

POPULATION VARIATION IN ESCAPE BEHAVIOR AND LIMB MORPHOLOGY OF COLLARED LIZARDS (*CROTAPHYTUS COLLARIS*) IN OKLAHOMA

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ABSTRACT: The evolution of the morphological traits underlying locomotor performance is often addressed at the level of species comparisons; however, examining variation in traits within a species and the underlying selective pressures that presumably mold those traits can offer great insight into the effects of natural selection, as well as the selective forces responsible for phenotypic changes. We studied limb morphology and escape behavior of three Oklahoma populations of collared lizards: Glass Mountains (GM), Sooner Lake (SL), and Wichita Mountains (WM). Predation differs among populations, with WM > SL >> GM. Habitat openness also varies, with SL > GM > WM. Our analysis of limb morphometrics revealed that WM had the longest hindlimb elements, GM lizards had the shortest, and SL lizards were intermediate. These differences are consistent with the hypothesis that predation pressure rather than habitat structure is most important in determining hindlimb morphology. WM lizards were found to have the longest approach distance among populations, but GM lizards ran the longest distances from predators. These differences in escape behavior support the hypothesis that predation pressure is important in determining population differences in behavior.

Key words: Antipredator behavior; Body shape; Body size; Ecomorphology; Geographic variation; Predation

INTRASPECIFIC correlations among morphology, behavior, and ecology can give great insight into the selective pressures that are important in different ecological contexts (e.g., Foster and Endler, 1999; Luyten and Liley, 1991; Van Damme et al., 1998). For example, predation, habitat structure, or the potential for sexual selection may differ among populations, and any or all of these may have far-reaching effects on the behavioral and morphological phenotypes found in a population (e.g., Baird et al., 1997; Endler, 1995; Herrel et al., 2001; Stoner and Breden, 1988).

For lizards, there often is a strong correlation between limb morphology and sprint speed (reviewed in Aerts et al., 2000; Garland and Losos, 1994; Irschick and Garland, 2001). Attempts to understand the selective pressures acting on these variables have focused primarily on either predation (e.g., Christian and Tracy, 1981; Irschick, 2000; Irschick and Losos, 1998; Warner and Andrews, 2002; Webb, 1986) or habitat structure (e.g., Herrel

et al., 2001; Irschick et al., 2005; Van Damme et al., 1998, 2003). We investigated population variation in limb morphology with a multifaceted approach, considering both predation pressure and habitat structure as hypotheses to explain phenotypic differences among populations.

Collared lizards (*Crotaphytus collaris*) represent an ideal species with which to investigate selective pressures on phenotypic traits. A great deal is known about their general ecology and behavior (e.g., Baird et al., 1996; Fitch, 1956; Yedlin and Ferguson, 1973), especially in four Oklahoma populations which have received extensive attention: Wichita Mountains (WM), Glass mountains (GM), Arcadia Lake (AL), and Sooner Lake (SL) (e.g., Baird et al., 1997; Husak et al., 2006; McCoy et al., 2003). Previous studies indicate that these populations differ in conspicuousness of color pattern (Macedonia et al., 2004), characteristics of their habitat (Baird et al., 1997; Macedonia et al., 2004), and predation pressure (Baird et al., 1997; Husak et al., 2006). Husak et al. (2006) examined attacks on lizard models and found that predation pressure varied by WM > SL >> GM. Considering these differences among populations, we formulated a set of hypotheses regarding escape behavior and limb morphology.

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Many potential selective pressures can affect escape behavior (Cooper, 2003a; Templeton and Shriver, 2004; Ydenberg and Dill, 1986). Sexual selection can affect escape behavior by favoring males that remain visible longer in the presence of predators (Cooper, 2003b; Martín and López, 1999). To stay visible, males should not run into refuges immediately, but should instead run away from predators. Furthermore, if sexual selection favors conspicuous coloration, conspicuous individuals may rely more strongly on fleeing while less conspicuous individuals may rely more strongly on crypsis (Martín and López, 1999). Among the Oklahoma populations studied, WM lizards are the most colorful and conspicuous (Macedonia et al., 2004) and experience the highest predation pressure (Husak et al., 2006). Hence, we predicted that they should rely more on fleeing to escape predators than the other populations. Specifically, we predicted that WM lizards would run when predators were further away and would not run as long a distance in comparison to other populations. SL lizards also have high predation pressure but are the most cryptic, so we predicted that they would run when predators are closer to them compared to WM. GM lizards experience little predation and are intermediate in their coloration and conspicuousness. Since there is pressure to remain visible for territory maintenance purposes, as also is true at the other two sites, we predicted that GM lizards would allow the closest approach, since predation is lowest, and run a longer distance when disturbed by a predator in order to remain visible to conspecifics.

We made two alternative hypotheses concerning population differences in morphology. Our first hypothesis is based on differences in predation pressure and our escape behavior predictions. Where there is greater predation pressure we predicted that lizards would experience strong selection for fast maximal sprint speed and, therefore, long hindlimbs (Bauwens et al., 1995; Bonine and Garland, 1999; Snell et al., 1988). Hence, we predicted that WM lizards would have the longest hindlimbs with the longest distal elements of the hindlimbs. We predicted GM lizards, which experience low predation pressure and likely do not experience strong selection for fast sprint speed, would have the shortest hind-

limbs with short distal hindlimb elements. We predicted SL lizards would be intermediate to the other two. Because collared lizards typically run bipedally when disturbed by a predator or responding to a conspecific (Yedlin and Ferguson, 1973), we predicted that there would be little selective pressure on forelimb length, and, hence, no difference among populations.

Our second hypothesis focused on effects of habitat openness on limb morphology. All populations of collared lizards in Oklahoma are saxicolous. However, there are large differences in the degree of openness in the habitat matrix surrounding the rocks on which they live (see Baird et al., 1997; Macedonia et al., 2004 for more specific habitat differences). WM lizards inhabit large boulders along slopes and flats of the Wichita Mountains, where rocks are surrounded by grass that is taller than at the other sites studied. Thus, for this population we predicted relatively short hindlimbs, especially proximal elements (Van Damme et al., 2003), for better maneuverability through the vegetated habitat when escaping predators or patrolling territories (e.g., see Newbold, 2005 for an example of locomotion differing due to habitat structure). At GM, lizards inhabit rocks on the tops of steep-sided gypsum buttes or boulders along the bases of those buttes. In either case, rocks are surrounded by loose soil, gravel, or short grass. The relatively open habitat at GM led us to predict that these lizards would have long hindlimbs with long distal elements (e.g., Melville and Swain, 2000; Van Damme et al., 2003). SL has a unique substrate, with lizards inhabiting a concrete-covered, rip-rap boulder dam that is very homogenous in structure. The habitat is completely open with vegetation only in a narrow strip along the top of the dam. Therefore, we predicted that SL lizards would have the longest hindlimbs with long distal elements. Hence, considerations of predation pressure and habitat structure separately give different predictions. Following habitat structure we would predict that hindlimb length should vary by $SL > GM > WM$, whereas following predation pressure we would predict $WM > SL > GM$.

MATERIALS AND METHODS

We studied adult and juvenile male and female lizards at the Glass Mountains (Glass

[Gloss] Mountains State Park; Major Co.), the Wichita Mountains (Ft. Sill Army base and Wichita Mountains Wildlife Refuge; Comanche Co.), and Sooner Lake (Pawnee Co.). Descriptions of the sites are given above and in Baird et al. (1997) and Macedonia et al. (2004). Our dataset consisted of two components: morphometric data and escape behavior data. We captured lizards by noosing and measured each with vernier calipers to the nearest 0.1 mm for snout-vent length, total hindlimb length, femur length, tibia length, hindfoot length, length of the longest toe on the hindfoot, and total forelimb length. All measurements were taken on the right side of the body by the same person (JFH).

We quantified two aspects of escape behavior, following a modification of Cooper (1997): approach distance and flight distance. The same individual (wearing similar clothing each time) walked toward a lizard at a constant pace and in a straight line until the lizard fled. If the lizard did not immediately seek refuge, the walking individual continued approaching it until it took refuge. We then measured the distance between the lizard's original location and where the observer was when the lizard fled (approach distance). We also measured the distance from where the lizard originally was, along its escape path, to where it took refuge (flight distance). Our method of estimating flight distance is a deviation from typical methodology used when quantifying escape behavior. However, we were interested in a measure of how long lizards would remain active and visible when disturbed by a predator. To avoid confusion, and to avoid creating more jargon, we use the term "flight distance" but acknowledge that there are differences in our meaning compared to traditional uses.

All morphological data were log transformed. Collared lizards are known to be sexually dimorphic in body size and limb dimensions (McCoy et al., 1994) and differ geographically in the degree to which they are sexually dimorphic (Baird et al., 1997), likely as a result of differing selective pressures, so we analyzed males and females in the same analyses to look for patterns of sexual dimorphism among populations. We performed a two-factor ANOVA to determine differences in SVL between sexes and among populations. To reduce potential biases due to collection of

different proportions of ages of lizards among sites, we used only the five largest lizards of each sex in the comparison of SVL (McCoy et al., 1994). For the remainder of the analyses we used all individuals. We obtained residuals for each (log-transformed) morphological variable regressed against (log-transformed) SVL for all populations and sexes combined. We then performed two-factor ANOVAs on the residual limb morphology variables, followed by Tukey's Honestly Significant Different (HSD) pairwise comparisons on significant variables. Approach distance and flight distance were compared in a similar manner with two-factor ANOVAs followed by Tukey's HSD pairwise comparisons for significant ANOVAs. If significant interactions were found in two-factor ANOVAs, we used the "SLICE" option in SAS version 8 (SAS Institute, 1999) to examine simple effects (Kuehl, 2000). All analyses were performed with SAS except the regressions, which were performed with SYSTAT 9 (SPSS, 1998). We report actual *P* values for independent tests; however, all *P* values reported as significant individually retained significance when adjusted for Bonferroni probabilities (Rice, 1989).

RESULTS

For SVL, there was a sex*population interaction ($F_{2,24} = 10.27$, $P = 0.0006$). In tests for simple effects, males were significantly larger than females at GM ($P = 0.010$), SL ($P < 0.0001$), and WM ($P < 0.0001$; Table 1). For females, there were no significant differences between GM and SL ($P = 0.411$) or GM and WM ($P = 0.870$), but SL females were marginally larger than WM females ($P = 0.055$; Table 1). GM males were significantly smaller than SL males ($P = 0.0002$) and WM males ($P = 0.0003$), but there was no significant difference between SL and WM males ($P > 0.90$; Table 1).

None of the variables for residual limb morphology had a significant sex*population interaction ($P > 0.18$ for all). Total forelimb length did not differ between the sexes or among populations ($P > 0.48$ for both factors; Table 2). All other variables had a significant effect of sex and population (Table 2), with males being larger than females (Table 1). Tukey's HSD pairwise comparisons between

TABLE 1.—Morphometric data (means in mm \pm 1 SE) for three populations of collared lizards (*Crotaphytus collaris*) in Oklahoma, U.S.A.

	Glass Mountains		Sooner Lake		Wichita Mountains	
	Male	Female	Male	Female	Male	Female
<i>n</i>	13	12	24	19	12	13
SVL	92.4 (\pm 3.17)	85.9 (\pm 3.27)	95.9 (\pm 2.50)	89.7 (\pm 1.67)	101.1 (\pm 2.30)	90.0 (\pm 1.31)
Total hindlimb	74.0 (\pm 2.07)	64.8 (\pm 1.73)	77.9 (\pm 1.34)	69.9 (\pm 0.74)	82.6 (\pm 1.21)	71.5 (\pm 1.05)
Femur	22.1 (\pm 0.83)	19.1 (\pm 0.51)	22.7 (\pm 0.55)	20.6 (\pm 0.39)	24.9 (\pm 0.55)	21.6 (\pm 0.33)
Tibia	26.5 (\pm 0.81)	23.7 (\pm 0.66)	28.3 (\pm 0.53)	25.0 (\pm 0.36)	29.8 (\pm 0.58)	25.7 (\pm 0.30)
Hindfoot	30.0 (\pm 0.81)	25.6 (\pm 1.22)	32.1 (\pm 0.42)	28.7 (\pm 0.21)	33.1 (\pm 0.87)	29.0 (\pm 0.45)
Toe	15.6 (\pm 0.59)	13.9 (\pm 0.32)	15.8 (\pm 0.26)	13.7 (\pm 0.18)	17.9 (\pm 0.28)	15.3 (\pm 0.28)
Total forelimb	40.1 (\pm 1.23)	36.6 (\pm 0.94)	41.9 (\pm 0.75)	38.2 (\pm 0.56)	41.3 (\pm 2.89)	38.6 (\pm 0.43)

populations revealed different patterns among sites, depending on the specific limb element. For residual total hindlimb length GM lizards were smaller than SL ($P = 0.006$) and WM lizards ($P < 0.0001$), but SL and WM lizards did not differ ($P = 0.112$; Table 2). For residual femur length WM lizards were larger than GM ($P < 0.0001$) and SL lizards ($P = 0.0005$), but GM and SL lizards did not differ ($P = 0.570$; Table 2). For residual tibia length, GM lizards were smaller than SL ($P = 0.025$) and WM lizards ($P = 0.0003$; Table 2), but SL and WM lizards did not differ ($P = 0.142$). For residual hindfoot length, GM lizards were smaller than SL ($P = 0.002$) and WM lizards ($P = 0.007$), but SL and WM lizards did not differ ($P > 0.9$; Table 2). For residual toe length, WM lizards were larger than GM ($P = 0.0006$) and SL lizards ($P < 0.0001$), but GM and SL lizards did not differ ($P = 0.249$; Table 2).

An ANOVA of approach distance revealed no significant sex*population interaction ($F_{2,65} = 0.37$, $P = 0.689$) and no significant difference between the sexes ($F_{1,65} = 1.31$, $P = 0.256$), but a significant difference among populations ($F_{2,65} = 6.20$, $P = 0.003$). Tukey's

HSD pairwise comparisons revealed that WM lizards had a significantly longer approach distance than SL lizards ($P = 0.003$) and a longer approach distance than GM lizards ($P = 0.0828$), but there was no difference between GM and SL ($P = 0.256$; Table 3). ANOVA of flight distance revealed a significant sex*population interaction ($F_{2,65} = 3.72$, $P = 0.030$; Table 3). Examination of simple effects indicated that males ran further than females at GM ($P = 0.010$), but not at the other sites ($P > 0.90$ for all; Table 3). GM males had a significantly longer flight distance than SL males ($P < 0.001$) and WM males ($P < 0.001$). SL males and WM males did not differ significantly ($P > 0.90$). There were no significant pairwise differences in flight distance between populations for females ($P > 0.75$ for all).

DISCUSSION

Determining the selection pressures that shape morphology can be difficult (e.g., Herrel et al., 2001; Schulte et al., 2004; Van Damme et al., 1997, 1998; Vanhooydonck and Van Damme, 2003). We used an intraspecific approach to test alternative hypotheses about

TABLE 2.—Results of analysis of variance, with sex and population as factors, on residual limb variables of collared lizards (*Crotaphytus collaris*) in Oklahoma, U.S.A. None of the sex*population interactions were significant. Pairwise comparisons represent the direction of order of magnitude; nonsignificant comparisons are indicated with an equals sign. GM = Glass Mountains, SL = Sooner Lake, WM = Wichita Mountains.

	Sex		Population		Pairwise comparisons
	$F_{1,87}$	<i>P</i> -value	$F_{2,87}$	<i>P</i> -value	
Total hindlimb	46.33	<0.0001	10.83	<0.0001	WM = SL > GM
Femur	18.51	<0.0001	11.20	<0.0001	WM > SL = GM
Tibia	39.72	<0.0001	8.41	0.0005	WM = SL > GM
Hindfoot	19.14	<0.0001	7.03	0.0015	WM = SL > GM
Toe	28.86	<0.0001	17.88	<0.0001	WM > SL = GM
Total forelimb	0.03	0.859	0.74	0.482	—

TABLE 3.—Mean approach distance (means in $m \pm 1$ SE) and flight distance (means in $m \pm 1$ SE) for three populations of collared lizards (*Crotaphytus collaris*) in Oklahoma, USA.

	Class Mountains		Sooner Lake		Wichita Mountains	
	Male	Female	Male	Female	Male	Female
<i>n</i>	14	8	11	8	16	14
Approach distance	8.27 (± 1.98)	6.79 (± 1.98)	5.26 (± 0.86)	4.83 (± 0.95)	13.43 (± 2.33)	9.81 (± 1.50)
Flight distance	24.17 (± 5.11)	8.53 (± 3.76)	4.02 (± 1.06)	2.89 (± 1.10)	3.89 (± 1.26)	2.56 (± 1.42)

selection in collared lizards. In our study, differences among populations in morphology and behavior were consistent with predictions based on predation pressure and inconsistent with predictions based on habitat structure.

Lizards that inhabit open, rocky habitats are expected to have long hindlimbs with relatively long hindfeet and toes that allow for more surface area during the initial acceleration of fleeing (Van Damme et al., 2003), but our morphometric data did not match this pattern. Instead, our results supported the prediction drawn from the hypothesis that predation pressure is responsible for hindlimb morphology. As predicted, WM lizards had the longest hindlimbs and longest distal hindlimb elements. As predicted based on the low predation pressure present at GM, GM lizards had the shortest hindlimbs and hindlimb elements. This result is likely due to weaker selection for fast sprint speed at GM compared to the other populations studied. Hindlimb morphology of SL lizards was intermediate between WM and GM lizards, as predicted by the predation hypothesis. SL lizards unexpectedly had the longest hindfeet but the shortest toes, implying that SL lizards have long metatarsals compared to the other populations. The reasons for this result are unclear.

The lack of significant differences in forelimb length among populations is not surprising considering the bipedal locomotion of collared lizards. When disturbed by a predator, male and female collared lizards typically utilize bipedal locomotion to escape (Fitch, 1956; J. F. Husak, unpublished data). Because of this mode of escape, there may be little selective pressure on forelimb length related to maximal locomotor capacity and, hence, no differences among populations.

Escape behavior differences also were as predicted based on our knowledge of predation pressure for the various populations (Husak et al., 2006). These results are consistent with

previous studies that found intraspecific differences in escape behavior corresponding to presumed population differences in predation pressure (Bulova, 1994; Snell et al., 1988). WM lizards experience the highest predation pressure, and we found them to flee when the simulated predator was further away compared to the other populations. GM lizards had the longest flight distance, and we interpret this as an evolutionary response to low predation intensity, because male collared lizards are extremely territorial, and there are likely strong sexual selection pressures for them to remain active and visible in their territories (Baird et al., 1996; Husak and Fox, 2003). Despite this expectation, we found sexual dimorphism in flight distance only for GM lizards. Surprisingly, there was no sexual dimorphism in approach distance for any of the populations. This result could be due to sexual differences in behavior that we did not measure such as time to re-emergence (e.g., Cooper, 1998). If males experience greater pressure than females to be visible in their environment for purposes of territory maintenance (Baird et al., 1996), then approach and flight distances need not differ if males can simply re-emerge sooner.

Reasons for sexual differences in hindlimb morphology are unclear. Since we found no sexual dimorphism in escape behavior except at GM, there may not be differing selective pressures between the sexes on hindlimb morphology for faster sprint speed. In fact, there is no sexual dimorphism in sprint speed for SL lizards (Husak, 2005; Peterson and Husak, 2006). This result may be attributable to compensation for the greatly enlarged heads of males as a result of intra-sexual selection (Lappin and Husak, 2005). This possibility deserves further study. We found no significant sexual dimorphism in forelimb length, which is not surprising in light of the fact that males and females rarely touch the ground with their forelimbs while sprinting.

We do not know the genetic basis of hindlimb morphology and escape behavior differences among populations of collared lizards, and differences may be the result of phenotypic plasticity (e.g., Losos et al., 2000). However, most results followed a priori predictions based on population differences in predation pressure and color conspicuousness, suggesting adaptive processes at work (Reilly and Wainwright, 1994) as a result of different selective regimes. Even if plasticity underlies population variation in collared lizard hindlimb length, the plasticity may be advantageous by producing phenotypes that function better in a given environment (Losos et al., 2000; Schlichting and Pigliucci, 1998). Certainly, insight into the genetic basis of such differences would add greatly to our understanding of the mechanisms involved in such dramatic intraspecific variation in numerous morphological and behavioral traits in this species and in others. Knowledge of differences in maximal sprint speed performance would be very enlightening for further clarification of our hypotheses and an understanding of functional tradeoffs in the face of differing selective pressures.

The role of predation pressure in shaping lizard limb morphology has received some attention. Van Damme et al. (1998) suggested that differences in predation pressure between island and mainland habitats might explain differences in locomotion between two populations of the lizard *Podarcis hispanica*. Schulte et al. (2004) outlined potential strategies for lizards that live in flat, open microhabitats and suggested that they may either remain motionless or run long distances from a predator, with hindlimb length being under selection only when the lizard species adopts the latter strategy. However, this model assumes that predation pressure does not vary greatly within the distribution of the species. We found that different collared lizard populations with differing predation pressures had different escape strategies based on predation pressure. Where predation pressure was weak (GM) lizards ran from predators, but the distances run were much longer on average than the other populations with greater predation pressure. Aligned with the relaxed predation pressure, GM lizards had the shortest limbs among the populations we studied.

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LITERATURE CITED

- AERTS, P., R. VAN DAMME, B. VANHOYDONCK, A. ZAAF, AND A. HERREL. 2000. Lizard locomotion: how morphology meets ecology. *Netherlands Journal of Zoology* 50: 261–277.
- BAIRD, T. A., M. A. ACREE, AND C. L. SLOAN. 1996. Age and gender-related differences in the social behavior and mating success of free-living collared lizards, *Crotaphytus collaris*. *Copeia* 1996:336–347.
- BAIRD, T. A., S. F. FOX, AND J. K. MCCOY. 1997. Population differences in the roles of size and coloration in intra- and inter-sexual selection in the collared lizard, *Crotaphytus collaris*: influences of habitat and social organization. *Behavioral Ecology* 8:506–517.
- BAUWENS, D., T. GARLAND, JR., A. M. CASTILLA, AND R. VAN DAMME. 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. *Evolution* 49:848–863.
- BONINE, K. E., AND T. GARLAND, JR. 1999. Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. *Journal of Zoology* 248:255–265.
- BULOVA, S. J. 1994. Ecological correlates of population and individual variation in antipredator behavior in two species of desert lizards. *Copeia* 1994:980–992.
- CHRISTIAN, K. A., AND C. R. TRACY. 1981. The effect of the thermal environment on the ability of hatchling Galápagos land iguanas to avoid predation during dispersal. *Oecologia* 49:218–223.
- COOPER, W. E., JR. 1997. Threat factors affecting antipredatory behavior in the broad-headed skink (*Eumeces laticeps*): repeated approach, change in predator path, and eye contact. *Copeia* 1997:613–619.
- . 1998. Risk factors and emergence from refuge in the lizard *Eumeces laticeps*. *Behaviour* 135: 1065–1076.
- . 2003a. Effect of risk on aspects of escape behavior by a lizard, *Holbrookia propinqua*, in relation to optimal escape theory. *Ethology* 109:617–626.
- . 2003b. Sexual dimorphism in distance from cover but not escape behavior by the keeled earless lizard *Holbrookia propinqua*. *Journal of Herpetology* 37: 374–378.
- ENDLER, J. A. 1995. Multiple-trait coevolution and environmental gradients in guppies. *Trends in Ecology and Evolution* 10:22–29.

- FITCH, H. S. 1956. An ecological study of the collared lizard (*Crotaphytus collaris*). University of Kansas Publications of the Museum of Natural History 8:213–274.
- FOSTER, S. A., AND J. A. ENDLER (Eds.). 1999. Geographic Variation in Behavior: Perspectives on Evolutionary Mechanisms. Oxford University Press, New York, New York, U.S.A.
- GARLAND, T., JR., AND J. B. LOSOS. 1994. Ecological morphology of locomotor performance in squamate reptiles. Pp. 240–302. In P. C. Wainwright and S. M. Reilly (Eds.), Ecological Morphology: Integrative Organismal Biology. University of Chicago Press, Chicago, Illinois, U.S.A.
- HERREL, A., J. J. MEYERS, AND B. VANHOODONCK. 2001. Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): a population-level analysis. Biological Journal of the Linnean Society 74:305–314.
- HUSAK, J. F. 2005. Ecological and Evolutionary Significance of Locomotor Performance in Collared Lizards (*Crotaphytus collaris*). Ph.D. Dissertation, Oklahoma State University, Stillwater, Oklahoma, U.S.A.
- HUSAK, J. F., AND S. F. FOX. 2003. Adult male collared lizards (*Crotaphytus collaris*) increase aggression towards displaced neighbours. Animal Behaviour 65: 391–396.
- HUSAK, J. F., J. M. MACEDONIA, S. F. FOX, AND R. C. SAUCEDA. 2006. Predation cost of conspicuous male coloration in collared lizards (*Crotaphytus collaris*): an experimental test using clay-covered models. Ethology: In press.
- IRSCHICK, D. J. 2000. Comparative and behavioral analyses of preferred speed: *Anolis* lizards as a model system. Physiological and Biochemical Zoology 73:428–437.
- IRSCHICK, D. J., AND T. GARLAND, JR. 2001. Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. Annual Review of Ecology and Systematics 32:367–396.
- IRSCHICK, D. J., AND J. B. LOSOS. 1998. A comparative analysis of the ecological significance of locomotor performance in Caribbean *Anolis* lizards. Evolution 52:219–226.
- IRSCHICK, D. J., B. VANHOODONCK, A. HERREL, AND J. J. MEYERS. 2005. Intraspecific correlations among morphology, performance, and habitat use within a green anole (*Anolis carolinensis*) population. Biological Journal of the Linnean Society 85:211–221.
- KUEHL, R. O. 2000. Design of Experiments: Statistical Principles of Research Design and Analysis. Duxbury, Pacific Grove, California, U.S.A.
- LAPPIN, A. K., AND J. F. HUSAK. 2005. Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). American Naturalist 166: 426–436.
- LOSOS, J. B., D. A. CREER, D. GLOSSIP, R. GOELLNER, A. HAMPTON, G. ROBERTS, N. HASKELL, P. TAYLOR, AND J. EITLING. 2000. Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. Evolution 54:301–305.
- LUYTEN, P. H., AND N. R. LILEY. 1991. Sexual selection and competitive mating success of male guppies (*Poecilia reticulata*) from four Trinidad populations. Behavioral Ecology and Sociobiology 28:329–336.
- MACEDONIA, J. M., J. F. HUSAK, Y. M. BRANDT, A. K. LAPPIN, AND T. A. BAIRD. 2004. Sexual dichromatism and color conspicuousness in three populations of collared lizards (*Crotaphytus collaris*) from Oklahoma. Journal of Herpetology 38:340–354.
- MARTÍN, J., AND P. LÓPEZ. 1999. Nuptial coloration and mate guarding affect escape decisions of male lizards *Psammodromus algirus*. Ethology 105:439–447.
- MCCOY, J. K., S. F. FOX, AND T. A. BAIRD. 1994. Geographic variation in sexual dimorphism of *Crotaphytus collaris*. Southwestern Naturalist 39:328–335.
- MCCOY, J. K., T. A. BAIRD, AND S. F. FOX. 2003. Sexual selection, social behavior, and the environmental potential for polygyny. Pp. 149–171. In S. F. Fox, J. K. McCoy, and T. A. Baird (Eds.), Lizard Social Behavior. Johns Hopkins University Press, Baltimore, Maryland, U.S.A.
- MELVILLE, J., AND R. SWAIN. 2000. Evolutionary relationships between morphology, performance and habitat openness in the lizard genus *Niveoscincus* (Scincidae: Lygosominae). Biological Journal of the Linnean Society 70:667–683.
- NEWBOLD, T. A. S. 2005. Desert horned lizard (*Phrynosoma platyrhinos*) locomotor performance: the influence of cheatgrass (*Bromus tectorum*). Southwestern Naturalist 50:17–23.
- PETERSON, C. C., AND J. F. HUSAK. 2006. Locomotor performance and sexual selection: individual variation in sprint speed of collared lizards (*Crotaphytus collaris*). Copeia 2006:216–224.
- REILLY, S. M., AND P. C. WAINWRIGHT. 1994. Conclusion: ecological morphology and the power of integration. Pp. 339–354. In P. C. Wainwright and S. M. Reilly (Eds.), Ecological Morphology: Integrative Organismal Biology. University of Chicago Press, Chicago, Illinois, U.S.A.
- RICE, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.
- SAS INSTITUTE. 1999. SAS OnlineDoc, version 8. SAS Institute, Cary, North Carolina, U.S.A.
- SCHLICHTING, C. D., AND M. PIGLIUCCI. 1998. Phenotypic Evolution: A Reaction Norm Perspective. Sinauer, Sunderland, Massachusetts, U.S.A.
- SCHULTE, J. A., J. B. LOSOS, F. B. CRUZ, AND H. NUNEZ. 2004. The relationship between morphology, escape behavior and microhabitat occupation in the lizard clade *Liolaemus* (Iguanidae: Trodidurinae: Liolaemini). Journal of Evolutionary Biology 17:408–420.
- SNELL, H. L., R. D. JENNINGS, H. M. SNELL, AND S. HARCOURT. 1988. Intrapopulation variation in predator-avoidance of Galapagos lava lizards: the interaction of sexual and natural selection. Evolutionary Ecology 2:353–369.
- SPSS. 1998. SYSTAT. Version 9. SPSS. Evanston, Illinois, U.S.A.
- STONER, G., AND F. BREDEN. 1988. Phenotypic differentiation in female preference related to geographic variation in male predation risk in the Trinidad guppy (*Poecilia reticulata*). Behavioral Ecology and Sociobiology 22:285–291.
- TEMPLETON, C. N., AND W. M. SHRINER. 2004. Multiple selection pressures influence Trinidadian guppy (*Poecilia reticulata*) antipredator behavior. Behavioral Ecology 15:673–678.

- VAN DAMME, R., P. AERTS, AND B. VANHOYDONCK. 1997. No trade-off between sprinting and climbing in two populations of the lacertid lizard *Podarcis hispanica* (Reptilia: Lacertidae). *Biological Journal of the Linnean Society* 60:493–503.
- . 1998. Variation in morphology, gait characteristics and speed of locomotion in two populations of lizards. *Biological Journal of the Linnean Society* 63:409–427.
- VAN DAMME, R., B. VANHOYDONCK, P. AERTS, AND F. DE VREE. 2003. Evolution of lizard locomotion: context and constraint. Pp. 267–282. *In* V. L. Bels, J.-P. Gasc, and A. Casinos (Eds.), *Vertebrate Biomechanics and Evolution*. BIOS Scientific Publishers, Oxford, U.K.
- VANHOYDONCK, B., AND R. VAN DAMME. 2003. Relationships between locomotor performance, microhabitat use and antipredator behaviour in lacertid lizards. *Functional Ecology* 17:160–169.
- WARNER, D. A., AND R. M. ANDREWS. 2002. Laboratory and field experiments identify sources of variation in phenotypes and survival of hatchling lizards. *Biological Journal of the Linnean Society* 76:105–124.
- WEBB, P. W. 1986. Locomotion and predator-prey relationships. Pp. 24–41. *In* M. E. Feder and G. V. Lauder (Eds.), *Predator-Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates*. University of Chicago Press, Chicago, Illinois, U.S.A.
- YDENBERG, R. C., AND L. M. DILL. 1986. The economics of fleeing from predators. *Advances in the Study of Behavior* 16:229–249.
- YEDLIN, I. N., AND G. W. FERGUSON. 1973. Variations in aggressiveness of free-living male and female collared lizards, *Crotaphytus collaris*. *Herpetologica* 29:268–275.

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