of Chicago Press.
COLLETTE, B. B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. Bulletin of the Museum of Comparative Zoology 125:137–162.
DAWSON, T. P., S. T. JACKSON, J. I. HOUSE, I. C. PRENTICE, AND G. M. MACE. 2011. Beyond predictions: biodiversity conservation in a changing climate. Science 332:53–58.
EIFLER, D. A., AND M. A. EIFLER. 2010. Use of habitat by the semiaquatic lizard, *Norops aquaticus*. Southwestern Naturalist 55:466–469.
FISHER, R. N., AND M. S. FOSTER. 2012. Study design and sampling. *In* R. W. McDiarmid, M. S. Foster, C. Guyer, J. W. Gibbons, and N. Chernoff (eds.), Reptile Biodiversity Standard Methods for Inventorying and Monitoring, pp. 27–50. University of California Press, USA.
FLEMING, T. H., AND R. S. HOOKER. 1975. *Anolis cupreus*: the response of a lizard to tropical seasonality. Ecology 56:1243–1261.
GUYER, C. 1988. Food supplementation in a tropical mainland anole, *Norops humilis*: effects of individuals. Ecology 69:362–369.
———. 1990. The herpetofauna of La Selva, Costa Rica. *In* A. H. Gentry (ed.), Four Neotropical Rainforests, pp. 371–385. Yale University Press, USA.
GUYER, C., AND M. A. DONNELLY. 2012. Visual encounter surveys. *In* R. W. McDiarmid, M. S. Foster, C. Guyer, J. W. Gibbons, and N. Chernoff (eds.), Reptile Biodiversity Standard Methods for Inventorying and Monitoring, pp. 218–220. University of California Press, USA.
HEATWOLE, H., E. ORTIZ, A. M. DIAZ-COLLAZO, AND A. R. JIMINEZ-VELEZ. 1962. Aquatic tendencies in the Puerto Rican pasture-lizard, *Anolis pulchellus*. Herpetologica 17:272–274.
HENDERSON, R. W., AND L. G. HOEVERS. 1977. The seasonal incidence of snakes at a locality in northern Belize. Copeia 1977:349–355.
HUEY, R. B. 1991. Physiological consequences of habitat selection. American Naturalist 137:S91–S115.
JENSSEN, T. A. 2002. Spatial awareness by the lizard *Anolis cristatellus*: why should a non-ranging species demonstrate homing behavior? Herpetologica 58:364–371.
KARMALKAR, A. V., R. S. BRADLEY, AND H. F. DIAZ. 2008. Climate change scenario for Costa Rican montane forests. Geophysical Research Letters 35:L11702.
LEAL, M., A. K. KNOX, AND J. B. LOSOS. 2002. Lack of convergence in aquatic *Anolis* lizards. Evolution 56:785–791.
LEVINGS, S. C., AND D. M. WINDSOR. 1996. Seasonal and annual variation in litter arthropods. *In* E. G. Leigh Jr., A. S. Rand, and D. M. Windsor (eds.), The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes, pp. 355–388. Smithsonian Institution Press, Washington, DC.
LISTER, B. C., AND A. G. AGUAYO. 1992. Seasonality, predation, and the behavior of a tropical mainland anole. Journal of Animal Ecology 61:717–733.

Losos, J. B. 2009. Lizards in an Evolutionary Tree, Ecology and Adaptive Radiation of Anoles. University of California Press, USA.

Madsen, T., and R. Shine. 1996. Seasonal migration of predators and prey—a study of pythons and rats in tropical Australia. Ecology 77:149–156.

Mazerolle, M. J., L. L. Bailey, W. L. Kendall, J. A. Royle, S. J. Converse, and J. D. Nichols. 2007. Making great leaps forward: accounting for detectability in herpetological field studies. Journal of Herpetology 41:672–689.

McDiarmid, R. W., and J. M. Savage. 2005. The herpetofauna of the Rincón area, Península de Osa, Costa Rica, a Central American lowland evergreen forest site. In M. A. Donnelly, B. I. Crother, C. Guyer, M. H. Wake, and M. E. White (eds.), Ecology and Evolution in the Tropics: A Herpetological Perspective, pp. 366–427. University of Chicago Press.

Morris, D. W. 1987. Ecological scale and habitat use. Ecology 68:362–369.

Perry, G. 1996. The evolution of sexual dimorphism in the lizard Anolis polylepis (Iguania): evidence from intraspecific variation in foraging behavior and diet. Canadian Journal of Zoology 74:1238–1245.

Pounds, J. A., M. P. L. Fogden, and J. H. Campbell. 1999. Biological response to climate change on a tropical mountain. Nature 398:611–615.

Rand, A. S., and E. E. Williams. 1969. The anoles of La Palma: aspects of their ecological relationships. Breviora 327:1–19.

Reagan, D. P. 1974. Habitat selection in the three-toed box turtle, Terrapene carolina triunguis. Copeia 1974:512–527.

Rodda, G. H. 2012. Population size and demographics. In R. W. McDiarmid, M. S. Foster, C. Guyer, J. W. Gibbons, and N. Chernoff (eds.), Reptile Biodiversity Standard Methods for Inventorying and Monitoring, pp. 283–322. University of California Press, USA.

Ruibal, R. 1961. Thermal relations of five species of tropical lizards. Evolution 15:98–111.

Sasa, M., D. K. Wasko, and W. W. Lamar. 2009. Natural history of the terciopelo Bothrops asper (Serpentes: Viperidae) in Costa Rica. Toxicon 54:904–922.

Savage, J. M. 2002. The Amphibians and Reptiles of Costa Rica: A Herpetofauna between Two Continents, between Two Seas. University of Chicago Press.

Schlaepfer, M. A. 2006. Growth rates and body condition in Norops polylepis (Polychrotidae) vary with respect to sex but not mite load. Biotropica 38:414–418.

Schlaepfer, M. A., and T. A. Gavin. 2001. Edge effects on lizards and frogs in tropical forest fragments. Conservation Biology 15:1079–1090.

Schoener, T. W., and A. Schoener. 1971. Structural habitats of West Indian Anolis lizards. I. Jamaican lowlands. Breviora 368:1–53.

Scott, N. J. 1976. The abundance and diversity of the herpetofauna of tropical forest litter. Biotropica 8:41–58.

Socci, A. M., M. A. Schlaepfer, and T. A. Gavin. 2005. The importance of soil moisture and leaf cover in a female lizard's (Norops polylepis) evaluation of potential oviposition sites. Herpetologica 61:233–240.

Spiller, D. A., J. Piovia-Scott, A. N. Wright, L. H. Yang, G. Takimoto, T. W. Schoener, and T. Iwata. 2010. Marine subsidies have multiple effects on coastal food webs. Ecology 91:1424–1434.

Vasconcelos, H. L., and F. J. Luizão. 2004. Litter production and litter nutrient concentrations in a fragmented Amazonian landscape. Ecological Applications 14:884–892.

Whitaker, R. H., S. A. Levin, and R. B. Root. 1973. Niche, habitat, and ecotope. American Naturalist 107:321–338.

Williams, E. E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. Evolutionary Biology 6:47–89.