

# Does survival depend on how fast you *can* run or how fast you *do* run?

J. F. HUSAK†‡

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

## Summary

1. Natural selection is generally thought to operate on organisms' maximal abilities to perform ecological tasks in nature (i.e. whole-animal performance). However, selection may instead operate on the manner in which that performance trait is used (i.e. 'ecological performance').
2. I tested whether survival of adult Collared Lizards (*Crotaphytus collaris*) depended on maximal sprint speed capacity or on the speed at which they actually performed two important ecological tasks: chasing a prey item and escaping a predator.
3. Maximal sprint speed did not significantly predict annual survival as determined by daily censuses of the site the following season, nor did speed while foraging, but speed while escaping a predator did. Survival also was positively related to the proportion of maximal capacity used while escaping.
4. These results suggest that selection may operate on ecological performance that is constrained, but not necessarily determined, by maximal performance capacity, suggesting that researchers should consider how organisms utilize maximal performance in nature when testing for a performance–survival relationship.

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## Introduction

The targets of natural and sexual selection are generally phenotypic traits that are the integration of lower levels of biological organization. Hence, the evolution of morphological and physiological traits is driven by selection on higher-level functional traits that constrain what an animal actually does in nature (Huey & Stevenson 1979; Arnold 1983; Pough 1989; Bennett & Huey 1990). This paradigm of thought has led many researchers to propose and empirically test hypotheses relating individual variation in fitness to individual variation in maximal ability to perform ecologically relevant tasks (i.e. whole-animal performance, Huey & Stevenson 1979; Arnold 1983; Emerson & Arnold 1989). Accordingly, such traits as maximal locomotor performance often predict survival, but not in all species or demographic groups within a species (e.g. Jayne & Bennett 1990; Le Galliard, Clobert & Ferrière 2004; Husak 2006). However, finding no relationship between maximal performance capacity and survival does not

necessarily mean that performance is unimportant to survival or not a target of selection.

'Behaviour' has been proposed to act as a filter between performance and fitness by many authors (reviewed in Garland, Bennett & Daniels 1990; Garland & Losos 1994; Irschick & Garland 2001), yet the connections among performance, behaviour, and fitness remain unclear, mostly due to a lack of empirical data and an incomplete theoretical framework from which to work (Webb 1986; Bennett 1989; Garland & Losos 1994; Kingsolver *et al.* 2001; Irschick *et al.* 2005). The hypothesized directional connections assume that maximal performance creates an upper limit on what an organism is capable of doing, but under which they may use a slate of variable behavioural options (Bennett 1989; Garland 1994; Garland & Losos 1994). Current hypotheses also assume that maximal capacity determines what an organism does while accomplishing a task in nature. For example, maximally faster individuals should escape predators faster than maximally slower individuals.

These issues are further complicated because there is not a clear operational distinction between 'behaviour' and 'performance' (see reviews in Irschick & Garland 2001; Lailvaux & Irschick 2006). The connection between performance and 'behaviour' is easier to quantitatively study when the behavioural trait of

†Author to whom correspondence should be addressed.

E-mail: husak@vt.edu

‡Present address: Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA.

interest is the use of maximal performance in nature (i.e. 'ecological performance'; Irschick 2003). For example, how fast do individuals run in nature compared with how fast they are able to maximally run in a laboratory? Given this example, 'performance' can be defined in the traditional sense as the maximal ability of an organism to accomplish an ecological task using dynamical motion (e.g. biting, running, flying or swimming) and 'ecological performance' can be defined as how an organism utilizes maximal performance in nature while accomplishing an ecological task (Irschick 2003). 'Behaviour' is a much more inclusive term that describes what an organism does, but does not quantify how *well* it does a given task (see Lailvaux & Irschick 2006 for a review). An example to distinguish among the three is an escape response by an animal. It has the ability to run away at some speed constrained by its morphology and physiology ('performance'), yet after assessing the situation runs away at a speed below its maximal abilities ('ecological performance'). The act of 'respond to predator' is the 'behaviour'. Because of the broadness and imprecision of the term 'behaviour' as used by others in discussions of morphological evolution, I henceforth use 'ecological performance' instead of 'behaviour' and encourage future workers to distinguish between the two in their own research with the acknowledgement that both are likely important to the evolution of morphological traits.

Lizard locomotion has served as a useful model system in evolutionary biology, especially in studies of selection on maximal performance traits (reviewed in Garland & Losos 1994; Aerts *et al.* 2000; Irschick & Garland 2001). Maximal sprint speed predicts survival for hatchling lizards in some species (Warner & Andrews 2002; Miles 2004; Husak 2006), but not in others (see Bennett & Huey 1990). However, the predictive power of maximal sprint speed on survival in adult lizards, a demographic group that has been through at least one round of selection, remains poorly studied. Maximal sprint speed capacity did not predict survival in adult Collared Lizards (*Crotaphytus collaris*) but it did in hatchlings (Husak 2006), suggesting that there are ontogenetic changes in the role of natural selection in the evolution of locomotor performance (see also Jayne & Bennett 1990). Further, how and when lizards utilize maximal sprint speed depends on ecological context, with individuals of some ages and sexes running fast while escaping predators or chasing rivals, but not while foraging (Irschick & Losos 1998; Irschick 2000; Irschick *et al.* 2000; Mattingly & Jayne 2004; Husak & Fox 2006). These observations raise the possibility that ecological performance rather than maximal performance may be the target of selection for some species or demographic groups within a species. Despite the potential for ecological performance to predict survival, no studies have to my knowledge tested whether maximal performance or ecological performance better predicts survival.

I tested the strength of selection on maximal performance and ecological performance in two contexts in adult Collared Lizards, a broadly distributed species in the south-western United States. Collared Lizards use sit-and-wait foraging to feed opportunistically on available arthropods (Blair & Blair 1941; Cooper *et al.* 2001), and are preyed upon by a variety of predators (Husak *et al.* 2006). Therefore, predator escape and prey capture may be contexts in which maximal sprint speed is subjected to selection. Conversely, as Collared Lizards do not, on average, utilize maximal sprinting capacity while foraging or escaping predators (Husak & Fox 2006), the speed at which lizards perform these tasks may be subjected to selection. On the other hand, absolute speeds used in nature may not be targets of selection; instead, the proportion of maximal capacity used in nature during certain tasks may be a target of selection. Therefore, I tested whether maximal sprint speed, speed while foraging, or speed while escaping predators predicted survival, and whether survival depended on age or sex. I then tested whether survival depended on the proportion of maximal capacity used in nature while foraging or escaping predators.

## Materials and methods

### SURVIVAL

The study was conducted on Sooner Lake dam in Pawnee County, Oklahoma, where the substrate consisted of concrete-covered boulders. In April–May 2003, I captured adult ( $\geq 2$  years of age) and yearling ( $\approx 1$  year of age) male and female lizards by noosing and permanently marked them by toe-clipping and applying a unique pattern of coloured paint spots on the hindlimbs for visual identification at a distance (a modification of Baird, Acree & Sloan 1996). To avoid effects of toe clipping on locomotor performance, I never clipped the longest toe on any lizard. The sprint speed of individuals was determined before toe-clipping early in the season and again later in the season after toe clipping, and there was no significant difference in maximal sprint speed (J. Husak unpublished data). Individuals that I captured the previous year before hatchlings emerged were considered  $\geq 2$  years of age. I examined survival for 60 adult and yearling lizards (14 yearling females, 15 yearling males, 18 females  $\geq 2$  years old, and 13 males  $\geq 2$  years old). The lizards analysed in this study represent a different sample of the same population as that examined in Husak (2006).

I determined survival in the field to the beginning of the next activity season by conducting daily censuses of the study site and surrounding areas of suitable habitat. The time between release and assessment of survival encompassed two ecologically important times during which lizards may have perished: (1) during the activity season (approximately late-March–early August) when predation, starvation or injuries associated with intra- or interspecific interactions may have caused

death, and (2) during overwintering (approximately mid-August to late-March) when lizards are quiescent and when mortality may have resulted from freezing, predation, infection or insufficient energy stores. My goal, however, was to determine what trait(s) best predicted survival over the entire year, not to predict survival during one or the other of the two ecological periods. Previous work with the population revealed that neither body size or body condition (or other morphological variables measured) predicted survival in yearling and adult Collared Lizards (Husak 2006), allowing me to focus my analyses in this study on performance variables that are potentially relevant.

#### 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 film (following Braña 2003), and later viewed the tapes and counted number of frames required to traverse 1-m intervals (the stability of frame speed recording for the camera and tapes used were verified by recording a stopwatch in a separate experiment, J. Husak unpublished data). The resulting speeds were comparable with those found by Peterson & Husak (2006) 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 split for each run was analysed. Following a run, I immediately confirmed 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 at the end of their third day of captivity. The best and second-best performances of each individual, regardless of the day on which they occurred, were highly correlated, indicating high repeatability ( $r = 0.90$ ,  $P < 0.001$ ).

#### FIELD SPEEDS

To determine field performance I followed the methods of Irschick & Losos (1998) and Husak & Fox (2006). I measured sprint speeds for all sex and age classes at the height of the breeding season in two contexts: (1) escaping a predator, and (2) foraging. No gravid females were used in these trials. The same generalized procedure of obtaining sprint speeds was used for all contexts. I used a video recorder to record the movements of the lizards, then reviewed the tape in the field so that I could use landmarks to measure the distance

ran for each movement. I counted the number of frames (30 frames  $s^{-1}$  recorded) per unit of distance measured in the field to obtain the sprint speed. Distances ran varied among individuals, so only runs  $\geq 3$  m were used for analysis to be comparable with laboratory measures of maximal speed. Speeds were calculated over approximate successive 1-m intervals (mean  $\pm$  SE =  $1.2 \pm 0.3$  m) to facilitate comparing those speeds with laboratory-measured speeds. We used the fastest approximate 1-m interval for analyses. If multiple movements occurred during a trial, I used the fastest speed. All trials were conducted when the substrate temperature was 30–40 °C, the optimal temperature range for Collared Lizards in central Oklahoma (Uzee 1990).

For the predator escape trials, a person (the same person in each case, wearing similar clothing) walked toward a lizard at a constant pace of approximately 40  $m\ min^{-1}$  (following Cooper 1997). The lizard was approached parallel with the orientation of the dam to avoid making lizards run up or downhill on the dam, the incline of which may affect behavioural antipredator strategies (Jayne & Ellis 1998) and sprint performance (Irschick & Jayne 1999).

To elicit foraging movements, I elicited a foraging attempt by tethering a fishing fly (without the hook) to the end of a 4-m pole and placing it 3 m away from the lizard, slightly wiggling it at the spot on which it was placed (e.g. Irschick 2000; Husak & Fox 2006). I used this distance to be comparable with that used in the laboratory for maximal performance measurement. Lizard movements toward the fishing fly were video recorded, and speeds were calculated in the manner described above.

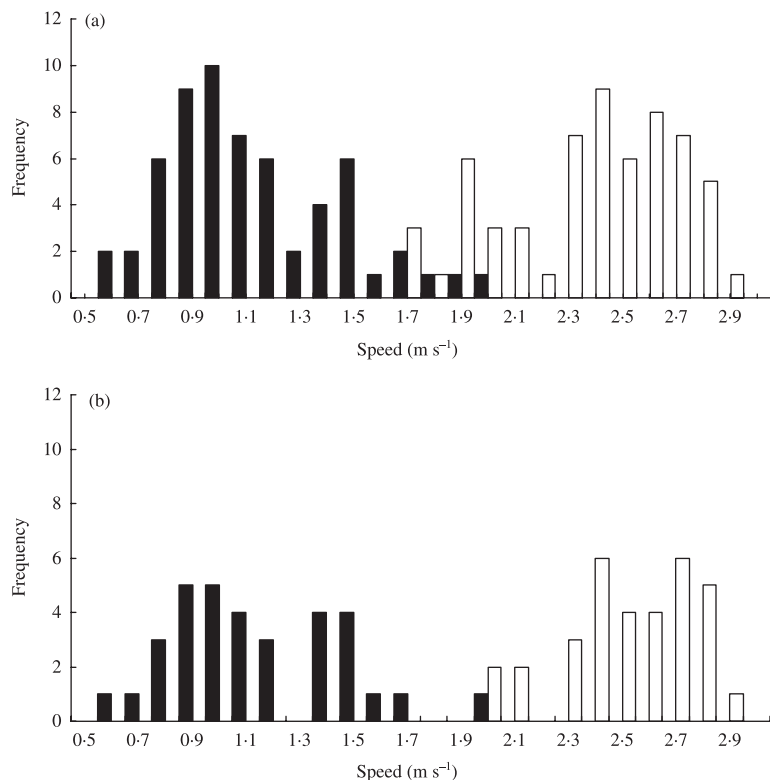
#### STATISTICAL ANALYSIS

I first used two-tailed *t*-tests to examine differences in traits between survivors and non-survivors. I used logistic regression (e.g. Janzen & Stern 1998) to test for both directional (linear) and stabilizing or disruptive (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). The linear selection logistic regression model included maximal sprint speed, sprint speed while foraging, sprint speed while escaping a predator, age (adult = 1, yearling = 0), and sex (male = 1, female = 0). The quadratic selection logistic regression model included squared values for each of the three sprint speed measurements. Where significant logistic regression models were obtained, the methods of Janzen & Stern (1998) were used to convert the standardized (i.e. multiplied by the pre-selection standard deviation of the trait,  $\sigma_z$ ) 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 ( $\beta_{avggrad}$ ) comparable with those obtained from multiple linear regression (Janzen & Stern 1998).

Selection may operate on the absolute speeds at which lizards ran in nature, or it may operate on the proportion of maximal capacity used. Hence, for each individual I divided each field speed by their corresponding maximal speed to obtain proportions of maximal sprint speed used while foraging and escaping. I then performed a second set of logistic regression analyses (both linear and quadratic as above) to determine if proportion of maximal capacity while foraging or escaping predicted survival. All analyses were conducted in SAS vs. 9.1 (SAS Institute Inc., Cary, NC, USA).

## Results

Of 60 lizards marked in 2003 and included in this study, 33 (55%) survived to 2004. Examining each demographic group, I found that eight (44%) adult females, six yearling females (67%), 13 adult males (65%) and six yearling males (46%) survived. Survivors and non-survivors did not significantly differ in maximal sprint speed capacity ( $t = 0.51$ , d.f. = 58,  $P = 0.61$ , Table 1) or speed while foraging ( $t = 0.50$ , d.f. = 58,  $P = 0.62$ , Table 1). However, survivors ran faster while escaping predators than non-survivors ( $t = 4.46$ , d.f. = 43.7,  $P < 0.001$ , Table 1). Analysis of the distribution of field speeds revealed that there was very little overlap in speeds used during the two activities (Fig. 1a), especially for individuals found to survive to the following year (Fig. 1b).



**Fig. 1.** Frequency distributions of speeds used in nature prior to selection while foraging (solid bars) and escaping a simulated predator (open bars) for (a) all individuals and (b) those individuals that survived to the following year.

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

Sprint speed (m s <sup>-1</sup> )	Survivors (33)	Non-survivors (27)
Maximal	3.38 $\pm$ 0.07	3.44 $\pm$ 0.09
Foraging	1.11 $\pm$ 0.05	1.08 $\pm$ 0.06
Escape	<b>2.47 <math>\pm</math> 0.04</b>	<b>2.14 <math>\pm</math> 0.06</b>

**Table 2.** Summary of linear selection analyses (directional selection) on demographic and performance traits of Collared Lizards using logistic regression. Coefficients represent  $\beta_{\text{avggrad}}$  (Janzen & Stern 1998). For sex, male = 1, female = 0; for age, adult = 1, yearling = 0

	Selection coefficient	$P$ -value
Age	-0.084	0.30
Sex	0.090	0.32
Maximal sprint speed	0.079	0.45
Foraging sprint speed	0.063	0.53
Escape sprint speed	0.383	< 0.001

The linear selection logistic regression model with maximal and field speeds as independent variables was significant ( $\chi^2 = 21.31$ , d.f. = 5,  $P < 0.001$ ) with only escape sprint speed significantly predicting survival (Table 2). The quadratic selection logistic regression model also was significant ( $\chi^2 = 23.39$ , d.f. = 8,  $P = 0.003$ ), but none of the partial regression coefficients were significant ( $P > 0.2$  for all), suggesting that the significant model was driven by the presence of escape sprint speed. Taken together, these results indicate directional selection on only escape sprint speed and no stabilizing or disruptive selection. The results are qualitatively the same if residual values are used (see also Husak 2006) or if yearlings and adult lizards are analysed separately and if males and females are analysed separately.

The linear selection logistic regression model with proportion of maximal capacity used while foraging and escaping as independent variables was significant ( $\chi^2 = 11.93$ , d.f. = 2,  $P = 0.003$ ) with proportion of maximal capacity used while escaping being significant ( $\beta_{\text{avggrad}} = 0.316$ ,  $P = 0.002$ ) and proportion of maximal capacity used while foraging being marginally significant ( $\beta_{\text{avggrad}} = -0.173$ ,  $P = 0.052$ ). The quadratic selection logistic regression model also was significant ( $\chi^2 = 12.12$ , d.f. = 4,  $P = 0.016$ ), but none of the partial regression coefficients were significant ( $P > 0.5$  for all), suggesting that the significant model was driven by the presence of the variables significant in the linear model. Taken together, these results indicate directional selection on the proportion of maximal capacity used while

performing ecological tasks but in differing directions, depending on the context. The results are qualitatively the same if yearlings and adult lizards are analysed separately and if males and females are analysed separately.

## Discussion

The results of this study revealed that selection can operate on ecological performance, emphasizing that studies seeking to better elucidate targets of selection should consider both maximal whole-animal performance traits themselves and ecological performance. Hence, studies that do not find a relationship between performance and survival should consider the relevance of that performance trait in nature to conclusively determine the role of that performance trait in the evolution of its underlying morphology. If selection does not operate on maximal performance, perhaps it operates on ecological performance, which is by definition determined and constrained by maximal performance.

The speed at which yearling and adult Collared Lizards escape predators appears to be more important to survival than how fast they can maximally run. This is in contrast to hatchling Collared Lizards in which survival is determined by maximal sprint speed (Husak 2006). The fate of hatchlings likely lies in the hands of their maximal sprinting capacities and not in their behavioural decisions because of their limited sprinting capabilities compared with older (and correspondingly larger) individuals (Carrier 1996; Husak 2006; Herrel & Gibb 2006). Yearlings and adults, which are able to run much faster than hatchlings, have more flexibility in the strategy they use to escape predators. Indeed, Collared Lizards older than 2 years use less of their maximal sprinting capacity when escaping predators than do yearlings (Husak & Fox 2006), implying that as Collared Lizards age they can attain a speed necessary to escape predators (i.e. reach a 'threshold' or 'adequate' escape speed; see Husak & Fox 2006) by using less of their maximal capacity. This ontogenetic change in ecological performance supports the idea that maximal performance provides a 'performance space' in which an animal's behavioural decisions are confined (Bennett 1989). As lizards age and increase in size this space likely increases, allowing more options for ecological performance to be expressed. These hypotheses suggest a more complex scenario of the presumed trickle-down effects of selection on ecological performance than if it were instead operating on just maximal performance. If escape speed is what selection acts on, then evolutionary change is expected in the musculoskeletal system of the locomotor apparatus, as well as in sensory systems associated with predator detection and the neural pathways to process such information and make 'appropriate' behavioural decisions (Lauder & Liem 1989; Lauder & Reilly 1996). Studies that seek to proximately connect all of these variables are greatly needed.

Despite the fact that faster escaping Collared Lizards survived better than those that escaped slower, faster escapers are not necessarily maximally faster individuals. There is not a positive relationship between escape speed and maximal sprint speed (Husak & Fox 2006), suggesting that maximal capacity *constrains* but does not necessarily *determine* what individuals ultimately do when responding to a predator. This is further supported by the fact that faster escapers were not faster foragers ( $r = 0.24$ ,  $P = 0.07$ ), though the relationship has a positive trend. Interestingly, there is a significant negative correlation between predator escape speed and the distance that Collared Lizards allow a simulated predator to approach (i.e. 'approach distance' calculated from our predator escape trials, following Cooper 1997;  $r = -0.63$ ,  $P < 0.001$ ) such that individuals that are slow escapers do not allow predators to approach as close as faster escapers. This implies different strategies in escaping predators among Collared Lizards, and the near-bimodal distribution of escape speeds prior to selection (Fig. 1a) provides some support of this observation. However, there was no detectable disruptive selection on escape speed or proportion of maximal capacity used while escaping. There is no significant relationship between escape speed and the distance that Collared Lizards run after approach by a simulated predator (i.e. 'flight distance' calculated from our predator escape trials; following Cooper 1997;  $r = 0.10$ ,  $P = 0.64$ ) nor between maximal sprint speed and either antipredator variable ( $P = 0.23$  for approach distance and  $P = 0.72$  for flight distance). However, despite the correlation between escape speed and approach distance, when approach distance is included in a logistic regression with the performance variables analysed above, approach distance is not a significant predictor of survival ( $\beta = 0.22$ ,  $P = 0.38$ ). These results emphasize our lack of understanding of how maximal performance influences ecological performance and the fitness consequences of behavioural decisions based on maximal capacities.

The finding that individuals using a higher proportion of their maximal speed while escaping survived better than those using less was somewhat surprising as using near-maximal capacity may be stressful or energetically detrimental. Because the proportion of maximal capacity used in nature is calculated as a ratio, a positive relationship between survival and proportion of maximal capacity used while escaping can be obtained in three ways. First, survival probability may increase as escape speed and maximal capacity both increase, but with escape speed increasing at a greater rate than maximal capacity. Second, survival probability may increase as escape speed remains constant but maximal capacity decreases. Third, survival probability may increase as escape speed increases but maximal capacity has no relationship with survival. The selection analyses on maximal and field speeds do not support the first two possibilities as there was no

relationship between maximal capacity and survival, and there was a positive relationship between survival and escape speed. The third possibility agrees with the selection analyses and supports the hypothesis that survival depends on attaining some speed sufficient to escape predators regardless of maximal capacity. The third scenario also implies that the positive relationship between survival and proportion of maximal capacity used while escaping is an artefact of escape speed being the numerator in the calculation of the proportion. However, my results are difficult to interpret in a comparative sense because few investigators have quantified selection on maximal performance, and none to my knowledge have quantified selection on ecological performance traits that may be constrained by maximal performance (Irschick & Garland 2001; Kingsolver *et al.* 2001). Future empirical and theoretical studies should attempt to reach beyond the conceptually simple (but logistically difficult) morphology–performance–fitness paradigm and the individual connections associated with it. If it is not maximal performance, but instead ecological performance that predicts survival, then mechanisms that proximately regulate the use of maximal performance should be investigated as links earlier in the chain. Future work should also consider how external factors simultaneously influence morphology, performance and ecological performance, and what consequences those effects have on each level of biological organization, and ultimately fitness.

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