Literature Cited

- Bailey, L.L., W.L. Kendall, D.R. Church, and H.M. Wilbur. 2004. Estimating survival and breeding probability for pond-breeding amphibians: A modified robust design. *Ecology* 85:2456–2466.
- Bruce, R.C. 1982. Egg-laying, larval periods and metamorphosis of *Eurycea bislineata* and *E. junaluska* at Santeetlah Creek, North Carolina. *Copeia* 1982:755–762.
- Folkerts, G.W. 1971. Ecotypic variation in salamanders of the southeastern U.S. Herpetological Review 3:106.
- Forester, D.C. 1977. Comments on the female reproductive cycle and philopatry by *Desmognathus ochrophaeus* (Amphibia, Urodela, Plethodontidae). *Journal of Herpetology* 11:311–316.
- Jones, T.R. 1980. A reevaluation of the salamander, Eurycea aquatica Rose and Bush (Amphibia: Plethodontidae). Unpubl. M.S. Thesis, Auburn University, Auburn, Alabama.
- Kozak, K.H., R.A. Blaie, and A. Larson. 2006. Gene lineages and eastern North American paleodrainage basins: Phylogeography and speciation of the *Eurycea bislineata* complex. *Molecular Ecology* 15:191–207.
- Mount, R.H. 1975. Amphibians and Reptiles of Alabama. Auburn Printing Co., Auburn, Alabama.

- Pauley, T.K. and M.B. Watson. 2005. Eurycea cirrigera, pp. 740–743. In: M. Lannoo (ed.), Amphibian Declines: Status of United States Species. University of California Press, Berkeley.
- Petranka, J.W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D.C.
- Rose, F.L. and F.M. Bush. 1964. A new species of *Eurycea* (Amphibia: Caudata) from the southeastern United States. *Tulane Studies in Zoology* 10:121–128.
- Sever, D.M. 2005a. Eurycea bislineata, pp. 735–738. In: M. Lannoo (ed.), Amphibian Declines: Status of United States Species. University of California Press, Berkeley.
- Sever, D.M. 2005b. Eurycea wilderae, pp. 770–772. In: M. Lannoo (ed.), Amphibian Declines: Status of United States Species. University of California Press, Berkeley.
- Timpe, E.K., S.P. Graham, and R.M. Bonett. 2009. Phylogeography of the Brownback Salamander reveals patterns of local endemism in southern Appalachian springs. *Molecular Phylogenetics and Evolution* 52:368–376.
- Wells, K.D. 2007. *The Ecology and Behavior of Amphibians*. University of Chicago Press, Chicago, Illinois.

Perch Height Differences among Female Anolis polylepis Exhibiting Dorsal Pattern Polymorphism

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Female-limited dorsal pattern variation within a species has been of interest to naturalists for years, and has been observed in animals ranging from spiders, damselflies, and dragonflies to frogs and lizards. Protection against predation by birds has been offered as a preliminary explanation for the evolution of these patterns, especially from birds that have acute color vision and which preferentially prey on females because they are less agile and more nutritious (Stamps and Gon 1983).



Fig. 1. Male *Anolis polylepis* with dewlap extended (right) and female *A. polylepis* (above) with the "diamond stripe" (ds) dorsal pattern (see text). Copyright © David Laurencio 2010. Used with permission.



Female-limited dorsal pattern variation is observed in many anoline lizards (Savage 2002, Losos 2009). In anoles, multiple dorsal patterns occur in females throughout a population, and these dorsal patterns are heritable (Calsbeek et al. 2008) and relatively fixed throughout a female's life (although the intensity of the pattern can change depending on light availability, humidity, and temperature; pers. obs.). Savage (2002) described some recurring dorsal pattern phenotypes seen widely in species of Costa Rican anoles.

Female *Anolis polylepis* from Las Cruces Biological Station in Costa Rica show a number of dorsal patterns. As part of a demographic study of *A. polylepis*, I captured and recaptured females that possessed different dorsal patterns and measured perch heights and other ecological variables to determine if females with different dorsal patterns differ in microhabitat use.

Study Site and Methods

During the dry season of 2003, I performed a capture-mark-recapture study of juvenile and adult *Anolis polylepis* (Fig. 1) in a 10,000-m² plot of primary forest within the boundaries of the Las Cruces Biological Station. The Station is located at an elevation of 1,200 m above sea level in San Vito, Coto Brus County, Puntarenas Province, in southern Costa Rica (8°47′7"N, 82°57′32"W). This mid-elevation site is comprised of more than 300 ha of Premontane Wet Forest habitat according to the Holdridge classification system.

I superimposed a Cartesian coordinate system over the plot and every five meters placed a survey flag that contained the Cartesian coordinates. I performed standardized searches for lizards on this plot by entering the plot from the same point during every search (the southeastern side) and slowly walking a zigzag pattern from one end to the other end of the plot. I continually searched the plot for lizards in this way from 0800-1130 h. When a lizard was observed during a standard plot search, I noted its location with respect to the nearest flag, and recorded whether the lizard was perched on the ground versus a trunk or branch of a tree. I measured the height of the perch and the diameter at breast height (DBH) of the tree on which the lizard was perched with a hand-held 5-m tape measure. I then captured the lizard (by hand or with a noose) and brought it back to the Las Cruces lab, where I measured its snout-to-vent length (SVL) in millimeters, mass in grams, and, if the lizard was a female, I noted if she was gravid (i.e., had a shelled egg in the right or left oviduct) or had yolking follicles. I collected data for 19 days from 3-24 March. I estimated home range sizes for females using the methods of Jennrich and Turner (1969).

Three dorsal patterns were common among female *A. polylepis*. I described and drew them in detail in my field notes (Fig. 2), and they appeared to be intermediate phenotypes of that described for female Costa

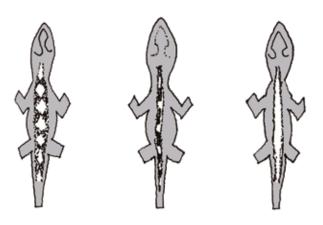


Fig. 2. Dorsal patterns observed in female *Anolis polylepis* in primary forests near Las Cruces Biological Station: ds = diamond stripe, cs = checkered stripe, ws = white stripe.

Rican anoles by Savage (2002). I defined the three common dorsal patterns as: (a) Diamond stripe (or "ds"), which consists of black diamonds, and is the dorsal pattern labeled "b" in Savage (2002); (b) checkered stripe (or "cs"), which consists of a white and black hyphen- or dash-like pattern, and appears to be a variation of dorsal pattern "e" in Savage (2002), with a black dash overlying the white stripe; and (c) white stripe (or "ws"), which consists of a bright white stripe bordered by black stripes, and is the dorsal pattern labeled "e" in Savage (2002).

To determine whether females with the three dorsal patterns differed in mass, SVL, perch height, DBH, and home range size, I performed one-way ANOVAs for each variable, with dorsal pattern type as the independent variable. To determine whether females with the three dorsal stripe patterns differed in being gravid or not or in the number of home range overlaps with other males and females, I used chi-square tests for each variable, with dorsal pattern type as the independent variable.

Results

Females of the three differing dorsal patterns did not differ in mass, SVL, DBH, home range size, gravidity status, or number of overlapping home ranges with male or females (Table 1). However, a dorsal pattern-specific difference in perch heights was evident. Females with the ds pattern perched the lowest, females with the cs pattern perched at intermediate heights, and females with the ws pattern perched the highest (Fig. 3).

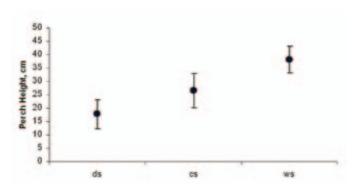


Fig. 3. Perch height differences among female *Anolis polylepis* with differing dorsal patterns at Las Cruces Biological Station. ds = diamond stripe, cs = checkered stripe, and ws = white stripe. Bars represent one standard error. One-way ANOVA showed these differences to be statistically significant at $p \le 0.05$).

Discussion

These data suggest that females that possess different dorsal patterns differ in perch height in *Anolis polylepis* at Las Cruces Biological Station. Furthermore, these females do not appear to differ according to other common ecologically relevant variables that were measured.

Avian predation has been hypothesized to be the key selective force responsible for the evolution of these dorsal polymorphisms in most species (Stamps and Gon 1983). That avian predation has an influence on population density (Andrews and Rand 1982), community structure (Adolph and Roughgarden 1983), and habitat choice (Wunderle 1981) in anoles has been recognized for years. Recently, Calsbeek et al. (2009) studied female-specific dorsal pattern polymorphism in Caribbean island populations of the closely related *Anolis sagrei*, and found that predation on particular patterns was frequency dependent and acted as a significant selective agent maintaining the frequency of pattern variants in the population. Unfortunately, the study did not attempt to study perch height differences in dorsal pattern variation. The authors speculated that particular dorsal patterns appear differentially conspicuous to predators in certain microhabitat conditions. Interestingly, the dorsal pattern variations observed in *A. sagrei* are different in shape and design than those in *A. polylepis*.

Table 1. Results of separate one-way ANOVAs and Chi-square analyses testing dorsal pattern differences in ecologically relevant dependent variables among female *Anolis polylepis*. Dorsal pattern type was the independent variable. Female dorsal patterns commonly observed at Las Cruces Biological Station were "ds" (diamond stripe), "cs" (checkered stripe) and "ws" (white stripe). N refers to number of individual females repeatedly observed with a particular dorsal pattern, and the number in parentheses refers to the total number of sightings for the particular dorsal pattern sighting. DBH = tree trunk diameter at breast height. An asterisk (*) marks results significant at $p \le 0.05$.

Dependent variable	F	df	P	N (ds)	N (ds)	N (ws)	
Mass	0.500	14	0.613	6 (26)	3 (20)	6 (21)	
SVL	1.431	14	0.259	6 (26)	3 (20)	6 (21)	
Perch height	3.955	14	0.039*	6 (26)	3 (20)	6 (21)	
DBH	0.200	14	0.821	6 (26)	3 (20)	6 (21)	
Home range	0.714	14	0.502	6 (26)	3 (20)	6 (21)	
	χ^2	df	P	N (ds)	N (cs)	N (ws)	
gravid / not-gravid	4.611	14	0.330	6 (26)	3 (20)	6 (21)	
# Male HR overlap	5.220	14	0.516	6 (26)	3 (20)	6 (21)	
# Female HR overlap	5.882	14	0.443	6 (26)	3 (20)	6 (21)	

The data I present here are consistent with an avian predation explanation — if the different dorsal patterns could be shown to be differentially conspicuous to avian predators in different microhabitats, and if different dorsal patterns experience differential mortality as a result of this conspicuousness. Future research on female dorsal patterns in anoles should therefore focus on the ecological significance of the female dorsal patterns with respect to avian visual systems.

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Literature Cited

Adolph, S.C. and J. Roughgarden. 1983. Foraging by passerine birds and *Anolis* lizards on St. Eustatius (Neth. Antilles): Implications for interclass competition, and predation. *Oecologia* 56:313–317.

Andrews, R.M. and A.S. Rand. 1982. Seasonal breeding and long-term fluctuations in the lizard *Anolis limifrons*, pp. 405–412. In: E.G. Leigh, Jr. and A.S. Rand (eds.), *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*. Smithsonian Institution Press, Washington, D.C.

Calsbeek, R., C. Bonneaud, and T.B. Smith, 2008. Differential fitness effects of immunocompetence and neighborhood density in alternative female lizard morphs. *Journal of Animal Ecology* 77:103–109.

Calsbeek, R., L. Bonvini, and R.M. Cox. 2009. Geographic variation, frequency dependent selection, and the maintenance of a female limited polymorphism. *Evolution*, early view, published online 3 August 2009.

Jennrich, R.I. and F.B. Turner. 1969. Measurement of non-circular home range. Journal of Theoretical Biology 22:227–237.

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

Stamps, J.A. and S.M. Gon III. 1983. Sex-biased pattern variation in the prey of birds. *Annual Review of Ecology and Systematics* 14:231–253.

Wunderle, J.M., Jr. 1981. Avian predation upon Anolis lizards on Grenada, West Indies. Herpetologica 37:104–108.