

Does speed help you survive? A test with Collared Lizards of different ages

J. F. HUSAK†

Department of Zoology, Oklahoma State University, Stillwater, OK 74078, USA

Summary

1. While it is generally accepted that the evolution of morphological traits is mediated by selection on whole-animal performance, few studies have examined how variation in performance explains variation in fitness. Most studies to date have studied how performance predicts survival, and these typically examine only a single age class.

2. Maximal sprint speed was measured for hatchling and adult Collared Lizards (*Crotaphytus collaris*), in addition to morphological measurements, in order to determine how well annual survival could be predicted by performance and whether the relationship between performance and survival differed between age classes.

3. Logistic regression revealed that no morphological trait or sprint speed performance predicted survival in adults. However, sprint speed predicted survival in hatchlings. Further, hindlimb length differed between survivors and non-survivors and correlated with sprint speed, suggesting that the evolution of hindlimb length in hatchlings may be driven by selection on sprint speed performance.

4. Selection on sprint speed may be mediated directly by predators where hatchlings cannot attain speeds sufficient to escape predators or indirectly where slower individuals use a greater proportion of their maximal capacity than faster individuals while escaping predators, perhaps causing elevated stress levels or a higher expenditure of energy stores.

Key-words: Fitness, foraging, locomotion, natural selection, performance, predation, survival, territoriality

Functional Ecology (2006) **20**, 174–179

doi: 10.1111/j.1365-2435.2006.01069.x

Introduction

Differential survival among individuals reflects variation in underlying morphological and physiological traits, but selection acts on the integrated manifestation of such traits (i.e. whole-animal performance; Huey & Stevenson 1979; Arnold 1983). Since Arnold (1983) described an operational framework for linking morphology, performance and fitness, many authors have extended and refined his paradigm (e.g. Bennett & Huey 1990; Wainwright & Reilly 1994; Irschick 2002). The link between morphology and performance has received considerable attention (reviewed in Garland & Losos 1994; Irschick & Garland 2001), whereas the link between performance and fitness has received comparatively little (Irschick & Garland 2001). The lack of studies is probably due to the difficulty of quantifying both physiological performance and lifetime fitness in the same individuals. Studies attempting to do so have focused on how performance predicts survival (e.g. Jayne & Bennett 1990; Miles 2004) typically within a specific age class. These studies have been

instructive regarding how natural selection may act on performance, and they have revealed dramatic ontogenetic differences in how selection acts on performance (Jayne & Bennett 1990; Kingsolver 1999; Warner & Andrews 2002; Kingsolver & Srygley 2000; Miles 2004). Locomotor performance predicted survival in hatchling lizards *Sceloporus undulatus* (Warner & Andrews 2002) and *Urosaurus ornatus* (Miles 2004), but not hatchlings of Garter Snakes, *Thamnophis sirtalis* (Jayne & Bennett 1990), or *S. occidentalis* and *S. merriami* hatchlings (unpublished studies cited in Bennett & Huey 1990). Juvenile endurance capacity predicted survival in the lizard *Lacerta vivipara* (Le Galliard, Clobert & Ferrière 2004). Among adults, locomotor performance predicted survival in garter snakes (Jayne & Bennett 1990), but flight performance did not predict survival in three butterfly species (Kingsolver 1999; Kingsolver & Srygley 2000). More studies that examine how performance predicts survival in different age classes of the same species are needed to assess the generality of ontogenetic shifts in selection on performance.

Ontogenetic differences in selection on performance would not be surprising given that absolute performance typically differs between juveniles and adults. Performance typically scales with body size such that

younger individuals are 'worse' absolute performers than adults owing to their smaller size (Garland & Losos 1994; Carrier 1996; Irschick 2000). Although there are many instances of juveniles using very different niches from those used by adults, juveniles in many vertebrate species often inhabit the same environment as adults where the two groups potentially compete for resources and experience the same potential predators (Werner & Gilliam 1984). The smaller size of juveniles may make them vulnerable to a larger suite of potential predators than adults and may limit the size range of prey that may be consumed, reducing competitive ability compared with adults (Schmidt-Nielsen 1984; La Barbera 1989). Such factors suggest that natural selection on performance traits affecting predator avoidance and foraging may be stronger on juveniles than adults (Carrier 1996). Studies that compare locomotor performance in nature between adults and juveniles support this hypothesis. Juvenile *Anolis lineatopis* lizards and subadult *Crotaphytus collaris* lizards run slower than adults, but they utilize a higher percentage of maximal sprint speed capacity than adults when escaping predators (Irschick 2000; Irschick *et al.* 2000; Husak 2005).

I examined how well morphological and performance traits predicted survival in hatchling and adult Collared Lizards (*Crotaphytus collaris*), a broadly distributed species in the south-western United States. Collared Lizards use sit-and-wait foraging to feed opportunistically on available arthropods and small vertebrates (Blair & Blair 1941; Husak & McCoy 2000; Cooper *et al.* 2001). Therefore, predator escape and prey capture may be contexts in which maximal sprint speed is subjected to selection. I tested whether body size and condition, hindlimb length or maximal sprint speed capacity predicted survival, and whether there were differences in what trait(s) predicted survival between the two age classes.

Materials and methods

GENERAL METHODS

The study site was a 2-ha area on Sooner Lake dam in Pawnee County, Oklahoma, where the substrate consisted of concrete-covered rip-rap boulders. In April–May 2003, adult (= 2 years of age) and yearling (~1 year of age) male and female lizards were captured by noosing and permanently marked with toe-clips and a unique pattern of coloured paint spots for visual identification at a distance (after Baird, Acree & Sloan 1996). Individuals that were captured and marked the previous year as hatchlings were considered yearlings, whereas those captured the previous year before hatchlings emerged were considered ≥ 2 years of age. I examined survival for 54 adult and yearling lizards (12 yearling females, 14 yearling males, 15 females ≥ 2 years old, and 13 males ≥ 2 years old). In August–October 2003, hatchlings ($N = 64$) were captured and marked as described above. Morphological traits potentially related to survival

were measured, including snout–vent length (SVL), body mass and hindlimb length. To remove effects of body size, log-transformed hindlimb length was regressed against log-transformed SVL, and residuals were used in subsequent analyses. The residuals from a regression of log-transformed mass against log-transformed SVL were used as an index of body condition.

MAXIMAL SPRINT SPEED

Lizards were transported to Oklahoma State University and held for 1 day to allow passage of gut contents. No gravid females were used. On the mornings of their second and third days of captivity, I placed lizards individually in net bags inside a lighted incubator at 37 °C. Three times a day, with trials separated by at least 2 h, each lizard was removed from the incubator and immediately chased down a 3-m racetrack into a black bag. The racetrack had a high-friction sandpaper substrate. I video taped runs on SONY Hi8 (Sony, Park Ridge, NJ, USA) film (following Braña 2003), and later viewed the tapes and counted number of frames required to traverse 1-m intervals (yearlings and adults) or 0.5-m intervals (hatchlings). The resulting speeds were comparable to those found by Peterson & Husak (in press) using a racetrack with infrared beams. I classified the quality of each run as 'good' or 'poor' (van Berkum & Tsuji 1987), and data from 'poor' runs (pauses, reversals) were discarded. Only the single fastest 1-m (for yearlings and adults) or 0.5-m (for hatchlings) split for each run was analysed. Following a run, I immediately measured the lizard's body temperature with a quick-read cloacal thermometer. All lizards were released at their exact point of capture after all trials were completed. The best and second-best performances of each individual, regardless of the day on which they occurred, were highly correlated, indicating high repeatability for adults and yearlings ($r = 0.95$, $P < 0.001$) and hatchlings ($r = 0.90$, $P < 0.001$). To remove the effects of body size, log-transformed sprint speed was regressed against log-transformed SVL, and residuals were used in subsequent analyses.

SURVIVAL

I determined survival in the field to the beginning of the next activity season. The time between release and assessment of survival encompassed two ecologically important times during which lizards may have perished. The first was during the activity season when predation, starvation or injuries associated with intra- or interspecific interactions may have caused death. The second was a period of overwintering when the lizards are quiescent and when mortality may have resulted from freezing, predation, infection or insufficient energy stores. This approximately spanned mid-August to late March for adults and yearlings and late October to late March for hatchlings. My goal was to determine what trait(s) best predicted survival over

these entire time periods, not to predict survival during one or the other of the two ecological periods. Hence, my estimate of condition has limited utility for how well it can accurately predict survival, especially for the later overwintering period (see Discussion). Body condition of lizards, especially territorial males, decreases over the activity season (e.g. Abell 2000), so my measure of condition early in the season may be important to survival up to overwintering, but it might not reflect winter survival. To test this hypothesis specifically, one would need to measure condition just prior to lizards overwintering, and after they have presumably increased body fat stores after activities associated with reproduction are completed (e.g. territorial patrol in males and egg production in females). Despite these limitations, I made predictions based on the data available. If most deaths were due to starvation (i.e. insufficient energy stores during the active season or over winter), I predicted that body condition or body size would best predict survival and sprint speed would be non-significant, whereas if selection pressures associated with activity were the primary cause of death, I predicted that sprint speed or body size would best predict survival.

ANALYSIS

I first used two-tailed *t*-tests to examine differences in traits between survivors and non-survivors, analysing hatchlings and adults separately. For subsequent analyses, unless indicated otherwise, adults and yearlings were combined into a single 'adult' category. I used logistic regression (e.g. Janzen & Stern 1998) to test for both directional (linear) and stabilizing (quadratic) selection (Lande & Arnold 1983). All independent variables were \log_{10} -transformed for analysis. The dependent variable was the untransformed probability of survival (i.e. 0 or 1). Separate logistic regressions were conducted for hatchlings and adults. The linear selection logistic regression model included SVL, residual hindlimb length, body condition, residual sprint speed and sex (male = 1, female = 0). In adult analyses, age (adult or yearling) was included as a variable. The results were qualitatively the same if body mass was included in the analysis instead of body condition. The quadratic selection logistic regression model included squared residual hindlimb length and squared residual sprint

speed. The results for the residuals were qualitatively similar to those obtained for absolute hindlimb length and sprint speed. Where significant logistic regression models were obtained, the methods of Janzen & Stern (1998) were used to convert the standardized (i.e. multiplied by the preselection standard deviation of the trait, σ_z) logistic regression coefficients into selection coefficients, using the average gradient of the estimated selection surface (i.e. the probabilities of survival). This results in selection coefficients (β_{avggrad}) comparable to those obtained from multiple linear regression (Janzen & Stern 1998). All analyses were conducted in S-Plus vs. 6.1 (Insightful Corporation, Seattle, WA).

Results

Of 54 adult lizards marked in 2003, 24 (44%) survived to 2004. Survivors and non-survivors did not significantly differ in SVL ($t = 0.05$, $df = 52$, $P = 0.96$, Table 1), residual hindlimb length ($t = -0.44$, $df = 52$, $P = 0.66$, Table 1), body condition ($t = 0.56$, $df = 52$, $P = 0.58$, Table 1) or residual sprint speed ($t = -0.49$, $df = 52$, $P = 0.63$, Table 1). The results are qualitatively the same if yearlings and adult lizards are analysed separately and if males and females are analysed separately. Of 64 hatchling lizards marked in 2003, 31 (48%) survived to 2004. Survivors and non-survivors did not differ significantly in SVL ($t = -1.30$, $df = 62$, $P = 0.20$, Table 1) or body condition ($t = 1.06$, $df = 62$, $P = 0.30$, Table 1). However, survivors had significantly larger hindlimb residuals ($t = -2.62$, $df = 62$, $P = 0.01$, Table 1) and significantly larger sprint speed residuals ($t = -8.41$, $df = 62$, $P < 0.001$, Table 1) than non-survivors.

The linear selection logistic regression model for adults was not significant ($\chi^2 = 5.85$, $df = 6$, $P = 0.44$), nor were any partial regression coefficients. Likewise, the quadratic selection logistic regression model for adults also was not significant ($\chi^2 = 7.20$, $df = 8$, $P = 0.52$). The results are qualitatively the same if yearlings and adult lizards are analysed separately. In contrast, the linear selection logistic regression model for hatchlings was significant ($\chi^2 = 13.00$, $df = 5$, $P = 0.02$) with only residual sprint speed predicting survival significantly (Table 2; a logistic regression model with absolute values resulted in $\beta_{\text{avggrad}} = 0.27$ for sprint speed, a coefficient very similar to that obtained for residual

Table 1. Descriptive statistics (mean \pm 1 SEM) for surviving and non-surviving hatchling and adult Collared Lizards (*Crotaphytus collaris*). Numbers in parentheses represent the number of individuals for that category. Bold values represent a significant difference in residual values between survivors and non-survivors using *t*-tests (see text)

	Hatchlings		Adults	
	Survivors (31)	Non-survivors (33)	Survivors (24)	Non-survivors (30)
SVL (mm)	66.25 \pm 1.38	63.53 \pm 1.80	93.06 \pm 1.89	93.11 \pm 1.52
Hindlimb length (mm)	54.83 \pm 1.22	51.39 \pm 1.42	73.32 \pm 1.59	73.14 \pm 1.45
Mass (g)	13.79 \pm 0.97	12.83 \pm 1.17	30.90 \pm 2.60	30.30 \pm 2.03
Condition	-0.0071 \pm 0.008	0.0067 \pm 0.01	-0.0086 \pm 0.01	0.0027 \pm 0.02
Sprint speed (m s ⁻¹)	3.33 \pm 0.06	2.50 \pm 0.06	3.34 \pm 0.09	3.38 \pm 0.07

Table 2. Summary of linear selection analyses (directional selection) on morphological and performance traits of hatchling Collared Lizards using logistic regression. Coefficients represent β_{avggrad} (Janzen & Stern 1998). For sex, male = 1, female = 0

	Selection coefficient	P-value
SVL (mm)	0.005	0.86
Residual hindlimb length	0.039	0.18
Condition	-0.034	0.24
Residual sprint speed	0.229	<0.001
Sex	-0.035	0.20

values). This indicates directional selection on residual sprint speed in hatchlings but not adults. The quadratic selection logistic regression model for hatchlings was not significant ($\chi^2 = 10.80$, $df = 7$, $P = 0.15$).

Discussion

This study revealed a positive relationship between locomotor performance and survival in hatchling but not adult lizards. This is consistent with the hypothesis that juveniles are likely under stronger selective pressure from predators and/or for foraging proficiency than adults. This could reflect a minimum range of speeds that individuals must attain for success in escaping predators and/or foraging. Correspondingly, the maximal sprint speed capacity of non-surviving hatchlings barely lies within the range of that measured for older age classes while foraging and escaping predators (Husak 2005). Yearlings and adults run on average between 0.8 and 1.3 m s⁻¹ while foraging and 2.0 and 2.5 m s⁻¹ while escaping predators (Husak 2005). Given these, it is unlikely that non-surviving hatchlings were unsuccessful at foraging since the maximal capacity of hatchling survivors and non-survivors (Table 1) was well above the average speeds used by older lizards. However, the average maximal speed of hatchling non-survivors was approximately equal to that used by older lizards while escaping predators in nature. Average maximal capacity of hatchling survivors was greater than what is used by older lizards while escaping predators. This suggests two possibilities for how maximal sprint speed may be under directional selective pressure from predators.

First, hatchling non-survivors simply may have been unable to attain speeds sufficient to escape predators. The primary predators of Collared Lizards are snakes and raptorial birds (Husak *et al.* in press), and hatchling Collared Lizards are likely vulnerable to a larger size range of snake predators compared with yearlings and adults. While modifying escape behaviour may be sufficient to compensate for poor locomotor performance in some instances (Husak 2005), if snake predators can approach close to hatchlings, then fast sprint speeds may be necessary for escape. The second way that sprint speed performance may be under selective pressure is indirect. Lizards might compensate for low maximal capacity by using escape speeds closer to maximal capacity (Irschick *et al.* 2000; Irschick 2002).

Frequent use of near maximal capacity may cause elevated levels of corticosterone or high expenditures of energy, both of which can reduce survivorship (e.g. Brown *et al.* 2005; Civantos & Forsman 2000). However, the consequences of using near-maximal capacity often are poorly understood and deserve further empirical attention.

Arnold's (1983) paradigm predicts a correlation between variation in fitness-related performance and variation in relevant morphological traits. For Collared Lizards, hindlimb length was positively correlated with sprint speed in hatchlings ($r = 0.28$, $P = 0.026$), but not in yearlings and adults ($r = 0.12$, $P = 0.39$). Correspondingly, survival was predicted by sprint speed in hatchlings but not adults. It would be instructive for future research to examine what determines sprint speed within these specific age classes. Muscle cross-sectional area or muscle fibre composition are possibilities (e.g. Bonine & Garland 1999). Variation in hindlimb length of hatchlings seems at least partially responsible for variation in sprint speed, indicating that selection on sprint speed influences the evolution of limb length in Collared Lizards. It is worth noting that the logistic regression analyses revealed that residual sprint speed, but not residual hindlimb length, predicted survival of hatchlings, yet *t*-tests revealed that both residual sprint speed and residual hindlimb length differed between survivors and non-survivors. These results emphasize the relatively more important role of whole-animal performance compared with morphological traits that underlie that performance in determining fitness.

Body condition did not significantly predict survival in either hatchlings or adults, but this result does not mean that body condition is unimportant to survival. My goal was to determine what traits, as measured at a discrete point in time, would predict survival in different age groups of lizards. Hence, I measured condition at the same time as the other traits measured, at the peak of the active season. Condition very likely changes over the course of the activity season (Abell 2000) when sexually mature lizards are involved in reproductive activities. If condition deteriorates during the season (Abell 2000) and then improves at the end of the season after reproduction has ceased, then my measure of condition may not be predictive of overwinter survival. However, condition as I measured it may be important during the time period from measurement to overwintering. To determine how well condition might influence survival accurately, one could take multiple measurements over the activity season. To determine how well fat stores influence overwinter survival one could measure condition as close to overwintering as possible and determine survival to the beginning of the next activity season. The utility and validity of body condition indices have been the subject of controversy (e.g. Green 2001; but see Schulte-Hostedde *et al.* 2005), so I cautiously interpret the significance (or the lack thereof) of my results relative to body condition and survival. Investigators studying the

evolution of phenotypic traits should clearly define what body condition indices mean and what their limitations are in studies of survival and selection.

Maximal locomotor capacity in lizards has been proposed to be under selective pressures related to predation and foraging proficiency (Christian & Tracy 1981; Webb 1986; Irschick & Losos 1998). My results suggest that predation pressure, but not foraging proficiency, is an important selective force operating on sprint speed performance of hatchling lizards, but less so in adults. The result is selection on underlying morphology that constrains performance. The finding that only linear selection is operating on the traits measured, and not quadratic selection, suggests that there is directional selection on performance and its underlying morphological basis.

The lack of a performance–fitness relationship in yearlings and adults raises some questions. Is performance of these older age classes under the influence of some other selective pressure(s)? If so, does the most important pressure differ between the sexes? Adult Collared Lizards are sexually dimorphic in relative hindlimb length (McCoy *et al.* 1994), with the development of sexual dimorphism beginning at sexual maturity. Previous work has shown that territorial adult males probably face strong sexual selection pressures to be fast for purposes of territory defence, whereas sprint speed of yearlings and adult females may be under selection for predator avoidance (Husak 2005). These results, together with the present study, suggest a complex scenario in which there are differing selective pressures operating at different intensities through ontogeny and between the sexes. Future work will reveal how general these ontogenetic and sexual differences in selection are among taxa and their ultimate effects on phenotypic expression.

Acknowledgements

I would like to thank Oklahoma Gas & Electric for access to the study site, P. Widder, M. Rouse and N. Rasmussen for help with field work, and S. Fox, T. A. Baird, A. Echelle and M. Palmer for comments on previous versions of the manuscript. This work was conducted with funding from the National Science Foundation (Dissertation Improvement Grant IOB-0407943) and Sigma Xi Grants-in-Aid of research. All work was conducted under an Oklahoma Department of Wildlife Conservation permit and Oklahoma State University Animal Care and Use Protocol No. AS031.

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Received 28 July 2005; revised 21 September 2005; accepted 24 September 2005

Editor: Charles W. Fox