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THE QUICK AND THE DEAD: CORRELATIONAL SELECTION ON MORPHOLOGY, PERFORMANCE, AND HABITAT USE IN ISLAND LIZARDS

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Natural selection is an important driver of microevolution. Yet, despite significant theoretical debate, we still have a poor understanding of how selection operates on interacting traits (i.e., morphology, performance, habitat use). Locomotor performance is often assumed to impact survival because of its key role in foraging, predator escape, and social interactions, and shows strong links with morphology and habitat use within and among species. In particular, decades of study suggest, but have not yet demonstrated, that natural selection on locomotor performance has shaped the diversification of *Anolis* lizards in the Greater Antilles. Here, we estimate natural selection on sprinting speed and endurance in small replicate island populations of *Anolis sagrei*. Consistent with past correlational studies, long-limbed lizards ran faster on broad surfaces but also had increased sprint sensitivity on narrow surfaces. Moreover, performance differences were adaptive in the wild. Selection favored long-limbed lizards that were fast on broad surfaces, and preferred broad substrates in nature, and also short-limbed lizards that were less sprint sensitive on narrow surfaces, and preferred narrow perches in nature. This finding is unique in showing that selection does not act on performance alone, but rather on unique combinations of performance, morphology, and habitat use. Our results support the long-standing hypothesis that correlated selection on locomotor performance, morphology, and habitat use drives the evolution of ecomorphological correlations within Caribbean *Anolis* lizards, potentially providing a microevolutionary mechanism for their remarkable adaptive radiation.

KEY WORDS: **correlational selection, island, natural selection, lizard, sprint speed.**

Recent reviews have reinforced the importance of natural selection as an agent of evolutionary change within animal populations (Hoekstra et al. 2001; Kingsolver et al. 2001). However, these studies also pointed toward key gaps in our understanding of how selection operates. For example, the vast majority of selection studies examine morphology, whereas fewer studies have examined selection on whole-organism traits, such as behavior or performance (Huey et al. 2003; Ghalambor et al. 2004; Le Galliard et al. 2004). Further, selection rarely acts on single traits alone (Arnold 1983; Lande and Arnold 1983; Phillips and Arnold 1989; Blows 2007), and understanding the complex interactions among traits and their resultant effects on fitness is of paramount importance for establishing how selection operates within populations. Even in cases in which researchers have successfully quantified selection on performance (e.g., Jayne and Bennett 1990; Watkins 1996; Le Galliard et al. 2004; Miles 2004; Husak et al. 2006;

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Irschick and Meyers 2007), they have not examined the interrelationships among performance, morphology, and resource use that influence fitness.

The importance of linking morphological variation with performance, and understanding how their interaction translates into fitness variation has been recognized for decades (Arnold 1983; Kingsolver and Huey 2003). Many studies have established strong links between morphology and performance, both within and among species. For example, morphology is known to influence locomotor performance in a variety of vertebrates (Billerbeck et al. 2001; Iriarte-Diaz 2002; Daley and Biewener 2003; Garland and Freeman 2005; Pontzer 2007) and invertebrates (Fish and Nicastro 2003; Berwaerts et al. 2006). Although many studies focus explicitly on trade-offs between or among traits (Vanhooydonck et al. 2001; Arnold 2003; McHenry and Lauder 2003; Wainwright et al. 2005) few studies have explicitly tested whether differences in local environments could influence which of several alternative solutions to a trade-off is optimal in terms of fitness (but see Miles 2004; Husak et al. 2006).

Performance traits such as running, swimming, and flight, often reflect the culmination of many underlying physiological processes and represent interactions among different traits (Arnold 1983; Ghalambor et al. 2003). The fitness effects of variation in such traits are rarely examined, in part because of the large amount of work involved (Irschick et al. 2007). Additional complexity stems from the fact that in some scenarios, selection may only act on performance in combination with other traits, or in concert with ecological variables such as temperature or habitat use (Karino et al. 2006; Watkins and Vraspir 2006). For example, the long caudal-fins of male guppies reduce swimming performance in areas of high water flow velocity. Females prefer to mate with long-tailed males, and thus selection acts on combinations of male morphology and habitat choice to reduce the performance costs incurred by these males (Karino et al. 2006). These results underscore the importance of studying the entire morphology-performance-fitness axis in a relevant ecological context.

An ideal group for studying how interactions among morphology, performance and habitat use influence fitness would be a group that displays marked variation in each trait, and one for which there are strong interactions among traits. Caribbean *Anolis* lizards fit these criteria closely, as they have been the subject of numerous studies of morphology, performance, and habitat use (Losos 1994; Irschick and Losos 1999). Within the Caribbean, nearly 150 species of anoles have repeatedly evolved into roughly six morphological classes termed "ecomorphs" (Williams 1983; Losos et al. 1998), which are based on correlations between morphology and habitat use. For example, anole ecomorphs with relatively long limbs tend to occupy habitats with broad perches, whereas ecomorphs with relatively short limbs tend to occupy habitats with narrow perches (Williams 1983). Prior work has shown a strong functional background to this niche partitioning, particularly in terms of locomotor performance (Mattingly and Jayne 2004). Ecomorphs with long limbs are fast sprinters on broad surfaces but experience dramatic declines in speed on narrow surfaces, whereas ecomorphs with short limbs are slow on broad surfaces, but experience little decline in speed when moving on narrow perches (Irschick and Losos 1998, 1999; Spezzano and Jayne 2004). The difference in sprint performance on alternative perching surfaces has previously been termed "sprint sensitivity" (Irschick and Losos 1999), a term we also use here.

Microevolutionary studies can play an important role in testing the tempo and mode of evolution within diverse clades. In the case of *Anolis* lizards, no studies have examined whether morphology, performance, and habitat use interact to influence fitness within a single species. This is despite a large body of evidence showing strong links among these traits in different individual anole species (Irschick et al. 2005). These strong linkages highlight the potential for these traits to affect fitness in an interactive fashion within *Anolis* lizards, but in the absence of microevolutionary selection data, the mechanisms that have led to this diverse group remain poorly understood. For example, although the trade-off between high-speed/long limbs/broad perches and sprint sensitivity/short limbs/narrow perches underlies most hypotheses concerning the diversification of Greater Antilles anoles (Losos 1990), the role that selection plays in shaping such performance differences (Arnold 1983) is only beginning to be understood (Losos et al. 2006).

We attempted to fill this void by measuring viability selection on morphology, running performance, and habitat use (perching diameter) in three island populations of a common "trunk-ground" ecomorph, the brown anole, *A. sagrei*. The brown anole is the most common anole in the Bahamas, and uses a wide array of habitat types including both broad and narrow perches (Calsbeek and Smith 2007), making it an ideal subject for studying selection. We tested whether natural selection acts on trade-offs in morphology and performance. In addition, we tested the hypothesis that these trade-offs should depend on the ecological context in which they are measured. Specifically, because performance variation in anoles has been linked to habitat use, we asked whether selection would act on interactions between morphology, performance, and habitat use. Our study therefore considers the entire morphology/performance/fitness axis as a whole, including the important influence of ecological variation on these traits.

Methods

FIELD WORK

Initial lizard captures took place from June 6 to June 20, 2006 on Kidd cay, an offshore island connected to the mainland by a >80 m cement causeway that contains no lizard habitat, and

at an adjacent site (2 km away) on mainland Great Exuma, Bahamas. We captured all *A. sagrei* lizards from our natural study population on Kidd cay ($N = 166$ female and 149 male), a small (approximately 1500 m^2) island near Georgetown Great Exuma. We supplemented these data by introducing additional populations to two smaller offshore-cays that served as replicates. We captured and measured an additional 170 male lizards from a site on Great Exuma adjacent to our Kidd cay study site, and introduced 80 and 90 of these individuals to Nightmare and Flamingo bay cays, respectively. Females were left at their natural population densities on all three islands. Each of the offshore cays is small (<700 m^2) and approximately equidistant from Great Exuma (approximately 500 m offshore). The cays were chosen for this study based on their similarity in temperature and precipitation to our natural study island, and they differ primarily in the relative paucity of broad-diameter trees compared with Kidd cay. For example, Flamingo bay and Nightmare cays are not large enough to support the stands of mature palm trees and Australian pine that are found primarily on the perimeter of Kidd cay. Kidd cay also supports at least two other species of anole (*A. carolinensis* and *A. distichus)* as well as a terrestrial lizard species (*Ameiva).* None of these other lizard species is present on Flamingo bay or Nightmare cays.

We recorded perch use at capture following Rand (1964, 1967). Perch use by *A. sagrei* (Fig. 1) in our natural study population is remarkably consistent through time (R. Calsbeek pers. obs.), and perch use at first capture is an excellent approximation of the perching diameter used by lizards throughout this study. We verified the consistency of perch use by recording dispersal events between territories during the study, defining dispersal as movement between localities separated by more than 10 m (the average diameter of a male's territory [Calsbeek and Marnocha 2006]). Only one such dispersal event was recorded and the mean distance moved over the four months of study was 1.94 m ± 0.34. In general, brown anoles are very sedentary (Paterson 2002) and were often resighted on the same perch site on consecutive days. We only report selection on habitat use for Kidd cay, because lizards on offshore cays were experimentally introduced, and habitat use at capture did not reflect habitat use for the period during which we measured viability selection.

All lizards were sexed, weighed with a Pesola spring scale (nearest g), and measured snout-vent-length (SVL; nearest mm) using a small metal ruler. Hind and forelimb lengths were measured with dial callipers from the point of insertion into the abdomen to the femoral-tibial and humero-radio-ulnar joints. We focus our analyses on hind limb length because kinematic and performance studies have shown that hind limb length is the primary driver of variation in locomotor performance in lizards (Spezzano and Jayne 2004). All measurements were made in the afternoon by one observer (RC), blind with respect to habitat use. Lizards

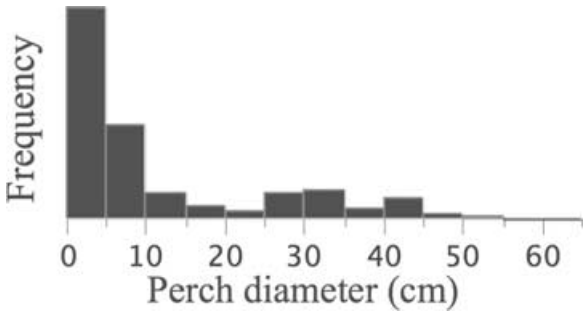

Figure 1. **Panel shows the distribution of perch diameters used by lizards in the study and illustrates the utility of using a 2.5 cm dowel to simulate a narrow perch in measures of sprinting performance.**

were injected with unique combinations of colored elastomer dye in the ventral side of the hind and forelimbs (Nauwelaerts et al. 2000). Tags serve as permanent identification in the wild, allowing us to track the fate of every individual over the course of the study. Lizards captured on Kidd cay were released within 4 h to their original point of capture. Lizards captured from Great Exuma were experimentally introduced to each of the two small offshore cays currently being used as part of a long-term study of natural selection (Calsbeek and Smith 2007). Populations were introduced at densities that can be considered biologically relevant (approximately 0.2–0.3 lizards/m^2) based on previous studies (Losos et al. 2001). We had previously cleared these cays of all naturally occurring male lizards such that none of the experimentally introduced lizards interacted with native residents.

We measured sprint speed on both broad (10 cm) and narrow (2.5 cm) diameter surfaces (Irschick and Losos 1999) and measured distance-running capacity on a flat circular racetrack (Le Galliard et al. 2004). During each afternoon following capture, lizards (maintained at ambient temperatures that were near their field optimum) (Huey 1983) were induced to run up a 1-m track that was either broad (i.e., a 10 cm wide plank) or narrow (i.e., a 2.5-cm diameter dowel), and that was marked at 10-cm increments. *Anolis* lizards tend to jump on horizontal surfaces (Perry et al. 2004) so both the broad and narrow tracks were inclined at approximately 20°. A darkened retreat site at the end of the track provided an escape route for lizards. The order of broad versus narrow diameter tracks used in trials was determined at random for the first lizard each day (coin toss), and was reversed in every odd trial.

Three trials on each surface were videotaped using a digital Sony handycam© recording at 32 frames/sec. We digitized all trials using MotionAnalysis© software (http://warthog.ucr.edu/) and recorded the maximum speed achieved over a 10-cm increment during all three trials. Only "good'' trials, in which the lizard actively cycled their limbs and kept their feet in contact with the

track across all 10 cm were used in the final analysis. Lizards were allowed 4 h of recovery time after sprinting trials. We then estimated the total running time to exhaustion (distance capacity) on a circular racetrack (approximately 3.7-m circumference) (Le Galliard et al. 2004). Lizards were motivated to run by gently tapping on the tail base with a soft brush and distance capacity was recorded as the total running time to exhaustion (nearest second) as determined by five failed attempts to motivate continued running and/or the loss of the righting response (Sinervo et al. 2000; Le Galliard et al. 2004).

In the analyses that follow, we use running speed on the narrow surface as a baseline indicator of maximum sprint speed. We then calculated the difference in sprint speed achieved on narrow and broad surfaces and we use this metric (Δspeed) as an index of "sprint-sensitivity" (Irschick and Losos 1999), which describes the decrease in speed as lizards move from broad to narrow dowels. Small (negative) values of Δspeed indicate that lizards ran slower on the narrow than on the broad surface, and were therefore less sprint-sensitive compared to lizards with large values of Δspeed. Distance capacity measures the total time that lizards are able to run at high speeds before reaching exhaustion, and is hereafter referred to as endurance (Garland 1999). All analyses were performed separately for each sex.

We measured viability selection over the next 4 months, an important period representing the time required to reach adulthood and the end of the first breeding season. We walked multiple daily transects on each study island, and conducted population censuses by capturing all surviving lizards over the course of 2 weeks. Those lizards that had been marked in the spring but were not recaptured during our census were considered dead (Janzen and Stern 1998). Census efficiency was determined by regressing the number of new lizards captured each day (log transformed) against the cumulative days of capture effort. We then estimated the number of lizards that would have been caught with one more day of the census. This number was less than three lizards on all islands.

We used general linear models to extract selection gradients (Lande and Arnold 1983; Brodie et al. 1995) for linear (β) and nonlinear ($\gamma_{1,1}$ and $\gamma_{1,2}$) forms of selection. Because the assumptions of parametric statistics may be violated for survival data (live/die), which tend to have nonnormally distributed errors, we computed significance values for selection gradients using logistic regression models (Janzen and Stern 1998). We included the independent variables sprint speed, sprint sensitivity, endurance, habitat use, hind limb length, and snout-vent-length to control for variation due to body size. We also corrected for body size in a separate set of models, by computing the residuals from the regression of log-transformed limb length on log-transformed snout-vent-length and using these residuals as estimates of size-corrected limb length. Prior to pooling data from multiple islands, we tested for any interaction between relevant terms and the factor for island. None of these were significant indicating that selection operated in the same way in all sites. We included "island id" as a random factor in all of the pooled analyses. We compared different models and chose parameters that minimized the Akaike information criterion (AIC) score (Akaike 1987). All variables used in selection analyses were standardized to mean 0 with unit standard deviation, except survival, which was scaled by the mean survival in each population. We visualized fitness surfaces using the cubic spline approach of Schluter and Nychka (1994). All statistical tests were performed with JMP version 6.0.2 for the Macintosh.

Results

CORRELATIONS BETWEEN MORPHOLOGY AND PERFORMANCE

Raw trait values are provided in the Appendix. Consistent with previous studies (Losos and Sinervo 1989; Sinervo and Losos 1991; Spezzano and Jayne 2004), maximum sprint speed depended on the diameter of substrate used in each trial ($\overline{X}_{\text{broad}} = 2.51$ m/sec. $\pm$ 0.52; $\overline{X}_{\text{narrow}} = 1.94$ m/sec. $\pm$ 0.49, paired t = 17.47, $P < 0.0001$). Sprint sensitivity was negatively correlated with hind limb length, but only for males ($r = -0.20$; $F_{2,293} = 12.91$, $P < 0.001$, no effect of island ($P = 0.52$); Fig. 2A), as was maximum sprint speed on the narrow perch ($r = -0.19$; $F_{2,296} = 10.23$, $P = 0.001$, no effect of island ($P = 0.49$); Fig. 2B). Lizards with longer hind limb lengths tended to sprint faster on the broad perch, although the relationship was weak and nonlinear reaching a maximum at intermediate limb lengths ($F_{2,296} = 2.18$, $P = 0.05$, effect of island $P = 0.48$). By contrast, endurance was positively correlated with hind limb length ($r = 0.33$; $F_{2,309} = 20.01$, $P < 0.0001$, effect of island $P < 0.0001$; Fig. 2C) and was negatively correlated with sprint sensitivity, although this relationship was not significant ($r = -0.11$; $F_{2,293} = 2.86$, $P = 0.09$, effect of island $P < 0.0001$; Fig. 2D). Finally, during sprint trials, long hind limbs increased the probability of falling off of the narrow perch (logistic regression $\chi^2 = 9.62$, $N = 315$, $P = 0.002$), but no lizards fell off of the broad perch regardless of limb length. All results remained significant when we used size-corrected limb length (Table 1, showing results based on residuals from the regression of limb length against SVL) except endurance, which varied by island, and sprint speed on the broad perch, which was not related to residual limb length. The relationship between endurance and residual limb length was positive and significant for lizards on the offshore cays, but nonsignificant on Kidd cay. In sum, male lizards with long hind limbs tended to be fast sprinters and also have high endurance, whereas lizards with short hind limbs tended to be less sprint-sensitive and exhibited low endurance.

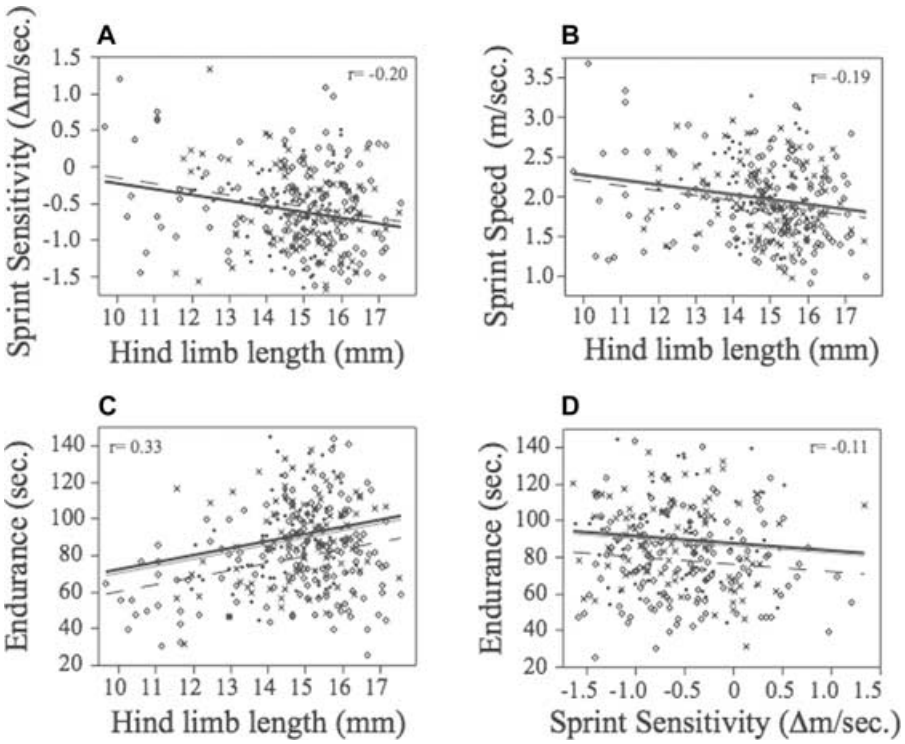

Figure 2. Correlations between morphology and locomotor performance measured in *Anolis sagrei* were consistent with those previously demonstrated among species in the adaptive radiation of Greater Antillean anoles (Irschick and Losos 1998, 1999; Spezzano and Jayne 2004). Both sprint sensitivity (Δspeed; panel A) and sprint speed on narrow surfaces (panel B) were negatively correlated with hind limb length. Endurance was positively correlated with hind limb length (C) but was traded off with sprint sensitivity (D). Sample sizes range from 296 to 315 lizards (eighteen lizards could not be scored for sprint speed; see methods). The effect of island was only significant for endurance. In panels A–D Flamingo bay, Nightmare, and Kidd cays are denoted by open circles and a heavy regression line, X's and a light regression line, and by points and a dashed regression line, respectively.

EFFECTS OF MORPHOLOGY AND PERFORMANCE ON SURVIVAL

Variation in sprint speed and sprint sensitivity had significant effects on survival to maturity but only in concert with other traits. Again, results were only significant in males. We detected correlational selection (i.e., interaction term $\gamma_{1,2}$; Lande and Arnold 1983; Brodie et al. 1995) between hind-limb length and sprint sensitivity (pooled results; hind limb × sprint sensitivity; $F_{1,290} = 2.60$, $\gamma_{1,2} = 0.14 \pm 0.05$, Wald $\chi^2 = 6.61$, $P = 0.01$, island effect $P = 0.02$, no interaction effects were significant). Similarly, we detected correlational selection acting between hind-limb length and sprint speed on the narrow perch (pooled results; hind limb × sprint speed; $F_{1,280} = 2.07$, $\gamma_{1,2} = 0.06 \pm 0.03$, Wald $\chi^2 = 3.65$, $P = 0.05$, island effect $P = 0.02$, no interaction effects were significant). Results were qualitatively the same on all three cays (Table 2) and the overall P-values were highly significant (Fisher's exact test $P < 0.0001$ for both tests). Correlational selection gradients indicated a survival advantage for both slower males with short hind limbs, and faster males with longer hind limbs (on the narrow dowel; Fig. 3A). Results remained significant when we used size-corrected hind-limb length (residual hind limb × speed $F_{1,291} = 2.52$, $\gamma_{1,2} = 0.16 \pm 0.06$; Wald $\chi^2 = 6.22$, $P = 0.01$). Moreover, the strength of selection (γ) was strongest in the analysis for Kidd cay, the island on which all lizards were natural residents ($F_{1,122} = 2.47$, $\gamma_{1,2} = 0.17 \pm 0.07$, Wald $\chi^2 = 6.97$, $P = 0.001$).

Table 1. Summary of male performance results using residual limb lengths from the regression of limb length versus snout-vent-length (both log transformed). Results using raw trait values are provided in the text. The column for "Island effect" refers to the interaction between the measured performance variable and the factor for island id and "Stumbles" refers to lizards that fell off of the narrow diameter perch. Sample sizes were 295 males for each sprint speed measure and 315 for stamina and stumbles.

Estimate	Test used	Test statistic	Island effect
Maximum speed	ANOVA	7.99***	6.21**
Sprint sensitivity	ANOVA	5.48**	3.21
Stamina	ANOVA	0.04	5.06***
Stumbles	χ^2	4.05*	

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 2. Linear (β) and nonlinear (γ) selection coefficients from the three independent study islands demonstrating the importance of correlational selection (interaction terms) on male limb length and sprint sensitivity. All traits were standardized to mean zero with unit variance prior to analysis. The combined *P*-value across all three sites was highly significant ($P < 0.001$).

W (Kidd cay) $N = 147$	β/γ	SE	χ^2	*P*
Intercept	0.41	0.05		
Hindlimb	0.02	0.04	0.399	0.53
Sprint sensitivity	0.03	0.04	0.066	0.79
Hindlimb^2	0.02	0.03	0.289	0.59
Sprint sensitivity^2	0.001	0.03	0.00	0.99
Hindlimb × Sprint sensitivity	0.07	0.04	3.15	0.07
W (Flamingo Bay cay) $N = 80$				
Intercept	0.27	0.07		
Hindlimb	0.05	0.06	1.67	0.19
Sprint sensitivity	–0.01	0.05	0.97	0.32
Hindlimb^2	0.04	0.06	0.06	0.91
Sprint sensitivity^2	–0.04	0.05	1.43	0.23
Hindlimb × Sprint sensitivity	0.16	0.07	6.32	0.01
W (Nightmare cay) $N = 90$				
Intercept	0.39	0.08		
Hindlimb	–0.06	0.05	2.73	0.09
Sprint sensitivity	0.03	0.05	1.85	0.17
Hindlimb^2	–0.06	0.05	0.77	0.38
Sprint sensitivity^2	–0.007	0.03	0.07	0.79
Hindlimb × Sprint sensitivity	0.05	0.06	1.13	0.28

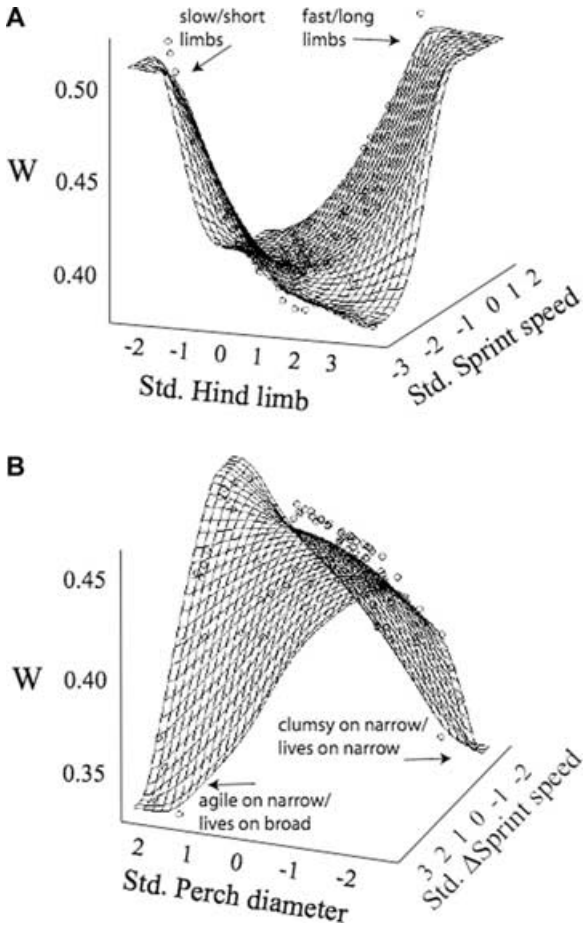

Figure 3. Multivariate fitness surfaces illustrating the way running performance, habitat use, and morphology translate into differences in survival. W represents the probability of survival, all traits were standardized to mean zero with unit variance, and fitness surfaces were fitted using generalized cross validation (Schluter and Nychka 1994). (A) Correlational selection (Lande and Arnold 1983; Brodie et al. 1995) acting on sprinting speed and hind limb length favored fast lizards with long hind limbs, and slower lizards with short hind limbs. Arrows indicate fitness optima (B) Selection also acted on the correlation between habitat use and sprint sensitivity creating a ridge of high fitness. However, lizards that were less sprint-sensitive on the narrow dowel but inhabited broad perches survived poorly, as did lizards that were clumsy on narrow surfaces and inhabited narrow perches. Arrows indicate fitness minima.

THE IMPORTANCE OF HABITAT USE

We also detected significant differences in survival as a function of the interaction between sprinting performance and habitat use. The fitness surface describing this variation in survival (Fig. 3B) indicates a ridge of high fitness across the range of available perch diameters (diameter × sprint-sensitivity; $F_{1,94} = 1.85$, $\gamma_{1,2} = -0.09 \pm 0.05$, Wald $\chi^2 = 4.18$ $P = 0.04$; Table 3), with fitness minima localized in the two extreme performance/habitat mismatch scenarios (i.e., lizards that are less sprint-sensitive on narrow surfaces but inhabit broad perches and vice versa). Thus, lizards enjoyed high survival over a relatively wide range of sprint performance, so long as their performance was well suited to their use of the available habitat. We initially restricted this test to lizards from Kidd cay, the only study island for which we had estimates of habitat use by lizards during the study. However, results were qualitatively similar when we pooled across all islands, using perch diameters scored at capture ($F_{1,291} = 2.24$, $\gamma_{1,2} = -0.12 \pm 0.07$, Wald $\chi^2 = 2.90$, $P = 0.08$).

Finally, we tested our prediction that selection on the morphology-performance-fitness axis should depend on the ecological context in which it was measured. That is, we tested for the presence of three-way interactions among locomotor performance, habitat use, and morphology. Indeed, we found strong evidence that natural selection acted on variation in all three of these elements together (sprint sensitivity × hind limb × perch diameter; $F_{1,247} = 2.08$, Wald $\chi^2 = 7.34$, $P = 0.007$) and (sprint speed × hind limb × perch diameter $F_{1,248} = 2.07$, Wald $\chi^2 = 6.61$, $P = 0.01$). Assuming that these traits are coded by genetic loci, these interactions represent a form of fitness epistasis (Whitlock et al. 1995; Sinervo and Svensson 2002). Results were significant for males only, and this was likely because the variation in limb length, which is the raw material for selection, was nearly twice

Table 3. Linear (β) and nonlinear (γ) selection coefficients demonstrating the importance of correlational selection (interaction terms) on perching diameter and sprint sensitivity. Data are from Kidd cay only, as this was the only island for which we could measure habitat use. All variables were standardized to mean zero and unit variance prior to analysis. Sample sizes for this test differ from those in Table 1 because we excluded all males who were not using a measurable perch when first observed (i.e., males on the ground or perched on leaves).

W (Kidd cay) $N = 96$	β/γ	SE	χ^2	P
Intercept	0.39	0.05		
Perch diameter	0.01	0.05	0.05	0.82
Sprint sensitivity	0.02	0.05	0.17	0.67
Perch diameter^2	–0.02	0.04	0.27	0.61
Sprint sensitivity ^{2}	–0.05	0.04	1.96	0.16
Perch diameter × Sprint sensitivity	–0.09	0.05	4.18	0.04

as high in males as in females ($CV_{male} = 12.4$ vs. $CV_{fem} = 6.8$, $P < 0.01$).

Discussion

The goal of most previous selection studies has been to understand how selection shapes variation in morphological traits (Hoekstra et al. 2001; Kingsolver et al. 2001). Our study contributes to the small but growing body of literature aimed at understanding selection on higher-level traits like behavior and performance (Benkman 2003; Grant and Grant 2006; Husak et al. 2006; Irschick and Meyers 2007). However, even among such studies, our results are unique in showing that selection acts not simply on performance per se, but rather on unique combinations of performance (sprinting speed, sprint sensitivity), morphology (hind-limb length), and habitat use (perch diameter) to create local adaptation (Irschick and Losos 1999). Indeed, selection acted on these trait combinations despite the lack of selection on individual performance or morphological traits. Thus, selection favored both male lizards with long hind limbs that sprinted well on broad substrates and tended to perch on broad surfaces, and lizards with short hind limbs that were less sprint-sensitive and tended to occur on narrow surfaces. It is not yet clear the degree to which habitat preferences may influence the strength of selection acting on these correlations.

The significant interactions between performance and morphology, and between performance and habitat use, are strong indicators that selection drives local adaptation in our study populations. Similarly the three-way interactions between morphology, performance, and habitat use with fitness add an important ecological dimension to traditional estimates of the way morphology and performance interact to influence fitness. These results underscore the importance of an ecological perspective when measuring performance effects in nature (see below). We feel confident in these conclusions because our mark–recapture methods provided robust estimates of survival because we captured nearly every lizard on each island during both the spring and fall (recapture rates of 97–99%; two lizards on Flamingo bay cay eluded recapture), and emigration off study islands is likely to be extremely rare except during major storms (Calsbeek and Smith 2003) none of which affected our study.

Although our results were significant only for males, previous performance work on anoles has focused almost exclusively on males (Losos 1990; Irschick and Losos 1999), and key ecomorphological correlations and consequent selection may be more important for males than females. We cannot offer a conclusive explanation as to the differences between males and females in the selection results, but one possible factor is the significantly higher variance in morphology, and size in general, exhibited by males compared to females. The lack of selection on females could have important evolutionary implications because traits that are under selection in only one sex would likely show a weaker response to selection. Genetic correlations between the sexes may slow the process of divergence considerably (Lande 1980) although even in the absence of direct selection, females should show a correlated genetic response with males. New evidence suggests that the extreme sexual dimorphism exhibited by *A. sagrei* may play an important role in species level diversification (Butler et al. 2007).

Sexual selection may also contribute to variation in selection pressures acting between morphology, performance, and habitat use. For example, effective territory defence may depend on the ability to move swiftly or sure-footedly through their habitat (Miles et al. 2001), and increased population densities might lead to heightened selection pressures on the ability to hold territories (Calsbeek and Smith 2007). Likewise, mate choice may involve assessment of an individual's physical performance (Vencl and Carlson 1998; but see Lailvaux and Irschick 2006), especially if females assess perch distributions to produce progeny with morphologies that match their local habitat. Future studies aimed at understanding the importance of sexual selection to selection on morphology and performance could shed light on these questions.

There has been considerable debate regarding the role of microevolutionary studies for understanding macroevolutionary patterns (e.g., Charlesworth et al. 1982; Eldredge 1989). Prior research with *Anolis* lizards has documented strong links between morphology, performance, and habitat use within and among species, and our results add to this picture by showing that selection also operates simultaneously on these traits. Indeed, our results show that the same correlations between morphology and performance that characterize interspecific variation among Caribbean anoles also exist within a single species, and that these correlations have likely arisen under the influence of

natural selection. As such, our results could provide a microevolutionary mechanism by which the patterns of diversity among *Anolis* species arose in the Greater Antilles (Schluter 1994; Losos et al. 1998). In the case of *Anolis* lizards, considerable diversification has taken place within small geographic areas that are relatively devoid of large geographic barriers to gene flow (e.g., Jamaica, Losos 1994). Some views of adaptive radiation posit that competition among sympatric species drives differentiation and speciation via natural selection for key morphological traits (Schluter 2000). Thus, population divergence may be driven by natural selection arising from competition and other ecological forces, and although our data are silent on the issue of competition, they suggest that natural selection may favor different sets of traits within a single population. This result also implies that if *A. sagrei* populations spanned dramatically different habitats, the stage could easily be set for the incipient stages of speciation. Further studies examining whether selection acts in the same manner for different populations of anoles, which occur in different habitats, would be useful for testing this idea.

Evolutionary biologists have debated whether selection acts on single traits, or on combinations in traits (see Blows 2007 for a recent review). Although most biologists are in agreement that selection acts on actions of the whole organism (i.e., how far a frog jumps to escape a predator), rather than on simple traits that drive the action (i.e., limb length), how one should quantify the force of selection remains challenging. Some authors have stressed the potential interactive role of different traits for influencing performance (e.g., Arnold 1983; Land and Arnold 1983; Phillips and Arnold 1989), but empirical examples are rare (Sinervo and Svensson 2002). In some cases, prior work has detailed how selection acts on several traits simultaneously, such as pheremones in *Drosophila* flies (Blows 2007). Other examples, such as key aspects of body organization, are likely cases in which phenotypic and genotypic correlations among traits are of paramount importance (Wagner and Altenberg 1996; Wagner and Schwenk 2000; Vincent et al. 2006).

Our results differ slightly from these prior discussions given our use of multiple unrelated traits (e.g., morphology, habitat use), as opposed to different interacting morphological traits (e.g., components of the skull; Cheverud 1982). Expanding the view of selection acting across vastly different suites of traits is an important advance, because it implies that selection on any given trait is highly dependent on other aspects of the organism's morphology, behavior, or ecology. By examining different traits, one is also drawn away from the perhaps overly facile view that selection acts on simple values of performance alone (i.e., high sprint speed; Irschick and Meyers 2007). Although the view that high sprint speeds results in high fitness has garnered some support (Jayne and Bennett 1990; Miles 2004; Husak et al. 2006), and may be relevant in some species, in other species complex interactive effects should also be considered. It is also possible that selection may not act on performance traits at all (Welbergen et al. 1992; Van Buskirk and Schmidt 2000; see also Bennett and Huey 1990). Although we have not yet provided evidence for the nature of genetic correlations in performance traits in our system, preliminary results from a laboratory breeding study suggest a negative genetic correlation exists between sprint speed and stamina (R. Calsbeek, pers. obs.). The correlational selection measured in the present study may ultimately underlie this genetic correlation. Alternatively, the correlation may have arisen by indirect selection acting through differences in habitat use. Making a distinction between these alternatives will require further work. Finally, in situations in which selection on morphology and performance is also linked to habitat use, one further implication is that social factors may dictate the direction and pace of selection (Svensson et al., 2006). For example, perch height is, in some species, dictated by social dominance, with more dominant males perching higher than less-dominant lizards (e.g., green anoles; Greenberg and Crews 1990). This implies that the strength and direction of selection may not be static within an individual's lifetime. Further work that examines selection on behavior (e.g., male display patterns or dominance), habitat use, performance, and morphology would be especially interesting in this regard.

A potential criticism of this study is that we have not documented the source of morphological variation measured among individuals. There are at least two possible sources for the reported variation in size. Some of the variation in body size may have an ontogenetic component. Growth is indeterminate in most reptiles, and body size tends to scale with age (Olsson and Shine 1996; Heino and Kaitala 1999; Charnov et al. 2001). *Anolis* lizards produce a single-egg clutch at approximately 2-week intervals from March through September (Jenssen and Nunez 1998), and the individuals measured in this study likely represent a range of age classes spanning several months. However, between-year survival is very low in our study population ($<10\%$) and we consistently marked all individuals on the island. Thus, we can be reasonably certain that we did not mix cohorts from different years in our analyses, although individuals within a year may span a range of several months age difference. Second, heritability estimates of limb length and body size reported elsewhere (R. Calsbeek et al., unpubl. ms; Calsbeek and Smith 2007) indicate that part of the variation in these traits certainly has a genetic basis. Results with both the size-corrected and uncorrected measures were similar in our study, and we have presented both analyses to emphasize that selection operates on interactions with limb length per se, and other aspects of variation in size that may be more directly linked to within-cohort age structure. However, one caveat is that we cannot unambiguously conclude the relative importance of selection on genetic versus ontogentic variation in size. Future studies on lizards of known age (e.g., those

hatched in the laboratory and released to the field) could resolve this dilemma.

Field studies of natural selection have conclusively shown that the pace of microevolution can be extremely rapid in nature (Endler 1986; Hendry and Kinnison 1999), but the vast majority of these studies have focused on single morphological traits (Kingsolver et al. 2001). We believe that our results make an important contribution to the broader field of natural selection by emphasizing the strong links among morphology, performance, and habitat use within populations. Our results also lend credence to the long-standing hypothesis that ecologically based natural selection on performance, morphology, and habitat use underlies the diversification of island lizard populations.

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Appendix. Raw trait values (with standard errors) for the three cays used in the study.

Trait	Kidd		Flamingo bay		Nightmare	
	Mean	SE	Mean	SE	Mean	SE
Hind limb (mm)	14.79	0.14	14.67	0.11	14.91	0.13
SVL (mm)	55.82	0.52	57.58	0.39	57.38	0.45
Stamina (sec.)	78	1.97	89.65	2.51	88.36	2.43
Sprint speed narrow perch (m/sec.)	1.9	0.46	1.99	0.54	1.96	0.47
Sprint speed broad perch (m/sec.)	2.42	0.43	2.58	0.59	2.56	0.57