



Size-Related Habitat Use by Nonbreeding *Anolis carolinensis* Lizards
Author(s): Thomas A. Jenssen, Katheryn A. Hovde, Kendall G. Taney
Reviewed work(s):
Source: *Copeia*, Vol. 1998, No. 3 (Aug. 3, 1998), pp. 774-779
Published by: [American Society of Ichthyologists and Herpetologists \(ASIH\)](http://www.asih.org/)
Stable URL: <http://www.jstor.org/stable/1447814>
Accessed: 12/01/2012 15:31

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



American Society of Ichthyologists and Herpetologists (ASIH) is collaborating with JSTOR to digitize, preserve and extend access to *Copeia*.

<http://www.jstor.org>

Size-Related Habitat Use by Nonbreeding *Anolis carolinensis* Lizards

THOMAS A. JENSSEN, KATHERYN A. HOVDE, AND KENDALL G. TANEY

Studies on sympatric anoline faunas as models of community structure have led to the progressive formulation of the “ecomorph” concept (Williams, 1969, 1972, 1983). Embodied in this term is the view that associated *Anolis* species, which characteristically partition the habitat (e.g., Haefner, 1988), converge on predictable phenotypes peculiar to each species’ particular habitat niche (e.g., crown-anoles, trunk-anoles, grass-anoles). Collette (1961) first suggested this ecomorphological correlation between a species’ limb and body morphology and its structural habitat niche. Behavioral (e.g., Moermond, 1979; Pounds, 1988) and physiological correlates (e.g., Garland and Losos, 1994) were further incorporated into the ecomorph concept, with Losos (1990a, 1990b, 1990c) testing the concept’s robustness across phylogenetic assemblages.

Most of the ecomorphology studies, however, have been based on (1) data from sympatric anoline faunas in which interspecific competition, particularly for food (e.g., Schoener, 1977), was inferred as a prime influence on ecomorph differentiation; (2) data usually from adults; and (3) data collected when proximate mechanisms of sexual selection might influence intraspecific habitat profiles because many anoline species are sexually active for most and sometimes all of the circannual cycle (see review in Jenssen and Nunez, 1994). To avoid some of the above issues and to further expand the ecomorph concept into a different ecological context, we made a simple set of habitat observations during the postbreeding period on all size classes of a habitat generalist with no endemic congeneric competitors. We hypothesized that, if habitat physiognomy is influencing interspecific habitat use, the same phenomenon should apply to different size classes within a species. In accord with this prediction, our data showed a nonrandom connection between the ontogeny of body size and microhabitat utilization. From these data, we suggest that the ecomorph concept may also have a developmental-ecological application within the perspective of the ontogenetic niche (sensu West and King, 1987).

MATERIALS AND METHODS

Our subject, *Anolis carolinensis*, is a widely distributed, habitat generalist, having adapted to

microclimates from subtropical Florida to temperate Oklahoma and Tennessee (Conant, 1975) as well as to arboreal habitats which include palmetto scrub, seagrape beach scrub, cypress-tupelo swamp, deciduous hardwoods, and human habitations and plantings. *Anolis carolinensis* densities are greatest in mesic, ecotonal, or edge situations, where bodies of water, trails, or fields create breaks in the canopy (Michaud, 1990). Being the most northerly distributed member of its tropical genus, *A. carolinensis* has a distinct four-month breeding period and no endemic congeners (though eight exotic *Anolis* species are currently in Florida; Meshaka et al., 1997).

Our observations were made in a species-typical, bottomland hardwood habitat along the Augusta canal (12 km northwest of Augusta, GA). Data collection occurred from late August to late September 1992, during the beginning of the postreproductive period (Jenssen et al., 1995a) when numbers of all size classes of lizards were maximally represented and reproductive activities had ceased. We performed a walking census (Rand, 1967) to locate subjects along a 2-km transect formed by the canal’s tow path. The path created an edge effect which enhanced a consistent, broad spectrum of *A. carolinensis* microhabitats.

During a census, we surveyed the vegetation on both sides of the path, from low growth annuals and herbaceous understory to the upper tree canopies. When a lizard was spotted, we estimated its body size, perch height, perch diameter, and type of microhabitat in which it was perching. Observer effect had no impact on the dataset because the observer-to-subject distances (> 2 m) never invoked flight behavior, though occasional subjects did show subtle intention movements for avoidance.

Variables were estimated in the following ways. Size (snout-vent length, SVL) was assigned visually to one of five classes: (1) hatchling, ≤ 22 mm; (2) small juvenile, 23–29 mm; (3) large juvenile, 30–39 mm; (4) subadult to small adult, 40–49 mm; and (5) medium to large adult, 50–70 mm. Because sexual size dimorphism of *A. carolinensis* is pronounced in adults (Jenssen et al., 1995b), we could also identify at a distance the sex for size-class 5 lizards. As a reference to calibrate our size estimates, a series of full-scale lizard silhouettes,

corresponding to the five size classes, was drawn on a cue card attached to our field clipboard. In addition, we occasionally noosed and measured a subject to check and maintain our SVL estimates. Perch heights and diameters were visually estimated using a 2-m pole and a 30-cm rule as references. The perch diameter of leaves posed a quantitative problem, given the disparity between width and thickness as possible dimensions. We chose width because leaf surface was what directly supported the lizard. As modified from Jenssen et al. (1984), we ranked the quality of the immediate microhabitat by assigning the subject's perch site to one of five habitat types: (1) grasses and low annuals; (2) low shrubs (< 2 m high); (3) tall shrubs (> 2 m high); (4) small trees (< 5 m high); and (5) large trees (> 5 m high).

A total of 599 habitat records were accumulated from nine censuses (approximately two per week) along the census route during daylight (0900–1600 h) and weather conditions when the lizards were active. Though the census route was long, the habitat complex, and each census separated by two or more days, there still remained the possibility that the same lizard may have been observed more than once at the same locality. Therefore, to cancel correlation effects due to the potential of replicate observations, we simply used the mean values from each size class ($n = 5$) and from each census ($n = 9$) as individual datum (total $n = 45$) for each variable. The class means for each variable were then plotted for the nine censuses to indicate a conservative estimate of intercensus variance across time. To examine for an ontogenetic shift in habitat use, selected statistical procedures were run with SAS software (Statistical Analysis Systems, vers. 6, Cary, NC, 1988, unpubl.).

RESULTS

Mean census values for all three habitat variables progressively increased with increasing body size (size classes 1–5) of *A. carolinensis* (Fig. 1). A multiple regression analysis (SAS, GLM procedure) based on census means for each size class was statistically significant ($P < 0.0001$) for all variables (perch height, $R^2 = 0.73$; perch diameter, $R^2 = 0.66$; habitat type, $R^2 = 0.85$). Across the ranked size-classes, a trend analysis (SAS, GLM procedure, Contrast) found a significant linear correlation ($P < 0.0001$) for perch heights and microhabitat types ($F = 63.69, 46.78$, respectively) and significant linear and quadratic correlations for perch diameters ($F = 44.10, P = 0.0001$; $F = 10.41, P = 0.0025$;

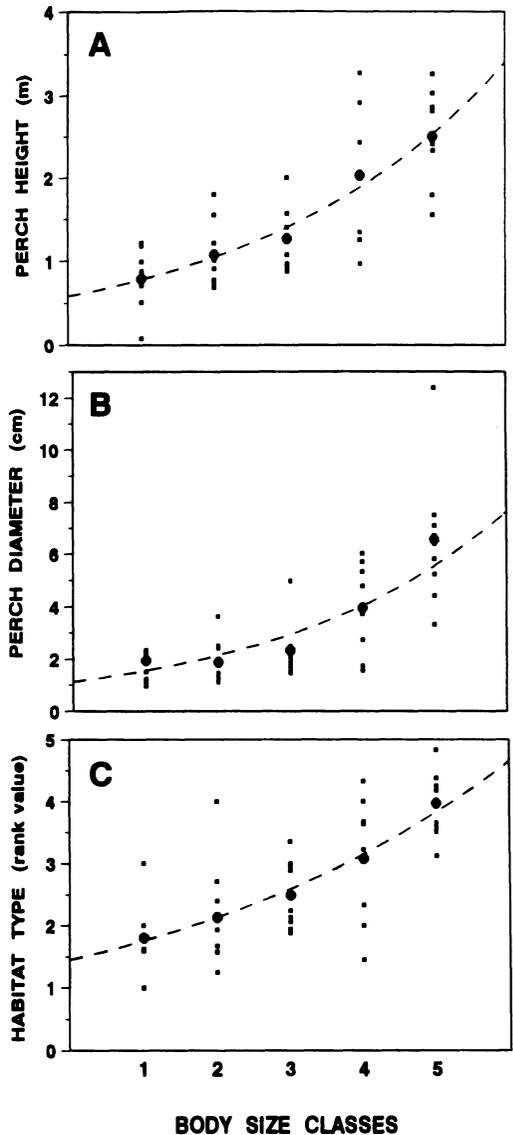


Fig. 1. Nine mean census values (based on 599 total observations) for each habitat variable: (A) perch height; (B) perch diameter; and (C) habitat type from five size classes (1, hatchlings; 2, small juveniles; 3, large juveniles; 4, subadults to small adults; and 5, medium to large adults) of nonbreeding *Anolis carolinensis* near Augusta, Georgia. Each large dot depicts the mean of mean size class censuses; dashed line is fitted to mean of means for each size class.

respectively; Fig. 1). In addition, the use of leaves as a supporting substratum progressively decreased with increasing body size; the proportion of leaf use by size class was as follows: (1) 62%; (2) 45%; (3) 38%; (4) 32%; and (5) 10%.

An intersexual comparison was made for size-

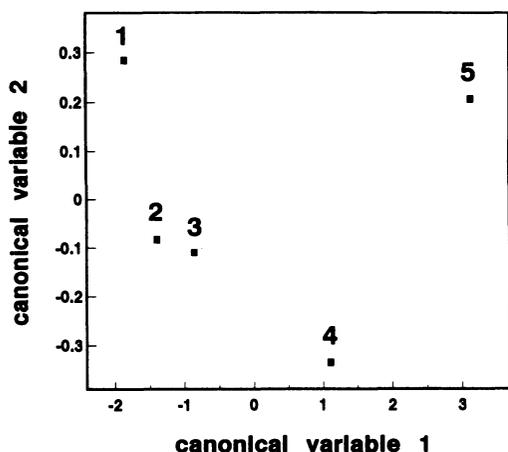


Fig. 2. Canonical discriminant analysis of mean values from nine censuses from three habitat variables for five size classes of nonbreeding *Anolis carolinensis*, where the numbered dots represent the centroids for the following: (1) hatchlings; (2) small juveniles; (3) large juveniles; (4) subadults to small adults; and (5) medium to large adults. Axis 1 portrays 98% of total variance.

class 5 adults (76 females, 109 males), with no significant differences (SAS, GLM procedure, Wilcoxon Rank Sums) in perch height ($Z = 0.78$, $P = 0.43$), perch diameter ($Z = -1.36$, $P = 0.18$), or habitat type ($Z = 1.31$, $P = 0.19$). The absence of an intersexual effect remained, even when comparing much different sized adults. A comparison of the smaller of the size-class 5 females (medium-sized, approximately 50–59 mm SVL, $n = 62$) with the largest of the size-class 5 males (large-sized, approximately 66–70 mm SVL, $n = 27$) revealed no significant differences for perch height ($Z = -1.20$, $P = 0.23$), perch diameter ($Z = -1.11$, $P = 0.27$), and habitat type ($Z = -1.18$, $P = 0.24$).

The three habitat variables, all of which were highly significant in the general linear model (see above), were integrated using a multivariate canonical analysis (SAS, CANDISC procedure). This analysis summarized the total variation and presented the between size-class variation graphically. The spatial relationship among the centroids (i.e., mean value for size-class variance) for the five size classes indicates the relative habitat segregation among the size classes with regard to habitat type and perch height and diameter (Fig. 2). The intercentroid spacing along the first canonical axis, which explains 97.9% of the model variance (eigenvalue 3.924), quantifies the progressive shift of growing lizards from low, thinly structured substrata to more elevated, structurally diverse substrata.

Centroids for size-classes 4 and 5 (subadults to large adults) have the greatest separation from the other size classes. Of lesser importance (2% of explained variance, eigenvalue 0.056) was the vertical separation of centroids along the second canonical axis on which only the small and large juveniles were clustered.

DISCUSSION

In their study of sympatric Jamaican anoles, Powell and Russell (1992) raised the question of ontogenetic effects on the structural niche of an ecomorph but found little evidence for intraspecific differences in structural niche use. Our data, however, document an ontological correlate to *A. carolinensis* habitat use. Our analysis was very conservative, and, though measured for a single population, the trend for higher and larger substrata with increasing body size is a reasonable generalization for the species.

Much speculation can be generated to explain habitat segregation by body size, but from current data, some possible causations are better supported for *A. carolinensis* than others. We address briefly the following hypotheses: competition avoidance, competitive interference, cannibalism, habitat-specific predation, and habitat-matrix model. The competition-avoidance hypothesis (e.g., Schoener, 1967, 1968), when applied to intraspecific responses for food, predicts the selection for sexual dimorphism in adult foraging habitat and body size (particularly trophic structures) to reduce competition for similar prey size and taxa. This hypothesis, which would have the most potential in food-limited communities (e.g., Andrews, 1976), was not supported in our study. There was no evidence of intersexual habitat segregation among the size-class 5 adults, even when comparing small females with large males. Further, a behavioral ecology study of our population (Nunez et al., 1997) revealed no indication of food as a limiting resource. Though *A. carolinensis* is sexually dimorphic, Jenssen et al. (1995b) found more evidence to infer a sexually selected size dimorphism than size dimorphism being the result of intersexual competition. Still, on a broader scale, there is the possibility that *A. carolinensis* food items (e.g., arachnids and insects; King, 1966) are distributed by size in the habitat in a parallel manner to that of lizard sizes and, as a result, are responsible for the ontological distribution of *A. carolinensis* habitat use. Although this potential cannot be dismissed, it would seem unlikely, given the diversity of arthropod species, their lifestyles, and

dispersal abilities. Anecdotally, from 218 observed foraging events by adults (Jenssen et al., 1995a; Nunez et al., 1997), prey size did not appear to be related to perch height. In addition, field notes contain examples of small prey occurring at height being taken by large lizards (e.g., aggregation of midges 3 m high on a limb being eaten by an adult male), whereas large potential prey occurring in low habitat could even be a threat to small lizards (e.g., a garden spider in tall grass having captured a hatchling lizard).

Competitive interference between size classes of lizards would be a directly observable expression of competition and could lead to habitat partitioning. For example, larger lizards might aggressively exclude juveniles from preferred arboreal perch sites in the canopy, leaving immatures to occupy less contested positions in the grass and shrubs. However, in extensive focal observations on our study site, no adult male or female (with one pathological exception; Jenssen and Hovde, 1993) was seen to directly approach or aggressively respond to a juvenile or hatchling (Jenssen et al., 1995a; Nunez et al., 1997). If lizards of the smaller size classes had a definite preference for the modal range of adult perch sites, there was opportunity both within the large volumes of adult female (8 m³) and male (69 m³) home ranges (Nunez et al., 1997) and in occasional clumps of adult-free habitat.

Cannibalism, another form of competitive interference, is a widespread phenomenon in reptiles (Mitchell, 1986). If the adults of a species had a tendency toward conspecific predation, then small lizards vulnerable to ingestion would be selected to avoid adult microhabitats. As indicated for the competitive interference hypothesis, no stalking or attack behavior has been observed for our population (Jenssen et al., 1995a; Nunez et al., 1997). In addition, a controlled study by Gerber (*Anolis* Newsletter IV:49–53, unpubl., 1989; pers. comm.) failed to observe cannibalism when *A. carolinensis* hatchlings were paired in cages with hungry adults for as long as 24 h. The experimental conditions were not necessarily inhibiting cannibalistic behavior because, in a parallel experiment, adult *Anolis sagrei* readily ate *A. carolinensis* juveniles.

Habitat-specific predation is a phenomenon observed by Stamps (1983), where juvenile *Anolis aeneus* occupy a separate habitat (open scrub) from conspecific adults (shaded forest). Stamps concluded that the ontogeny-related divergence in *A. aeneus* habitat was caused by a large lizard (*Anolis richardi*), syntopic with the adult *A. aeneus*, which preyed on those juvenile

A. aeneus who shifted into the adult habitat before reaching a nonvulnerable size. This model does not exactly fit our pattern of size-related habitat use because there is no bimodal habitat segregation between small and large *A. carolinensis* (Fig. 1), and there is no apparent habitat-specific predator (Jenssen et al., 1995a; Nunez et al., 1997).

The habitat-matrix model (e.g., Pounds, 1988), a restatement of the ecomorph concept, is a biomechanical perspective which postulates that a species' structural habitat matrix selects for a predictable morphological phenotype, optimizing whole body performance within the given microhabitat (for experimental evidence, see Losos et al., 1997). The predictions of this model are consistent and most parsimonious with our observations of *A. carolinensis* habitat use, not in the context of convergent evolution but rather within the context of ontogeny.

As examples, anoline species that use narrow branches and twigs are smaller with shorter hind limbs than anoles that use wide branches and tree trunks (e.g., Irschick and Losos, 1996), and sprint speeds also drop off with decreasing perch diameters, including those for adult *A. carolinensis* (Losos and Irschick, 1996). Thus, as a matter of scale and mass, the small bodies of hatchlings and juveniles would have uncompromised locomotion performance, including running and jumping thrust, on small diameter and flexible substrata (e.g., leaves and blades of grass). Conversely, adult *A. carolinensis* should not frequent low, narrow, and less rigid habitat substrata, where maneuvering agility for foraging and escape would degrade. In accord with the habitat-matrix model, our data show a progressive increase of larger (and higher) perch dimensions with increasing body size, as well as a decreased use of leaves with increasing body size.

Hatchling and juvenile locomotion may be optimal within the low grass/bush habitat matrix, but presumably larger and more rigid substrata of the adult perches would suffice for small bodies as well as for large ones. Why smaller individuals are not more widely dispersed in the entire range of the available habitat is less evident under the habitat-matrix model. Perhaps the small body size, with its slower sprint speed and lower thermal inertia, is best suited in the dense stem/leaf structure of the grass/bush microhabitat. There, small juvenile *A. carolinensis* may find better crypsis, more immediate escape routes, and a finer mosaic of sun and shade than in the trees with their more open matrix of trunks and branches.

ACKNOWLEDGMENTS

We appreciate the suggestions of M. Lovern and K. Passek, the consultants at the Virginia Tech Statistics Consulting Center, J. Arnold, K. Hinkelmann, and E. Smith, and the research opportunity and support provided by J. Congdon and the Savannah River Ecology Laboratory through the Financial Assistance Award Number DE-FC09-96SR18546 from the U.S. Department of Energy to the University of Georgia Research Foundation.

LITERATURE CITED

- ANDREWS, R. M. 1976. Growth rate in island and mainland lizards. *Copeia* 1976:477-482.
- COLLETTE, B. B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. *Bull. Mus. Comp. Zool.* 125:137-162.
- CONANT, R. 1975. A field guide to reptiles and amphibians of eastern and central North America. Houghton Mifflin Co., Boston, MA.
- GARLAND, T., AND J. B. LOSOS. 1994. Ecological morphology of locomotor performance in squamate reptiles, p. 240-302. *In: Ecological morphology: integrative organismal biology.* P. C. Wainwright and S. M. Reilly (eds.). Univ. of Chicago Press, Chicago.
- HAEFNER, J. W. 1988. Assembly rules for Greater Antilles *Anolis* lizards: competition and random models compared. *Oecologia* 74:551-565.
- IRSCHICK, D. J., AND J. B. LOSOS. 1996. Morphology, ecology, and behavior of the twig anole, *Anolis angusticeps*, p. 291-301. *In: Contributions to West Indian herpetology: a tribute to Albert Schwartz.* R. Powell and R. W. Henderson (eds.). Society for the Study of Amphibians and Reptiles, Ithaca, NY.
- JENSSEN, T. A., AND K. A. HOVDE. 1993. *Anolis carolinensis* (Green Anole). *Social Pathology Herpetol. Rev.* 24:58-59.
- , AND S. C. NUNEZ. 1994. Male and female reproductive cycles of the Jamaican lizard, *Anolis opalinus*. *Copeia* 1994:767-780.
- , D. L. MARCELLINI, C. A. PAGUE, AND L. A. JENSEN. 1984. Competitive interference between the Puerto Rican lizards, *Anolis cooki* and *Anolis cristatelus*. *Ibid.* 1984:853-862.
- , N. GREENBERG, AND K. A. HOVDE. 1995a. Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. *Herpetol. Monogr.* 9:41-62.
- , J. D. CONGDON, R. U. FISCHER, R. ESTES, D. KLING, AND S. EDMANDS. 1995b. Morphological characteristics of the lizard, *Anolis carolinensis*, from South Carolina. *Herpetologica* 51:401-411.
- KING, F. W. 1966. Competition between two south Florida lizards of the genus *Anolis*. Unpubl. Ph.D. diss., Univ. of Miami, Coral Gables, FL.
- LOSOS, J. B. 1990a. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecol. Monogr.* 60:369-388.
- . 1990b. The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* 44:1189-1203.
- . 1990c. Concordant evolution of locomotor behaviour, display rate, and morphology of *Anolis* lizards. *Anim. Behav.* 39:879-890.
- , AND D. J. IRSCHICK. 1996. The effect of perch diameter on escape behaviour of *Anolis* lizards: laboratory predictions and field tests. *Ibid.* 51:593-602.
- , K. I. WARHEIT, AND T. W. SCHOENER. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature* 387:70-73.
- MESHAKA, W. E., R. M. CLOUSE, B. P. BUTTERFIELD, AND J. B. HAUGE. 1997. The Cuban anole, *Anolis porcutus*: a new anole established in Florida. *Herpetol. Rev.* 28:101-102.
- MICHAUD, E. 1990. Geographic variation of life history traits in the lizard, *Anolis carolinensis*. Unpubl. Ph.D. diss., Univ. of Tennessee, Knoxville.
- MITCHELL, J. C. 1986. Cannibalism in reptiles: a worldview review. *Study Amphib. Reptiles Herpetol. Cir.* 15:1-23.
- MOERMOND, T. C. 1979. Habitat constraints on the behavior, morphology, and community structure of *Anolis* lizards. *Ecology* 60:152-164.
- NUNEZ, S. C., T. A. JENSSEN, AND K. ERSLAND. 1997. Female activity profile of a polygynous lizard (*Anolis carolinensis*): evidence of intersexual asymmetry. *Behaviour* 134:205-223.
- POUNDS, J. A. 1988. Ecomorphology, locomotion, and microhabitat structure: patterns in a tropical mainland *Anolis* community. *Ecol. Monogr.* 58:299-320.
- POWELL, G. L., AND A. P. RUSSELL. 1992. Locomotor correlates of ecomorph designation in *Anolis*: an examination of three sympatric species from Jamaica. *Can. J. Zool.* 70:725-739.
- RAND, A. S. 1967. Ecology and social organization in the iguanid lizard *Anolis lineatopus*. *Proc. U.S. Nat. Mus.* 122:1-79.
- SCHOENER, T. W. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* 155:474-477.
- . 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49:704-726.
- . 1977. Competition and the niche, p. 35-136. *In: Biology of the Reptilia. Ecology and behaviour A.* Vol. 7. C. Gans and D. W. Tinkle (eds.). Academic Press, New York.
- STAMPS, J. A. 1983. The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). *Behav. Ecol. Sociobiol.* 12:19-33.
- WEST, M. J., AND A. P. KING. 1987. Settling nature and nurture into an ontogenetic niche. *Devel. Psychol.* 20:549-562.
- WILLIAMS, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *Q. Rev. Biol.* 44:345-389.
- . 1972. The origin of faunas: evolution of lizard congeners in a complex island fauna—a trial analysis. *Evol. Biol.* 6:47-89.
- . 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*, p.

326–370. *In*: Lizard ecology: studies of a model organism. R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.). Harvard Univ. Press, Cambridge, MA.

(TAJ, KGT) BIOLOGY DEPARTMENT, VIRGINIA TECH, BLACKSBURG, VIRGINIA 24061; AND

(KAH) UNIVERSITY OF GEORGIA, SAVANNAH RIVER ECOLOGY LABORATORY, DRAWER E, AIKEN, SOUTH CAROLINA 29802. E-mail: tjenssen@vt.edu. Send reprint requests to TAJ. Submitted: 24 April 1997. Accepted: 21 Nov. 1997. Section editor: S. T. Ross.