

Intrapopulation variation in endurance of Galápagos lava lizards (*Microlophus albemarlensis*): evidence for an interaction between natural and sexual selection

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ABSTRACT

Variation in the risk of predation may profoundly affect the evolution of anti-predator behaviours. Theory predicts that selection would favour enhanced locomotor capacity in high-risk environments, such as open habitats. An earlier study demonstrated significant intrapopulation and intersexual variation in wariness and sprint speed among the lava lizards (*Microlophus albemarlensis*) that was concordant with presumed risk of predation on Isla Plaza Sur in the Galápagos Archipelago. In particular, males and females from sparsely vegetated areas had greater approach and flight distances than those of more highly vegetated areas; males were also faster than females. We now compare endurance capacities of males and females from the same population on Isla Plaza Sur. We predicted the higher presumed risk of predation in the sparsely vegetated region would favour enhanced performance capacities. In addition, we predicted that sexual selection for territory defence would favour males that had the ability to flee long distances. Lizards from the sparsely vegetated area did have higher endurance than those from the vegetated area. Males had higher endurance times than females, but this difference was an outcome of body size, which was inconsistent with the sexual selection hypothesis. The significant differences in endurance between locations combined with the absence of dimorphism in performance suggest that the intrapopulation differences are an outcome of natural selection for predator escape.

Keywords: endurance capacity, Galápagos, individual variation, lizard, *Microlophus albemarlensis*, natural selection, predation, sexual selection.

INTRODUCTION

Animals avoid predators by using numerous behaviours, including crypsis, refugia and locomotion. Many studies have focused on locomotor performance, because of the

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presumed importance of locomotion in predator avoidance (Christian and Tracy, 1981; Bennett and Huey, 1990; Jayne and Bennett, 1990; Garland and Losos, 1994). Although a substantial literature exists on variation in performance, scant data are available on how performance affects habitat use, prey capture or predator avoidance (Hertz *et al.*, 1988; Irschick and Losos, 1998, 1999). Direct demonstrations that enhanced locomotion ensures predator avoidance are rarely feasible (see Watkins, 1996). However, one may compare locomotor capacities of individuals that inhabit different predator milieus (Krupa and Sih, 1999). Presumably, an animal occupying a complex environment may have numerous refugia, hence locomotor performance may not be as strongly favoured by selection as in a more open area, with fewer refugia. Recent theory predicts that organisms in high-risk predator environments should allocate more energy to behaviours that are related to predator escape (Lima and Bednekoff, 1999).

Estimating the impact of predator avoidance on patterns in locomotion may be complicated by sexual differences in performance (Cullum, 1998). Males and females differ in size in many species (Fairbairn, 1997). In vertebrates, sexual size dimorphism is often male-biased (Stamps, 1983; Watkins, 1996; Fairbairn, 1997; Zamudio, 1998). If locomotor performance and body size are correlated (Sinervo and Huey, 1990), then, *a priori*, larger males are expected to have greater performance capacities than females, because of the difference in size. However, locomotor performance in males may exceed females for reasons other than size. Males tend to patrol territories, engage in displays to displace intruding males and perform courtship displays to secure females. These behaviours may place males in more exposed areas. The increase in activity from social displays and agonistic encounters may increase the vulnerability of males to predation (Martin and Lopez, 2000). Sprint speed, endurance or both may be greater in males than females, because of differential predation risk induced by sexual behaviours. Selection from predation should favour the evolution of enhanced sprint and endurance performance and therefore longer limbs in males more so than in females (Miles, 1994).

In a previous analysis, Snell *et al.* (1988) examined variation in sprint speed in relation to sexual and natural selection in a population of lava lizards (*Microlophus albemarlensis*) on Isla Plaza Sur in the Galápagos Archipelago. They compared sprint speed, approach distance and flight distance between male and female lava lizards that occupied two divergent habitat types. The eastern region of the island was sparsely vegetated, which presumably corresponded with a higher risk of predation; the western region was more heavily vegetated. Predator diversity tends to be lower on Galápagos islands with woody vegetation (Stone *et al.*, in press). In 1988, 94% (85/90) of observed predation episodes were due to Great Egrets (*Casmerodius albus*; H.L. Snell, personal observation). Snell *et al.* (1988) hypothesized that sexual selection for territory defence would favour short approach distances in males, but natural selection would favour increased hindlimb size and speed. Because reproductive success in female lava lizards is not tied to territory status, a change in locomotor performance was not expected. Approach and flight distances of lizards from the sparse area were greater than in those in the vegetated area. Males from the sparse area were significantly faster than males from the vegetated area. Sprint speed did not differ in females from the sparse and vegetated areas. Longer hindlimbs in males (after adjusting for body size) was a proximate correlate of the differences in speed between the sexes. Snell *et al.* (1988) proposed that the presumably higher predation rates on males was the primary selective agent favouring enhanced locomotor performance. The difference in sprint per-

formance was facilitated by natural selection favouring longer hindlimbs, which presumably minimizes the chance of capture by a predator.

Here, we compare another measure of predator escape behaviour, endurance capacity, among individuals from the same population of Galápagos lava lizards studied by Snell *et al.* (1988). We captured lizards in the same locations as Snell *et al.* (1988). The study sites were approximately 1000 m apart. We focus on endurance because of the strong relationship between endurance and activity patterns in lizards (Garland, 1999). Endurance is likely to relate to duration of distance moved, flight from predators and other aspects of predator avoidance (Garland, 1999; Sinervo *et al.*, 2000). For example, endurance should correlate with flight distances, which require sustained aerobic activity. The longer flight distances observed in lizards from the sparsely vegetated region of Plaza Sur, especially by males, suggests that endurance should vary between male and female lizards and between sites. In addition, endurance is correlated with social dominance and agonistic interactions, which may determine the success of territory and mate acquisition (Garland *et al.*, 1990; Robson and Miles, 2000). We predicted that lizards inhabiting high-risk environments should allocate more energy to predator escape behaviours (Lima and Bednekoff, 1999) and should therefore have higher endurance. Because males are likely to engage in higher levels of activity, which elevates their exposure to predators, we also expected males to show greater endurance than females.

METHODS

Field methods

We conducted the study during July 1993. Lava lizards were captured between 07.30 and 13.30 h while they were basking or active. We sampled the western region of the island for 3 days and the eastern side over the course of 2 days. Lizards were held in net bags no longer than 1–3 h before estimating endurance capacity. We measured snout–vent length to 0.1 mm, body mass to 0.2 g and left hindlimb length as the distance from the anterior portion of the preacetabular process to the tip of the longest digit.

Measurement of endurance capacity

For estimates of endurance capacity, we followed Garland (1994) and Miles (1994). Since body temperature affects performance (Bennett, 1980), we maintained lizards in a temperature chamber (36°C) for 1 h (Garland, 1994; Garland and Losos, 1994). The lizards were raced at a temperature of 36°C, which is the mean field active body temperature of these lizards (Snell *et al.*, 1988). We measured endurance by coaxing the lizards to run at a constant speed (approximately 0.5 km·h⁻¹) on a treadmill and recording the time until exhaustion. The lizards were placed on a moving canvas belt (20 × 25 cm) and induced to run by gently tapping the hind legs. We assayed the lizards for fatigue in two ways. First, when a lizard failed to maintain its position on the moving belt despite prodding at least three times. Second, we tested for loss of righting response (the ability to flip over when placed on their back), which is an accurate assay of exhaustion in ectotherms (Sinervo *et al.*, 2000). The lizards were released soon after recovery.

Statistical analyses

We first assessed whether the variables conformed to the assumptions of analysis of variance (ANOVA) models. We performed a test of the homogeneity of variances (Levene's test; Sokal and Rohlf, 1997) and a test of normality for each variable. Then, we used a two-factor ANOVA to test for sex-specific and location differences in snout–vent length and body mass. We examined the effects of sex and location on endurance capacity and hindlimb length in a two-factor analysis of covariance (ANCOVA) with snout–vent length as a covariate. Among-site comparisons were based on least-squared means generated from an ANCOVA with snout–vent length as a covariate. All *t*-tests were two-tailed unless stated otherwise. Finally, we used a multiple regression analysis to determine whether potential differences in endurance between sexes or localities were affected by body mass or hindlimb length. All statistical analyses used SAS (SAS Institute, 1989) or JMP (version 3.21).

RESULTS

Analysis of sexual and microgeographic variation in body size

Males had a significantly greater snout–vent length (two-way ANOVA: $F_{1,65} = 137.8$; $P < 0.001$) and body mass ($F_{1,45} = 144.64$; $P < 0.001$) than females (Table 1). Neither males nor females differed in snout–vent length ($P = 0.63$) or body mass ($P = 0.39$) between the sparse and vegetated sides of the island. Notably, lizards in the vegetated area were in better condition (where condition is defined as the residuals from a regression of body mass against snout–vent length) than those from the sparse area (ANOVA: $F_{1,65} = 7.06$; $P = 0.01$).

Analysis of endurance capacity

Lizards from the sparse side of the island had greater endurance than those on the vegetated side ($F_{1,68} = 31.05$; $P = 0.001$). Males had significantly greater endurance than females

Table 1. Sexual and microgeographic comparisons of snout–vent length, body mass and hindlimb length (mean \pm *s*)

	Males	Females
Snout–vent length (mm)		
Sparse	91.4 \pm 3.68 (<i>n</i> = 19)	70.7 \pm 3.54 (<i>n</i> = 9)
Vegetated	87.3 \pm 7.71 (<i>n</i> = 27)	73.0 \pm 4.94 (<i>n</i> = 17)
Body mass (g)		
Sparse	23.5 \pm 2.67 (<i>n</i> = 19)	10.2 \pm 1.21 (<i>n</i> = 9)
Vegetated	23.3 \pm 5.91 (<i>n</i> = 27)	11.8 \pm 2.41 (<i>n</i> = 17)
Hindlimb length (mm)		
Sparse	67.5 \pm 2.97 (<i>n</i> = 19)	53.7 \pm 2.56 (<i>n</i> = 9)
Vegetated	65.7 \pm 4.46 (<i>n</i> = 27)	54.7 \pm 1.76 (<i>n</i> = 17)
Stamina (s)		
Sparse	224.4 \pm 53.2 (<i>n</i> = 19)	208.4 \pm 81.4 (<i>n</i> = 9)
Vegetated	151.9 \pm 46.2 (<i>n</i> = 27)	129.3 \pm 41.8 (<i>n</i> = 17)

independent of site ($F_{1,68} = 10.46$; $P < 0.002$). The larger size of males appears to be the factor affecting the dimorphism in performance. A comparison of size-adjusted endurance showed no difference in performance between the sexes (ANCOVA: $F_{1,65} = 0.17$; $P = 0.68$) (Fig. 1). The difference in endurance between sites could be an outcome of lizards from the vegetated area carrying more mass, as suggested by their higher condition index. This hypothesis is unlikely, because we found that the difference in endurance between the sites persisted after including condition index as a covariate in an ANCOVA. If the pattern in endurance was due to sexual selection, then only males and not females should have shown an increase in endurance. However, both sexes from the sparse side had greater endurance than those from the vegetated side (one-tailed t -test: males, $t_{44} = 4.5$; $P < 0.01$; females, $t_{26} = 3.6$; $P < 0.01$) (Fig. 1). Indeed, the endurance of females from the sparse side was greater than that of males from the vegetated area ($F = 3.4$; $P < 0.01$). The interaction between location and sex was not significant ($F_{1,68} = 0.27$; $P < 0.6$).

Proximate causes of variation in endurance capacity

Endurance capacity is likely to be affected by the distance moved per stride and the energetic cost of each stride (Snyder, 1954; White and Anderson, 1994). Variation in limb length represents a key morphological trait for indirectly assessing the proximate causes of variation in endurance capacity. Longer limbs would increase stride length and, therefore, the distance moved per limb cycle. Thus, a lizard would take fewer strides per unit distance, which reduces the cost of transport and enhances the time and distance a lizard could move.

Lizards from the sparse and vegetated sides of the island did not differ in hindlimb length ($F_{1,63} = 0.14$; $P = 0.79$). The hindlimbs of males were significantly longer than females, even after adjusting for body size ($F_{1,62} = 27.45$; $P < 0.001$). Males did not differ in relative hindlimb length (least squares t -test: $t_{44} = 0.39$; $P < 0.4$). Hindlimb length was significantly correlated with endurance (Fig. 2). A stepwise multiple regression with log snout–vent length, log mass and log hindlimb length as predictor variables resulted in a significant partial regression coefficient only for snout–vent length ($\beta = 2.04$; $t = 2.03$; $P < 0.05$). Thus,

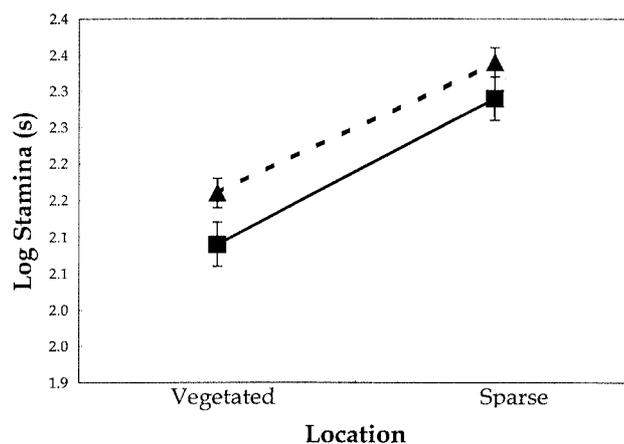


Fig. 1. Least square means for log stamina. ▲, males; ■, females.

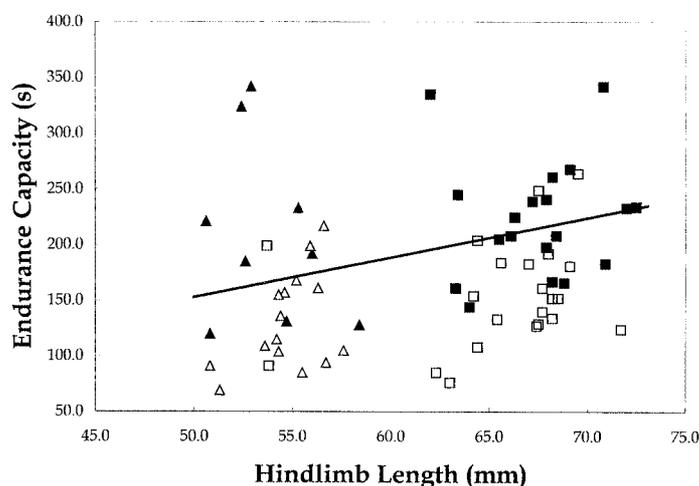


Fig. 2. Linear regression of endurance capacity against hindlimb length ($b = 1.25$, $F_{1,46} = 8.59$, $P < 0.01$). \blacktriangle , sparse females; \blacksquare , sparse males; \triangle , vegetated females; \square , vegetated males.

the association between endurance and hindlimb length is due to an indirect correlation with snout–vent length.

DISCUSSION

Our results show that lizards inhabiting the sparsely vegetated area of Isla Plaza Sur had higher endurance than lizards in the densely vegetated area of the island. In addition, males had higher absolute endurance than females. The difference in performance between sexes was a consequence of body size. However, the location differences in performance remained after controlling for body size. Hindlimb length was not associated with endurance either between locations or sexes. Thus, variation in morphology is not a suitable causal mechanism for the observed spatial patterns in performance. We suggest that other traits, such as muscle composition or muscle mass, may differ across the island. Alternatively, spatial variation in endurance could be a training effect. That is, lizards in the sparse area have better endurance because of their greater activity. Past studies did not support the hypothesis of a training effect in lizards (Gleeson, 1979; Garland *et al.*, 1987). Therefore, we find it unlikely that the lizards in the sparse area have higher endurance because of better physiological training.

The observed difference in performance occurs across a relatively short geographic scale. There are two possible explanations. First, the population is panmictic and hence there is gene flow across the island. Therefore, lizards from the sparse area experience intense selection, with the survivors having high endurance. Second, the differences are genetically based and the intrapopulation variation represents local adaptation maintained by selection. Three types of analyses could test these alternative explanations. First, data on the genetic structure of the population are necessary. These data would provide information on patterns of gene flow and levels of genetic differentiation between the vegetated and sparse sites (Garland and Adolph, 1991). Second, a longitudinal analysis of locomotor

performance is critical for generating estimates of the selection gradient – that is, the covariation between performance and fitness. Also, evidence of fixed differences in performance in hatchlings between the vegetated and sparse sites would support a genetic component. Third, it may also be that thermal and hydric conditions in the nest vary across sites. Therefore, a common garden experiment would complement both the genetic and ontogenetic analyses. Environmental conditions experienced by lizard embryos during incubation can have a profound influence of many phenotypic traits, including performance (Downes and Shine, 1999; Qualls and Shine, 2000).

Snell *et al.* (1988) noted sexual differences in sprint speed with respect to presumed differential risk of predation. Males from the sparsely vegetated area of Plaza Sur were faster than males in the heavily vegetated area. In addition, females did not differ in performance between sites. In contrast, we found that the absolute endurance of both male and female lizards from the sparse area exceeded the endurance of lizards from the vegetated area. If sexual selection was responsible for affecting endurance, then we should expect males, but not females, to differ in performance. However, both males and females from the sparse region had greater endurance. We conclude that the microgeographic differences in endurance have been shaped by natural selection and not sexual selection favouring predator escape.

Predator risk and locomotor performance

The type of anti-predator response used by an individual may be an outcome of the perceived risk of predation. Generally, species inhabiting environments characterized by a high risk of predation are predicted to invest more energy to enhance anti-predator behaviour (Lima and Bednekoff, 1999), which may include increasing speed or endurance (Krupa and Sih, 1999).

Although previous studies have emphasized maximal sprint capacity, endurance may also be a relevant trait used by lizards and other taxa for predator avoidance. First, approach distance and flight distance are two measures of wariness that covary with risk of predation in lizards (Snell *et al.*, 1988; Blazquez *et al.*, 1997). In other populations of Galápagos *Microlophus*, wariness, flight distance and hindlimb length were positively correlated with number of sympatric predators (Stone *et al.*, 1994, in press). Second, interspecific analyses substantiate the inverse relationship between risk of predation and endurance capacity. Lizards with low endurance, notably the Australian skink *Egernia cunninghami*, tend to remain close to cover (Garland, 1994). Conversely, lizards that inhabit open areas with little cover and thus must travel great distances to reach refugia tend to have high endurance (Jayne and Bennett, 1990; Garland, 1994). Third, species that are very active or move long distances also have higher endurance (Garland, 1999).

In our system, lizards in the sparsely vegetated zone of Isla Plaza Sur inhabit an environment with a potentially high risk of predation (Snell *et al.*, 1988). The pattern of intra-island variation in endurance performance is consistent with predictions generated from theory. The long distances lizards must travel to reach refugia should favour lizards with high endurance. Alternatively, the patterns of endurance may be consistent with different levels of activity between the study sites. Therefore, endurance may be an index of activity capacity. Male and female lizards from the sparse area have a lower condition index (mass carried per unit of snout–vent length). This, in turn, may be a consequence of lower food availability. Lizards from the sparse area may require larger home ranges or spend more

time foraging relative to the lizards from the vegetated area. Nevertheless, the greater time spent patrolling territories or feeding increases the exposure of lizards to potential predators. Various studies have shown a link between home range size, activity and endurance (e.g. Sinervo *et al.*, 2000). Thus, we suggest endurance provides an index to both activity capacity and predator escape.

Sexual dimorphism and sexual selection

Many activities related to reproduction may necessitate high endurance. These include territorial defence, mate acquisition, courtship and male–male interactions (Garland *et al.*, 1990; Garland, 1999; Robson and Miles, 2000). For example, male *M. albemarlensis* engage in prolonged episodes of territorial defence (H.L. Snell and D.B. Miles, unpublished observations), which includes push-ups and tail whipping. In addition, males are more brightly coloured and, therefore, are more conspicuous than females. The elevated activity combined with the conspicuous colouration increase the predation risk for males (Martin and Lopez, 1999). Hence, one should see enhanced performance being favoured by sexual selection.

Territory-holding males have a higher probability of mating. Sexual selection would favour males that were less wary, because males unlikely to erroneously flee their territory are expected to have higher mating success than males that move to a refuge in the presence of a predator. Natural selection would favour males that had longer limbs and therefore greater flight speeds to compensate for the short approach distances males tolerated (Snell *et al.*, 1988). One could extend this argument and suggest that the longer distances separating refugia would favour lizards that could sustain high exertion and were more likely to reach safety before the onset of fatigue. The high endurance in male *M. albemarlensis* could be a consequence of sexual selection. However, the absolute endurance of males and females from the sparse area was not statistically different, which is inconsistent with the sexual selection explanation. Once a lizard has decided to flee a predator, the distances separating refugia are greater in the east than the west. Males and females from the sparse area had similar flight distances. We interpret the similar patterns of performance in males and females as an outcome of natural selection.

The patterns of endurance are inconsistent with the significant sexual differences in sprint speed recorded in the same population. How can this contrast be reconciled? Two points are worth noting. First, recent studies have shown that maximum speed and endurance are uncorrelated in among-individual comparisons (Garland *et al.*, 1990; Robson and Miles, 2000). Therefore, selection may operate independently on these two locomotor traits. Second, higher maximum speeds may be critical in the initial evasion of a predator. Males have a shorter approach distance than females (Snell *et al.*, 1988) and thus have less time to flee successfully from a predator. Higher maximum speed may allow lizards a larger margin of safety in successfully fleeing a predator. Therefore, maximum velocity may be critical for the initial stages of predator avoidance, whereas endurance capacity is critical for successfully reaching a refuge.

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