The race goes to the swift: fitness consequences of variation in sprint performance in juvenile lizards

Donald B. Miles*

Department of Biological Sciences, Ohio University, Irvine Hall, Athens, OH 45701, USA

ABSTRACT

Locomotor performance is a fundamental link between an animal and its environment. Considerable evidence has accumulated about the biomechanical, physiological and morphological causes of variation in sprint speed and endurance in animals. Yet little information is available about the ecological role of locomotion and its relationship to fitness. This is largely due to the difficulty of acquiring survivorship data in known demographic populations. To address the selective significance of locomotor performance, I estimated the covariation between sprint speed and survivorship of juveniles in a population of the lizard, *Urosaurus ornatus*. Selection analyses based on mark–recapture data revealed significant directional selection for burst velocity and stride length. Faster lizards with longer stride lengths realized a survival advantage over slower lizards regardless of size. Significant non-linear selection was detected on initial velocity and mean velocity. The selection surface for initial velocity was concave up, hence juveniles with intermediate values for initial velocity had lower fitness. Conversely, the selection surface for mean velocity was concave down, thus juveniles with intermediate values for mean velocity had higher survivorship. I hypothesize that the differences in sprint performance influence prey capture and predator escape. Faster lizards may also select warmer microhabitats during favourable conditions, which may enhance growth rates but entail higher risks of predation.

Keywords: body size, fitness, lizard, locomotor performance, survivorship, *Urosaurus ornatus*.

INTRODUCTION

Locomotor performance is presumed to influence fitness, because of its likely role in affecting escape from predators or acquiring prey (Bennett and Huey, 1990; Garland and Carter, 1994; Bauwens *et al.*, 1995; Irschick and Garland, 2001; Van Damme and Vanhooydonck, 2001). Several studies of physiological performance provide support that traits such as sprint speed should have a profound effect on fitness. Measures of performance such as sprint speed and stamina show considerable inter-individual variation (Huey *et al.*, 1990; Hayes and Jenkins, 1997). Longitudinal analyses have shown that variation in locomotor traits have high repeatabilities both over short and long periods ($\approx$ 1 year; Huey

* e-mail: dmiles2@ohio.edu

and Dunham, 1987; Van Berkum *et al.*, 1989; Brodie and Russell, 1999). In addition, locomotor performance has been shown to have significant heritabilities (Garland, 1988; Tsuji *et al.*, 1989). Comparative analyses also indicate that maximum velocities observed in the laboratory closely correspond with escape performance in the field (Irschick and Losos, 1998).

Results from field studies and laboratory experiments suggest that variation in maximum velocity is correlated with predation rates (Christian and Tracy, 1981; Snell *et al.*, 1988; Watkins, 1996). However, inferences based on field data are derived from comparisons of sprint data from populations that differ in estimated predation risk; therefore, such evidence only lends indirect support to speed being a significant predictor of survivorship. Despite the probable selective importance of locomotor performance, evidence from field studies linking relative fitness to locomotor performance remains elusive (Garland and Losos, 1994; Miles, 1994). To date, only two studies have shown that sprint speed is a significant predictor of survivorship in a natural population (Jayne and Bennett, 1990; Warner and Andrews, 2002), but the association was evident in only certain age classes. Determining the fitness consequences of variation in performance is critical, because many studies assume that locomotor performance is an adequate proxy for fitness (Temple and Johnston, 1998).

Here I report the results of a study designed to determine whether locomotor performance affects fitness in the wild. I compared the survivorship of individuals from a natural population of *Urosaurus ornatus* with respect to their body size and estimated locomotor capacities. I restricted the analysis to juveniles, because their small size and presumed elevated risk of predation, and hence high mortality, suggest that selection should be more intense on the younger age classes (Carrier, 1996). Elucidation of the direct effect of locomotor capacities on fitness may be confounded by the influence of body size. Various measures of performance (e.g. maximum velocity or endurance) may be positively correlated with body size (Snell *et al.*, 1988; Huey *et al.*, 1990; Garland and Losos, 1994; Miles, 1994). Evolutionary theoretical models predict that offspring survival should be strongly related to offspring quality, as described by larger body size (Ferguson and Fox, 1984; Packard and Packard, 1988; Laurie and Brown, 1990; Sinervo *et al.*, 1992; Forsman, 1993; Janzen, 1993, 1995; Sorci and Clobert, 1999). Consequently, faster lizards may exhibit a survival advantage as an indirect consequence of body size rather than an advantage due to performance. Therefore, two predictions were tested in this study. First, an *a priori* prediction derived from theory is that large-sized offspring should have higher survivorship – that is, the 'bigger is better' hypothesis. Second, faster lizards should exhibit higher survivorship after controlling statistically for the effects of size. Thus, this study provides the opportunity to disentangle the relative contribution of size and sprint performance in predicting differential survivorship.

METHODS

Data collection

I collected hatchling and juvenile *Urosaurus ornatus* from Saguaro National Park near Tucson, Arizona, between 4 and 14 November 1987. *Urosaurus ornatus* is known to be active throughout the year in south-east Arizona (Asplund and Lowe, 1964). Lizards are active in early to mid-November when temperatures exceed 22°C. Although censuses were

conducted in the late morning and early afternoon when ambient temperatures were highest, the sample size was constrained by the low number of lizards seen during the study. All hatchlings and juvenile lizards observed in the field ($n = 45$) were captured and brought back to the laboratory for the performance experiments. I permanently marked each lizard with a unique toe clip to facilitate identification in subsequent censuses. I found no relationship between the number of toes clipped and survivorship in *U. ornatus* (unpublished data). The snout-to-vent length and body mass of each individual were measured before assessing sprint performance.

Analysis of locomotor performance

Estimates of sprint performance were made using well-established protocols (Miles and Smith, 1987; Bennett and Huey, 1990; Miles, 1994). I induced lizards to run down a 2 m long raceway by gently tapping the tail or hind limb. Eight infrared photocells spaced 10–25 cm along the length of the track recorded lizard movement. Elapsed times between successive photocells were stored on a computer and used to calculate sprint speed. All performance trials were conducted on lizards with a body temperature of 36°C, which was the measured field active body temperature (D.B. Miles, unpublished observation). Lizards were allowed to rest for at least 1 h before another run. Eight runs were obtained for each individual. Trials in which the lizards failed to sprint or reversed direction were excluded from the analysis. I used the fastest speed over any 25 cm segment as an estimate of burst velocity. Furthermore, I designated the initial velocity as the fastest speed along the first 25 cm of the racetrack; initial velocity provides an index of acceleration. The average speed, or mean velocity, attained by a lizard down the length of the 2 m track was also determined. Mean velocity is a measure of the ability of lizards to maintain speed over a relatively longer distance. Furthermore, mean velocity may also include a behavioural component. For example, lizards that use flight to avoid predators should have high average velocities. However, a lizard that uses crypsis or manoeuvrability to avoid predators may not sprint rapidly in a direct path, but zigzag down the track, which would result in low average velocity. I used sand as a substrate, which facilitated measuring stride length (the distance between successive footfalls) directly from the spoor (Huey, 1982; Miles, 1994). The maximum stride length that coincided with the fastest run was used in the analysis. All the measures of locomotor performance have high and significant repeatabilities. The intra-class correlation coefficients for initial and burst velocity are 0.36 and 0.48, respectively (D.B. Miles, unpublished data).

Estimation of survival

Lizards were released at the site of capture after the completion of the performance measurements, which was usually no longer than 2 days after capture. Lizards typically recovered completely from the trials before being released. I used survival to first reproduction (late spring to early summer) as an estimate of fitness. The time interval between initial capture and recapture spans two key episodes in the life cycle of *U. ornatus*. First, lizards enter a period of winter quiescence (mid-November to late February), which may be interspersed with activity. For example, juvenile lizards may be active, basking and foraging, between November and February if ambient temperatures exceed 22°C (Asplund and Lowe, 1964). In the time period included in this study, lizards were inactive for intervals not

exceeding 10 days (mean ± standard deviation = 4.8 ± 2.9 days), based on temperature records (NOAA). Survival through winter may therefore require substantial energy stores. Second, lizards begin territory establishment and mate acquisition in March and April (M'Closkey *et al.*, 1987a,b); during this period, lizards are very active and move considerably from tree to tree. The high activity and conspicuous dominance behaviours increase the exposure and vulnerability of lizards to predators. To determine survivorship, I monitored the study site during the late spring and early summer of 1988 by regular censuses conducted every 2 weeks. I made every effort to survey the sites of capture within the study area as well as a 50 m zone around the site. Lizards that were not captured by the end of the fourth census were presumed to have died.

Analysis of selection

I estimated the fitness gradient (i.e. the covariance between the performance traits and relative fitness) using logistic regression rather than multivariate regression (Janzen and Stern, 1998). Logistic regression can test for whether the fitness surface is linear or curvilinear (i.e. quadratic). However, description of the various forms of selection – directional, quadratic and correlational – may involve estimation of a large number of parameters, even for a rather small suite of traits. Even in large data sets, a complete specification of all combinations of trait values may be impossible. Furthermore, in many circumstances the fitness surface is likely to have a complex shape, which cannot be estimated using parametric methods. Therefore, I also used a non-parametric method, projection pursuit regression, to estimate the fitness surface developed by Schluter and Nychka (1994). Projection pursuit regression does not specify the form of the fitness surface, which makes it suitable for using non-normal estimates of fitness, such as survival data. Two advantages of the projection pursuit are it determines the form of multivariate selection on all the measured traits simultaneously and can detect correlational selection. The vectors of loading, **a**, and their standard errors were estimated by the program PP (Schluter and Nychka, 1994). Confidence intervals were generated by bootstrapping.

In all selection analyses, I defined fitness as the survival of individuals from November to June. Survivors were assigned a score of 1 and non-survivors a score of 0. All variables were standardized to a mean of 0 and unit variance. I used snout-to-vent length and body mass as estimates of body size in both the logistic and projection pursuit regressions. Because fat stores may be critical in determining annual survival in lizards, I included body condition in the analyses. Body condition was estimated as the regression of log(body mass) on log(snout-to-vent length).

I first used logistic regression to provide an overall test of the covariation between relative fitness and size and locomotor variables. As suggested by Brodie *et al.* (1995), I ran two separate regressions to estimate the linear and non-linear (quadratic) fitness gradients. The linear (i.e. directional) selection gradient was described using a model that included only linear terms for the variables. The non-linear (i.e. quadratic) fitness gradient was estimated by including the squared locomotor trait values in the regression model. Separate regressions are necessary to estimate the linear and quadratic terms because of the potential for the coefficients to be correlated if the data are not multivariate normally distributed (Brodie, 1992; Brodie *et al.*, 1995). I used JMP (version 4) for these statistical analyses. The non-parametric selection analysis was completed using projection pursuit regression. The

significance of the first axis from the projection pursuit regression was determined using standard errors based on bootstrap resampling.

RESULTS

The censuses of 1988 resulted in the recapture of 11 of the 45 lizards obtained in the 1987 census. This represents a survivorship of 24.4%, which is within the upper range of published values for the species (Dunham, 1982). Mean snout-to-vent length of lizards measured in 1987 and surviving to 1988 was longer than that of non-survivors ($t_{43} = 2.2$, $P < 0.03$; Table 1). Survivors were also heavier than non-survivors, but the difference was not significant ($t = 1.52$, $P = 0.14$). Logistic regression analysis revealed that juvenile snout-to-vent length significantly predicted survivorship ($\chi^2 = 4.67$, $P < 0.03$). Alternatively, variation in body condition rather than size may be a better predictor of survival. The condition index was unrelated to survival ($\chi^2 = 0.07$, $P = 0.79$).

Body size is strongly correlated with many phenotypic and physiological traits (Calder, 1984; Sinervo and Huey, 1990), including sprint performance ($r = 0.56$, $P < 0.001$; Fig. 1).

Table 1. Body size and locomotor traits for survivors and non-survivors (mean ± standard deviation)

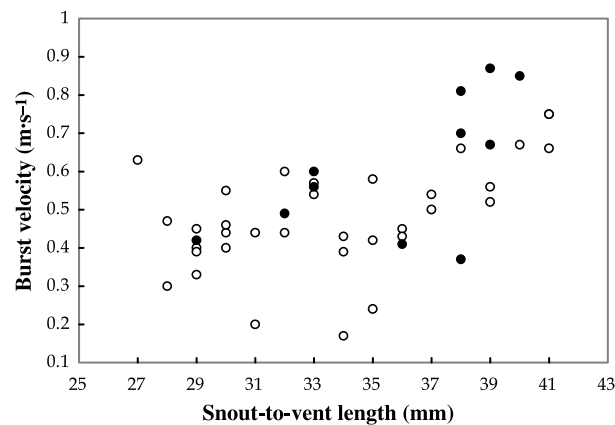| Trait	Survivors ($n = 11$)	Non-survivors ($n = 34$)
Snout-to-vent length (mm)	36.6 ± 3.5	33.6 ± 4.2
Mass (g)	1.36 ± 0.43	1.13 ± 0.46
Initial velocity (m·s^{-1})	0.36 ± 0.16	0.35 ± 0.15
Burst velocity (m·s^{-1})	0.62 ± 0.18	0.48 ± 0.14
Mean velocity (m·s^{-1})	0.39 ± 0.14	0.29 ± 0.11
Stride length (mm)	89.4 ± 14.6	71.8 ± 13.1

Fig. 1. Relationship between body size (snout-to-vent length) and burst velocity. ●, survivors; ○, non-survivors.

Therefore, size and performance are likely to be conflated. If body size and speed are correlated, then the fitness advantage attributed to sprint performance may be an indirect effect due to selection favouring large body size and not to an independent effect of speed. A key question is whether size or speed has a greater influence on survivorship. Results from a logistic regression showed that locomotor performance was a significant predictor of survivorship ($\chi^2 = 3.81$, $P < 0.05$). However, the regression coefficient for snout-to-vent length in the same analysis was not significant ($\chi^2 = 1.59$, $P = 0.24$), which suggests that speed was a better predictor of survival than body size. An analysis of covariance, with burst velocity as a covariate, revealed no difference in size among survivors and non-survivors ($F_{1,42} = 0.49$, $P = 0.48$). This argues that the fitness advantage due to size may be an outcome of elevated performance.

I identified the targets of selection by measuring the fitness gradient using logistic regression. Because logistic regression controls for correlations among the predictor variables, the partial regression coefficients estimate direct rather than indirect selection (Arnold, 1983; Endler, 1986). The overall logistic regression model estimating linear (directional) selection was significant ($P < 0.01$), with an R^2 of 0.31; therefore, the null hypothesis that survival was unrelated to locomotor performance was rejected. Only stride length was significantly associated with survival (Table 2). Snout-to-vent length, initial velocity, burst velocity and mean velocity were not associated with survival. These results suggest that juvenile lizards which took longer stride lengths tended to survive to 1988 (Table 2).

The logistic regression model that included quadratic terms was also highly significant ($\chi^2 = 28.10$, $P < 0.0001$; $R^2 = 0.57$). Of the five traits included in the analysis, only the coefficients for initial velocity and mean velocity were statistically significant (Table 2). Stride length also had a large regression coefficient, but it was only marginally statistically significant ($P = 0.08$). Both initial velocity and stride length had a positive regression coefficient, which may be interpreted as suggesting disruptive selection. That is, surviving juveniles were either slow initially or attained high velocities rather rapidly. The quadratic regression coefficient for mean velocity was negative, which may be interpreted as suggesting stabilizing selection (Table 2). Juveniles with intermediate values for mean velocity had higher fitness.

The projection pursuit regression model suggested a single axis describing the major patterns of variation in performance in relation to survival. Examination of the fitness

Table 2. Summary of selection analyses on body size (snout-to-vent length) and four locomotor performance traits

Trait	Linear term (directional selection)	Quadratic term (non-linear selection)
Snout-to-vent length (mm)	0.20	−0.06
Initial velocity (m·s^{-1})	0.24	0.55**
Burst velocity (m·s^{-1})	0.11	0.19
Mean velocity (m·s^{-1})	0.02	−1.21***
Stride length (mm)	0.24*	0.55[+]
R^2	0.31**	0.57***

Note: The values are coefficients for the selection gradient ($\beta_{avggrad}$) (Janzen and Stern, 1998).
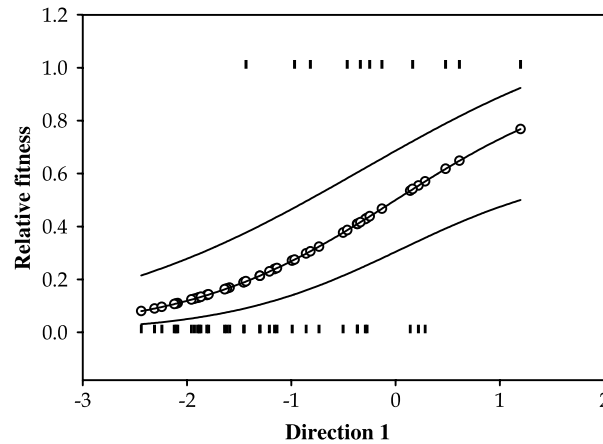[+]$0.05 < P < 0.10$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Fig. 2. Fitness response surface of initial velocity, burst velocity, mean velocity and stride length for juvenile *U. ornatus*. Confidence intervals were estimated from 1000 bootstrap replications.

Table 3. Fitness surface estimation using projection pursuit regression

Trait	Direction a_1
Snout-to-vent length	−0.10
Initial velocity	**−0.48**
Burst velocity	0.27
Mean velocity	0.27
Stride length	**0.83**
$\ln(\lambda) - 1.54$	

Note: Terms in **boldface** were significantly different from zero.

surface shows that selection was largely directional (Fig. 2), which is consistent with the pattern found above. Two variables, stride length and initial velocity, were significantly associated with fitness (Table 3). The larger coefficient for stride length indicates it had the greatest contribution to fitness. The opposite signs for the coefficients indicate negative correlational selection. That is, a long stride length relative to low initial velocity had a strong connection with survival. I used a principal components (PC) analysis to visualize the patterns of negative correlational selection (Fig. 3). Two principal components axes extracted from the covariance matrix explained 89% of the total variation (Table 4). All the performance variables had positive loadings on the first axis (Table 4), which may be interpreted as an overall index of 'speed'. The results from a logistic regression analysis indicated that PC axis 1 significantly predicted survivorship ($\chi^2 = 4.79$, $P < 0.02$). Therefore, faster lizards had higher fitness. The second PC axis represents a contrast between initial velocity and stride length (Table 4). Survivors had significantly higher scores on PC axis 2 ($\chi^2 = 7.69$, $P < 0.005$). Juveniles with low initial velocities and long stride lengths were most likely to survive.
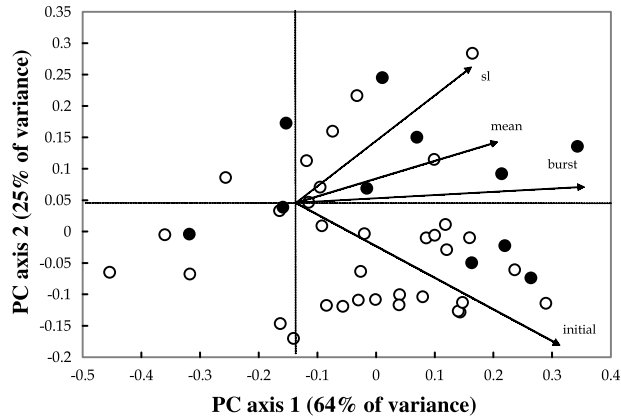
Fig. 3. Performance space defined by the first two axes from a principal components analysis using the covariance matrix based on four locomotor size-adjusted performance variables. ●, survivors; ○, non-survivors. The vectors portray the direction and magnitude of the loadings for each of the size-adjusted variables on each of the two PC axes. PC axis 1 represents a composite of the four measures of sprint performance (stride length, sl; mean velocity; burst velocity; initial velocity). PC axis 2 contrasts initial velocity against stride length and burst velocity. The results demonstrate that the surviving juveniles were faster and had longer stride lengths than the non-surviving lizards.

Table 4. Loadings from a principal components analysis based on the four standardized performance variables

Trait	PC axis 1	PC axis 2
Initial velocity	0.38	−0.81
Burst velocity	0.54	0.17
Mean velocity	0.58	0.08
Stride length	0.41	0.56
Eigenvalue	2.51	0.90
Variance explained (%)	63.0	22.0

DISCUSSION

Two key patterns emerged from the analysis of differential survivorship in juvenile *U. ornatus*. First, larger individuals were more likely to survive than smaller individuals. However, inclusion of the performance data also indicated that size alone did not completely explain the patterns of survival. Including body size and burst velocity simultaneously in a regression analysis resulted in only burst velocity significantly predicting survivorship. This result indicates that performance is a better predictor of survivorship in juvenile lizards than body size. Second, the selection analyses revealed a complex pattern of linear, quadratic and correlational selection on locomotor performance. There was evidence for strong directional selection on stride length. However, the quadratic selection analyses revealed a disparate pattern of selection acting on locomotor performance. Disruptive selection was apparent for initial velocity, whereas mean velocity was

under stabilizing selection. Only two traits, initial velocity and stride length, were under correlational selection and the observed relationship was negative.

Selection on body size

The selective advantage of large size in hatchling or juvenile individuals is predicted from theoretical models. One advantage of large size would be the ability to evade predators. Food acquisition may be another advantage to large size. Several empirical studies have provided support for a selective advantage of large size in lizards and other taxa, because larger juveniles may have higher fat stores or higher rates of energy acquisition leading to higher survivorship during poor environmental conditions or extended periods of inactivity (Ferguson and Fox, 1984; Jayne and Bennett, 1990; Laurie and Brown, 1990; Forsman, 1993; Janzen, 1993; Civantos and Forsman, 2000). However, other studies have failed to support the 'bigger is better' pattern (Sinervo *et al.*, 1992; Zamudio *et al.*, 1995; Wikelski and Trillmich, 1997; Sorci and Clobert, 1999). The lack of sufficient fat stores may be due to the inability to successfully capture prey. Alternatively, feeding activity may have been constrained by risks attributable to predation.

The pattern of selection on body size is consistent not only with the 'bigger is better' hypothesis, but also supports the hypothesis that earlier clutches are better than later clutches (Olsson and Shine, 1997). Female *U. ornatus* may lay up to three clutches per year in arid habitats during favourable years (Dunham, 1982). Based on incubation time and hatchling size (D. Vleck, personal communication), I inferred that the smallest individuals in the sample must have emerged from eggs oviposited in late September or early October. The larger individuals in the sample were progeny produced from earlier clutches that hatched in late August. Previous studies have found that second or later clutches had fewer eggs, which produced smaller-sized offspring and exhibited lower post-hatching survivorship (Sinervo *et al.*, 1992; Olsson and Shine, 1997; Sinervo, 1999). Some of the variation in offspring quality may be due to maternal characteristics, for example changes in allocation of resources to reproduction. It may also be a consequence of different environments the eggs were exposed to during incubation. For example, previous studies have also shown that thermal and hydric qualities of the nest environment can have profound implications for offspring snout-to-vent length and performance (Elphick and Shine, 1998).

Selection on locomotor performance

The results showed that locomotor performance, irrespective of size, is associated with fitness of juvenile lizards. This is consistent with other studies examining the covariance between locomotion and survival in younger age classes (Jayne and Bennett, 1990; Warner and Andrews, 2002). However, some studies have reported no selection on speed in hatchlings (e.g. *Sceloporus occidentalis*; Bennett and Huey, 1990). The standardized fitness gradient revealed that the selection on burst velocity was the result of indirect selection; the direct target of selection was stride length. An outcome of this study is that significant phenotypic selection may act on performance traits that are likely to directly modulate speed – that is, stride length rather than velocity. Biomechanical models show that lengthening the hind limb, which, in turn, increases stride length, can enhance speed. Therefore, the pattern of selection matches the predictions emerging from functional morphology (White and Anderson, 1994). This result highlights the need to include multiple measures of

locomotor performance and not simply measures of velocity (Garland and Carter, 1994; Garland and Losos, 1994).

The quadratic and correlational selection analyses revealed conflicting selection on locomotor traits. Non-linear selection on initial velocity was disruptive, which suggests two types of behaviours facilitated survival. For some surviving juveniles, speed in the first few centimetres, which would accompany fast starts, may have a role in avoiding predators or prey capture. For example, *U. ornatus* is a classic sit-and-wait predator and quick initial speed may affect the ability to capture prey successfully. However, some lizards with low initial velocities survived. These lizards may have used behavioural adjustments – for example, increased wariness or crypsis – to compensate for low performance. The analyses also demonstrated stabilizing selection on mean velocity. Because mean velocity is a measure of sustained speed (i.e. the average speed over 2 m), it seems intuitive that slow runners would have a lower survivorship. The low survivorship for lizards with high values of sustained speed appears to be counterintuitive. Mean velocity is a measure of sustained performance over a 2 m long track. Juveniles that have high mean velocities may also be very active. Thus, sustained performance may correlate with behaviour, such that highly active lizards are at greater risk of predation (Snell *et al.*, 1988; Sinervo *et al.*, 2000; Miles *et al.*, 2001). In addition, tree lizards may simply try to outrun a predator. Lizards with intermediate values of mean velocity may use both speed and manoeuvrability to flee from a predator. The behaviour of tree lizards supports this conjecture. Some lizards will run from a predator in a single, straight dash. Other lizards rapidly move away from a predator by running around a tree branch or trunk. This behaviour places the lizard further from the predator and hidden from view. Finally, two traits provided an example of correlational selection, as shown by the projection pursuit regression. Juveniles that had low values for one trait and high values for the other trait were more likely to survive and vice versa.

The results presented in this study demonstrate the selective importance of locomotor performance, which supports the assumptions of many studies of sprint speed (e.g. Christian and Tracy, 1981; Van Damme and VanHooydonck, 2001). Rapid initial starts and fast speed are likely to correlate with survival; faster juveniles are expected to have an advantage in prey capture and predator avoidance relative to slow juveniles. The pattern of selection on initial velocity supports the conclusions from a simulation study on the ecological consequences of acceleration (Huey and Hertz, 1984). Small lizards are predicted to enhance their escape from large quadruped predators by rapid acceleration on level or uphill slopes (Huey and Hertz, 1984).

Determining the ecological role of performance – that is, whether sprint performance enhances predator avoidance or prey capture – requires additional study. A first step towards this goal would be to identify the direct targets of selection in subsequent experiments, including phenotypic manipulations and predator encounters. These experiments could clarify whether locomotor performance confers a survival advantage through resource accrual or predator avoidance. Thus, additional data are necessary to link variation in performance with specific agents of selection.

ACKNOWLEDGEMENTS

REFERENCES

Arnold, S.J. 1983. Morphology, performance and fitness. *Am. Zool.*, **23**: 347–361.

Asplund, K.A. and Lowe, C.H. 1964. Reproductive cycles of the iguanid lizards *Urosaurus ornatus* and *Uta stansburiana* in southeastern Arizona. *J. Morph.*, **115**: 27–34.

Bauwens, D., Garland, T., Jr., Castilla, A.M. and Van Damme, R. 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological and behavioral covariation. *Evolution*, **49**: 848–863.

Bennett, A.F. and Huey, R.B. 1990. Studying the evolution of physiological performance. In *Oxford Surveys of Evolutionary Biology*, Vol. 7 (D.J. Futuyma and J. Antonovics, eds), pp. 251–284. Oxford: Oxford University Press.

Brodie, E.D., III. 1992. Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. *Evolution*, **46**: 1284–1298.

Brodie, E.D., III and Russell, N.H. 1999. The consistency of individual differences in behaviour: temperature effects on antipredator behaviour in garter snakes. *Anim. Behav.*, **57**: 445–451.

Brodie, E.D., III, Moore, A.J. and Janzen, F.J. 1995. Visualizing and quantifying natural selection. *Trends Ecol. Evol.*, **10**: 313–318.

Calder, W.A. 1984. *Size, Function, and Life History*. Cambridge, MA: Harvard University Press.

Carrier, D. 1996. Ontogenetic limits on locomotor performance. *Physiol. Zool.*, **69**: 467–488.

Christian, K.A. and Tracy, C. 1981. The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. *Oecologia*, **49**: 218–223.

Civantos, E. and Forsman, A. 2000. Determinants of survival in juvenile *Psammodromus algirus* lizards. *Oecologia*, **124**: 64–72.

Dunham, A.E. 1982. Demography and life history variation among populations of the iguanid lizard *Urosaurus ornatus*: implications for the study of life history phenomena in lizards. *Herpetologica*, **38**: 208–221.

Elphick, M.J. and Shine, R. 1998. Long term effects of incubation temperatures on the morphology and locomotor performance of hatchling lizards (*Bassiana duperreyi*, Scincidae). *Biol. J. Linn. Soc.*, **63**: 429–447.

Endler, J. 1986. *Natural Selection in the Wild*. Princeton, NJ: Princeton University Press.

Ferguson, G.W. and Fox, S.F. 1984. Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: its causes and evolutionary significance. *Evolution*, **38**: 342–349.

Forsman, A. 1993. Survival in relation to body size and growth rate in the adder, *Vipera berus*. *J. Anim. Ecol.*, **62**: 647–655.

Garland, T., Jr. 1988. Genetic basis of activity metabolism. I. Inheritance of speed, stamina and antipredator displays in the garter snake *Thamnophis sirtalis*. *Evolution*, **42**: 335–350.

Garland, T., Jr. and Carter, P.A. 1994. Evolutionary physiology. *Annu. Rev. Physiol.*, **56**: 579–621.

Garland, T., Jr. and Losos, J.B. 1994. Ecological morphology of locomotor performance in squamate reptiles. In *Ecological Morphology* (P. Wainwright and S.M. Reilly, eds), pp. 240–302. Chicago, IL: University of Chicago Press.

Hayes, J.P. and Jenkins, S.H. 1997. Individual variation in mammals. *J. Mammal.*, **78**: 274–293.

Huey, R.B. 1982. Phylogenetic and ontogenetic determinants of sprint performance in some diurnal Kalahari lizards. *Koedoe*, **25**: 43–48.

Huey, R.B. and Dunham, A.E. 1987. Repeatability of locomotor performance in natural populations of the lizard *Sceloporus merriami*. *Evolution*, **41**: 1116–1120.

Huey, R.B. and Hertz, P.E. 1984. Effects of body size and slope on acceleration of a lizard (*Stellio stellio*). *J. Exp. Biol.*, **110**: 113–123.

Huey, R.B., Dunham, A.E., Overall, K.L. and Newman, R.A. 1990. Variation in locomotor performance in demographically known populations of the lizard *Sceloporus merriami. Physiol. Zool.*, **63**: 845–872.

Irschick, D.J. and Garland, T., Jr. 2001. Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *Annu. Rev. Ecol. Syst.*, **32**: 367–396.

Irschick, D.J. and Losos, J.B. 1998. A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution*, **52**: 219–226.

Janzen, F.J. 1993. An experimental analysis of natural selection on body size of hatchling turtles. *Ecology*, **74**: 322–341.

Janzen, F.J. 1995. Experimental evidence for the evolutionary significance of temperature-dependent sex determination. *Evolution*, **49**: 864–873.

Janzen, F.J. and Stern, H.S. 1998. Logistic regression for empirical studies of multivariate selection. *Evolution*, **52**: 1564–1571.

Jayne, B.C. and Bennett, A.F. 1990. Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution*, **44**: 1204–1229.

Laurie, W.A. and Brown, D. 1990. Population biology of marine iguanas *Amblyrhynchus cristatus*. II. Changes in annual survival rates and the effects of size, sex, age, and fecundity in a population crash. *J. Anim. Ecol.*, **59**: 529–544.

M'Closkey, R.T., Baia, K.A. and Russell, R.W. 1987a. Tree lizard *Urosaurus ornatus* territories: experimental perturbation of the sex ratio. *Ecology*, **68**: 2059–2062.

M'Closkey, R.T., Baia, K.A. and Russell, R.W. 1987b. Defense of mates: a territory departure rule for male tree lizards following sex-ratio manipulation. *Oecologia*, **73**: 28–31.

Miles, D.B. 1994. Covariation between morphology and locomotory performance in Sceloporine lizards. In *Lizard Ecology* (L.J. Vitt and E.R. Pianka, eds), pp. 207–235. Princeton, NJ: Princeton University Press.

Miles, D.B. and Smith, R.G. 1987. A microcomputer-based timer and data acquisition device for measuring sprint speed and acceleration in cursorial animals. *Funct. Ecol.*, **1**: 281–286.

Miles, D.B., Snell, H.L. and Snell, H.M. 2001. Intrapopulational variation in endurance of Galápagos lava lizards (*Microlophus albemarlensis*): evidence for an interaction between natural and sexual selection. *Evol. Ecol. Res.*, **3**: 795–804.

Olsson, M. and Shine, R. 1997. The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why early clutches are better. *J. Evol. Biol.*, **10**: 369–381.

Packard, G.C. and Packard, M.J. 1988. The physiological ecology of reptilian eggs and embryos. In *Biology of the Reptilia* (C. Gans and R.B. Huey, eds), pp. 523–605. New York: Alan R. Liss.

Schluter, D. and Nychka, D. 1994. Exploring fitness surfaces. *Am. Nat.*, **143**: 597–616.

Sinervo, B. 1999. Mechanistic analysis of natural selection and a refinement of Lack's and Williams's principles. *Am. Nat.*, **154**: S26–S42.

Sinervo, B. and Huey, R.B. 1990. Allometric engineering: an experimental test of the causes of interpopulational differences in performance. *Science*, **248**: 1106–1109.

Sinervo, B., Doughty, P., Huey, R.B. and Zamudio, K. 1992. Allometric engineering: a causal analysis of natural selection on offspring size. *Science*, **258**: 1927–1930.

Sinervo, B., Miles, D.B., Frankino, W.A., Klukowski, M. and DeNardo, D.F. 2000. Testosterone, endurance, and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Horm. Behav.*, **38**: 222–233.

Snell, H.L., Snell, H.M., Jennings, R.D. and Harcourt, S. 1988. Intrapopulation variation in predator avoidance performance of Galapagos lava lizards: the interaction of sexual and natural selection. *Evol. Ecol.*, **2**: 353–369.

Sorci, G. and Clobert, J. 1999. Natural selection on hatchling body size and mass in two environments in the common lizard (*Lacerta vivipara*). *Evol. Ecol. Res.*, **1**: 303–316.

Temple, G.K. and Johnston, I.A. 1998. Testing hypotheses concerning the phenotypic plasticity of escape performance in fish of the family Cottidae. *J. Exp. Biol.*, **201**: 317–331.

Tsuji, J.C., Huey, R.B., Van Berkum, F.H., Garland, T., Jr. and Shaw, R.G. 1989. Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis*): quantitative genetics and morphometric correlates. *Evol. Ecol.*, **3**: 240–252.

Van Berkum, F.H., Huey, R.B., Tsuji, J.S. and Garland, T., Jr. 1989. Repeatability of individual differences in locomotor performance and body size during early ontogeny of the lizard *Sceloporus occidentalis* Baird and Girard. *Funct. Ecol.*, **3**: 97–105.

Van Damme, R. and Vanhooydonck, B. 2001. Origins of interspecific variation in lizard sprint capacity. *Funct. Ecol.*, **15**: 186–202.

Warner, D.A. and Andrews, R.M. 2002. Laboratory and field experiments identify sources of variation in phenotypes and survival of hatchling lizards. *Biol. J. Linn. Soc.*, **76**: 105–124.

Watkins, T.B. 1996. Predator mediated selection on burst swimming performance in tadpoles of the Pacific tree frog, *Pseudacris regilla*. *Physiol. Zool.*, **69**: 154–167.

White, T.D. and Anderson, R.A. 1994. Locomotor patterns and costs as related to body size and form in teiid lizards. *J. Zool.* (*Lond.*), **233**: 107–128.

Wikelski, M. and Trillmich, F. 1997. Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. *Evolution*, **51**: 922–936.

Zamudio, K.R., Huey, R.B. and Crill, W.D. 1995. Bigger isn't always better: body size, developmental and parental temperature and male territorial success in *Drosophila melanogaster*. *Anim. Behav.*, **49**: 671–677.