

# An ecological twist on the morphology–performance–fitness axis

Ryan Calsbeek\*

*Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA*

---

## ABSTRACT

**Hypothesis:** Natural selection shapes correlations between morphology and performance through variation in ecology (habitat use).

**Organism:** *Anolis sagrei* lizards (the brown anole).

**Field site:** A small offshore island near Great Exuma, Bahamas.

**Methods:** I measured morphology, physiological performance [e.g. sprint speed, sprint sensitivity (the change in speed on broad versus narrow surfaces), running endurance], and habitat use (perching diameter) in natural populations of male and female lizards. I released lizards to their original sites of capture and measured differences in survival (natural selection) in each sex as a function of morphology, performance, and estimates of habitat use. Survival differences were recorded over 4 months (June–September), a period that includes the greater part of the breeding season.

**Results:** Natural selection acted on correlations between morphology and performance that were associated with differences in habitat use among males. In most cases, selection acted on trait correlations despite the lack of any measurable selection on individual morphological or performance traits. However, morphology and performance were not correlated in females, nor did selection operate on performance variables or most morphological traits in females. Thus, hypotheses concerning selection on morphology, performance, and habitat use were supported by data for males but not females.

*Keywords:* anole, island, lizard, locomotor performance, selection.

## INTRODUCTION

Recently, several reviews (Hoekstra *et al.*, 2001; Kingsolver *et al.*, 2001; Hereford *et al.*, 2004) have highlighted an important shortcoming in our understanding of natural selection. Whereas a growing number of studies have demonstrated the strength of linear selection in nature, few have explored the importance of non-linear, and in particular correlational, selection pressures (selection acting on the covariance between traits). Moreover, most studies of selection continue to focus on one or a few key morphological traits, and we therefore know little about the importance of the joint action of selection acting on behavioural and

---

\* e-mail: ryan.calsbeek@dartmouth.edu

Consult the copyright statement on the inside front cover for non-commercial copying policies.

---

performance traits in natural populations. This shortcoming requires attention, because multivariate and/or correlational forms of selection are considered to be of central importance to the origin of intraspecific, and eventually interspecific, diversity (Lande, 1981; Brodie, 1993; Jones *et al.*, 2003; Roff and Fairbairn, 2007).

Intraspecific diversity in the form of phenotypic or genetic polymorphism is maintained within populations by correlational selection (Sinervo and Svensson, 2002). Correlational selection favours trait combinations with high fitness (Brodie, 1992; Brodie *et al.*, 1995; Blows and Brooks, 2003) and culls alternative low-fitness trait combinations. Different adaptive suites of traits are resolved as multiple peaks on a fitness landscape (Phillips and Arnold, 1989; Schluter and Nychka, 1994), and may be the selective basis that maintains intraspecific variation (Shuster and Wade, 1992; Sinervo and Lively, 1996; Svensson *et al.*, 2006) and ultimately leads to diversification among species [e.g. character displacement (Grant, 1968; Grant, 1990; Schluter, 1995, 1996); ecological niche partitioning (Losos, 1994; Losos *et al.*, 2003; Seehausen and Schluter, 2004)]. The evolution of correlated suites of traits depends on chronic selection that is strong enough to generate disequilibrium across multiple loci and still overcome recombination (Charlesworth and Charlesworth, 1975).

Given the importance of non-linear and correlational selection, Kingsolver *et al.* (2001) called for additional studies that measure multivariate selection, especially in systems where there is some *a priori* reason to anticipate correlational selection. One could recognize these systems as being characterized by selection pressures acting on differential investment in traits that are traded off (Sinervo and Svensson, 2002), and in which strong interactions among traits influence fitness. *Anolis* lizards from the Bahamas fit these criteria and thus provide an excellent group with which to address the causal links between morphology, performance, and fitness.

Nearly 150 species of anole are found on islands throughout the Caribbean and comprise a clear example of adaptive radiation. *Anolis* lizards have undergone extensive morphological diversification, with most attention having been paid to traits that are correlated with habitat use (e.g. limb length, body size). Morphologically similar species, termed 'ecomorphs' (Williams, 1983), have evolved repeatedly and independently on different islands in the Greater Antilles. Anole ecomorphs with relatively long limbs are most often found perching on broad diameter substrates (e.g. tree trunks), while ecomorphs with relatively shorter limbs are more often found on narrow diameter substrates (e.g. scrubby vegetation and twigs). The correlations between morphology and habitat use are thought to have arisen through natural selection favouring fast-moving, long-limbed lizards in open habitats, and more slow-moving, short-limbed lizards in scrubby habitats (Moermond, 1979; Williams, 1983; Losos, 1990). Thus, the classical view of diversification in anoles includes explicit predictions linking trade-offs between morphology and running performance to fitness through variation in habitat use (Williams, 1983; Losos *et al.*, 1998).

Significant progress has been made in understanding the relationships between morphology, performance, and fitness, and a growing number of studies have shown, for example, how variation in morphological and physiological traits can influence locomotor performance (Bennett *et al.*, 1984; Garland, 1984, 1985; Irschick and Losos, 1998, 1999; Van Buskirk and Schmidt, 2000; Kingsolver and Huey, 2003; McHenry and Lauder, 2003; Lailvaux *et al.*, 2004) or how performance affects fitness (Christian and Tracy, 1981; Benkman and Lindholm, 1991; Smith, 1997; Miles, 2004; Husak *et al.*, 2006). Traits related to performance (e.g. sprinting speed, running endurance, bite force) are often proposed as fitness proxies because they are likely to culminate from many underlying physiological processes and should therefore represent whole-animal vigour (Bartholomew, 1964; Arnold, 1983). In

the case of *Anolis* lizards, there is an important ecological thread that weaves each of these correlations together. For example, Calsbeek and Irschick (2007) have shown that selection does not simply favour the fastest lizards (Miles, 2004; Husak *et al.*, 2006). Rather, trade-offs mediated by habitat use illustrate that selection may favour speedy male lizards on broad surfaces, but also favour slower, more sure-footed male lizards on narrow surfaces. The trade-off between speed and ‘sprint sensitivity’ – that is, the degree to which differences in perching diameter affect sprinting velocity (Irschick and Losos, 1999) – arises because although long limbs enhance maximum velocity, short limbs facilitate navigation through narrow and complex habitats (Losos and Sinervo, 1989; Sinervo and Losos, 1991). Data on females were not reported by Calsbeek and Irschick (2007).

There is growing appreciation that habitat-based selection pressures may differ between the sexes. Male and female *A. sagrei* use different elements of the habitat; males typically perch higher in the vegetation than females. Females also spend substantially more time on the ground than males. These differences in habitat use are likely to lead to sex-specific differences in selection on locomotor traits (Butler *et al.*, 2007) given the differing potential for constraints on running performance. Although little attention has been paid to variation in performance and selection on females, recent work (Butler and Losos, 2002; Butler *et al.*, 2007) suggests that differences in selection acting on males and females serve to facilitate interspecific diversification in much the same way that ecological conditions have previously been shown to drive sexual dimorphism (Temeles *et al.*, 2000).

Here I use the brown anole, *Anolis sagrei*, to test the hypothesis that correlations between morphology and performance are moulded by different selection pressures acting on males and females in different habitats. Given the differences in habitat use exhibited by males and females, I build on previous work (Calsbeek and Irschick, 2007) and explore tests of the hypothesis separately for each sex. I then compare results previously reported for males (Calsbeek and Irschick, 2007) with the new data presented here on females.

## METHODS

### Fieldwork

*Anolis sagrei* is a small (snout-to-vent length 40–70 mm), semi-arboreal lizard with a broad tropical and sub-tropical distribution. It is the most common anole in the Bahamas and is one of the species in the Greater Antilles adaptive radiation (a ‘trunk-ground’ ecomorph). Most lizards in this study population (~85%) mature and die in a single year, with most mortality occurring during the summer months from May to October (Calsbeek and Smith, 2003). During May 2006, I captured all sub-adult male ( $n = 149$ ) and female ( $n = 166$ ) lizards from Kidd Cay, an offshore island near Great Exuma, Bahamas. The island is small (~0.084 km<sup>2</sup>) and near Great Exuma, Bahamas (23°31'N, 75°49.5'W). Kidd Cay supports a diverse habitat made up of both broad diameter vegetation like palm trees (*Pseudophoenix* spp.) and Australian pine trees (*Casuarina equisetifolia*) (mean perch diameter = 230 mm), as well as narrow diameter vegetation like sea-grape (*Coccoloba uvifera*), sea hibiscus (*Hibiscus tiliaceus*), and buttonwood (*Conocarpus erectus*) (mean perch diameter = 25 mm). I chose this primary site for study because selection pressures arising due to performance differences in these alternative habitat types are thought to underlie the diversification of anoles (Losos *et al.*, 1997; Schluter, 2000). For this reason, I measured characteristics of the habitat (i.e. perching diameter, nearest millimetre) in which each lizard was captured. *Anolis sagrei*

are highly territorial and perching diameter at first capture is a reliable estimate of habitat use (Calsbeek *et al.*, 2007).

Following capture, all lizards were sexed (males have enlarged post-anal scales), weighed with a Pesola spring scale (to the nearest gram), and measured for snout-to-vent length (SVL; nearest millimetre) using a small plastic ruler. I measured hind- and forelimb lengths (Calsbeek *et al.*, 2007) with dial calipers and marked each lizard with a unique combination of coloured elastomer dyes in the ventral side of the hind- and forelimbs (Nauwelaerts *et al.*, 2000). These tags serve to permanently identify individuals in the field, and allowed me to track each lizard throughout its lifetime. I released all lizards back to their original point of capture within 6 h.

### Running performance

During each afternoon following capture, I measured sprinting velocity by motivating lizards [maintained at ambient temperatures (25–30°C) near their performance optimum (Huey, 1983, report from a related species)] to run up a 1-m long track that was either broad (i.e. a 10-cm wide plank) or narrow (i.e. a 2.5-cm diameter dowel). Both surfaces were inclined at ~20° (Van Berkum, 1983; Perry *et al.*, 2004). Lizards were provided with a darkened retreat site at the far end of the track. The order of track diameters to begin trials each day was determined randomly and alternated between trials. For each lizard, I videotaped three trials on each surface with a digital Sony handycam<sup>®</sup> recording at 32 frames per second and trials were digitized with MotionAnalysis<sup>®</sup> software (<http://warthog.ucr.edu/>). I used the maximum speed achieved over a 10-cm increment during the three trials for analysis. Trials in which lizards did not actively cycle their limbs or keep their feet in contact with the track across all 10 cm were not used in any analyses. Four hours after sprint trials, I measured the running time to exhaustion (stamina) on a circular racetrack (circumference ~3.7 m) (Bennett, 1980; Le Galliard *et al.*, 2004). Stamina was recorded as the running time to exhaustion (seconds), determined by five failed attempts to motivate continued running and/or the loss of the righting response.

In all statistical analyses, I refer to maximum sprinting speed on the narrow dowel as a measure of maximum sprint speed. I calculated the difference in maximum speeds achieved on broad and narrow surfaces as an index of ‘sprint-sensitivity’ (Irschick and Losos, 1999), the reduction in speed experienced as lizards move from broad to narrow dowels. All analyses were performed using JMP v. 6.0.2 and were conducted separately for males and females after testing for sex effects in pooled analyses.

### Selection analyses

I conducted censuses of all surviving lizards 4 months later (late September) by walking multiple daily transects across the entire island. The period from May to September includes the time to reach sexual maturity and the end of the first breeding season. Censuses can be considered exhaustive because I recaptured all uniquely tagged (colour marks) lizards from the study island. Lizards that were not recovered during censuses were considered to have died. This is a reasonable assumption since emigration from the island is probably very rare (Calsbeek and Smith, 2003). Although most surviving lizards were captured within the first 3 days, censuses continued for 2 weeks, until three consecutive days of searching had turned up no new marked lizards.

I calculated selection gradients (Lande and Arnold, 1983; Brodie *et al.*, 1995) for linear ( $\beta$ ) and non-linear ( $\gamma_{1,1}$  and  $\gamma_{1,2}$ ) forms of selection using standard parametric tests. However, since the assumptions of parametric statistics are likely violated by the binomial dependent variable (live/die), I assigned significance values to selection gradients using logistic regression (Janzen and Stern, 1998) and visualized selection using projection pursuit and cubic splines (Schluter, 1988). I included the independent variables running performance, habitat use, hindlimb and forelimb lengths, and snout-to-vent length to control for variation due to body size. I estimated selection on size-corrected traits by incorporating the residuals from a regression of log-transformed limb length on log-transformed snout-to-vent length. These regressions were performed separately for each sex and then compared in pooled analyses. I standardized all variables used in selection analyses to a mean of 0 and unit standard deviation, except survival, which was scaled by the mean survival in each population.

### Path analysis

I used path analysis (Wright, 1934; Li, 1975) to examine direct effects (partial regression coefficients), indirect effects (product of direct effects), and total effects (sums along paths) of morphological, performance, and habitat variables on survival. I constructed *a priori* hypotheses for a set of models based on the ecology of anoles (Schoener, 1969; Losos, 1990; Losos and Irschick, 1996) and previous studies of morphological performance (Irschick and Losos, 1999; Calsbeek and Irschick, 2007). I compared competing models using Akaike's information criterion [AIC (Akaike 1987)], and chose the model that minimized the AIC score and whose score was at least 2 points lower than that of the next best model (Langerhans *et al.*, 2007). Significance tests for path models were based on comparisons in which the covariance structure of each model was tested against the covariance that would be expected under the assumption that the model was correct (Gomez and Zamora, 2000). A significant difference in this comparison indicates that the model in question provides a poor fit to the data. Path analyses, including significance tests, were performed using the CALIS procedure in SAS v8.

## RESULTS

*Anolis sagrei* from this population are highly sexually dimorphic in body size (mean  $\pm$  standard error: snout-to-vent length at first capture,  $SVL_{\text{male}} = 55.68 \pm 0.39$  mm,  $SVL_{\text{female}} = 43.12 \pm 0.37$  mm;  $F_{1,313} = 530$ ,  $P < 0.0001$ ). The dimorphism also extended to habitat use and running performance, with males generally perching on larger diameter surfaces higher off of the ground, and having higher maximum sprinting velocities and higher running endurance (Table 1). However, dimorphism in some performance traits was largely explained by the aforementioned differences in body size, and only sprinting speed remained different between the sexes after accounting for body size variation (based on residuals from regressions of log-transformed variables versus log-SVL; Table 1). Finally, in addition to the significant difference in mean size, male body size was also more variable than female body size ( $CV_{SVL} = 11.8$  for males and 5.5 for females;  $P < 0.05$ ).

Calsbeek and Irschick (2007) have shown that the same locomotor performance traits measured in the present study are correlated with limb length in male *A. sagrei*. However, these relationships were not significant in females. For example, maximum sprint speed, which was negatively correlated with male hindlimb length ( $r = 0.19$ ,  $P = 0.0001$ ) (Calsbeek and Irschick, 2007), was not related to female limb length ( $r = 0.03$ ,  $P = 0.74$ ,  $n = 159$ ), though it was

**Table 1.** Males and females differed in their use of the habitat (perch height and diameter) as well as in their running performance. However, differences in stamina and sprint sensitivity were no longer significant after correcting for body size. Residuals scores from the regression of performance variables against body size (snout-to-vent length)

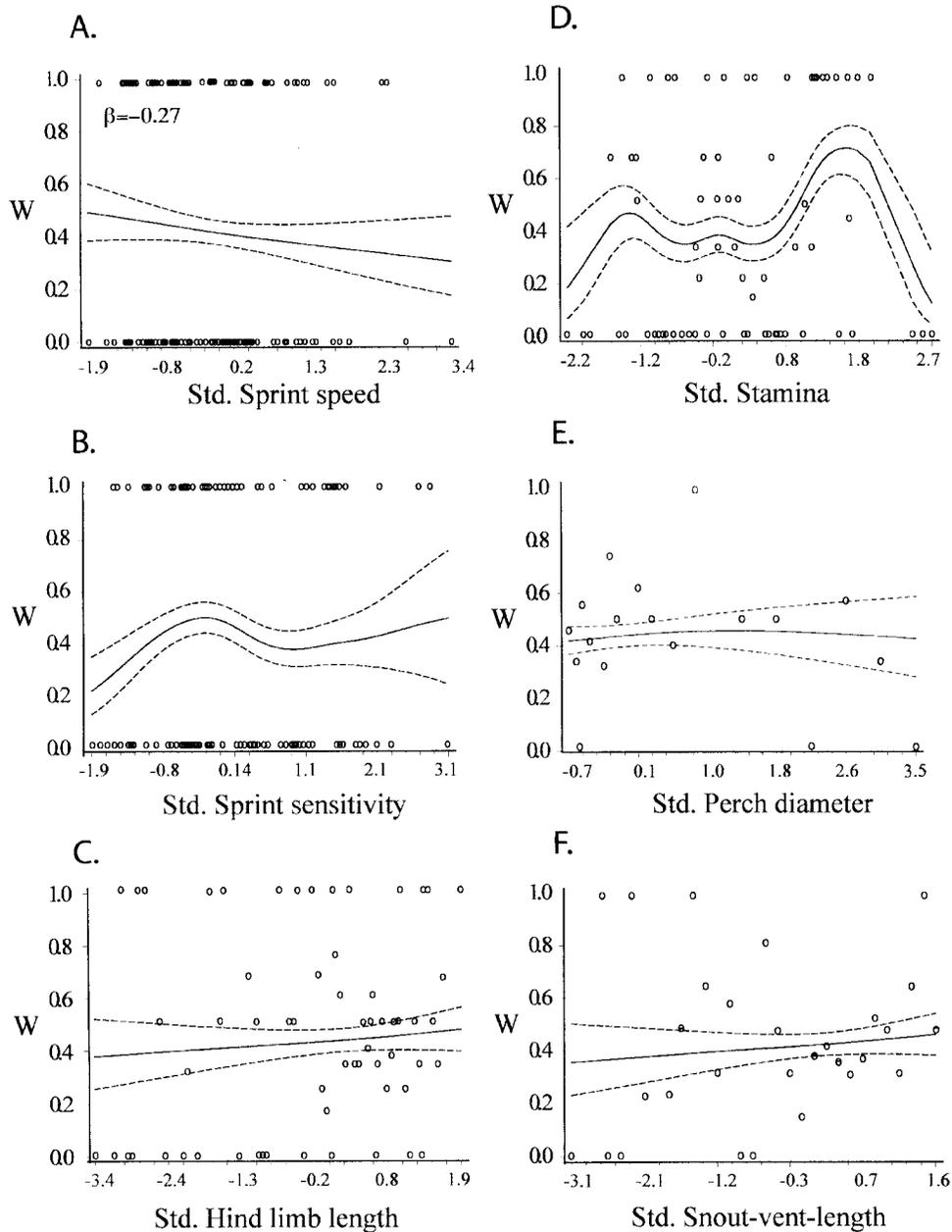
Variable	Sex	<i>n</i>	Mean	Standard error	<i>F</i>	<i>P</i>																																																																																																
Perch height (m)	F	163	0.46	0.05	12.06	0.0006																																																																																																
	M	149	0.71	0.05			Perch diameter (mm)	F	163	4.69	0.81	9.79	0.002	M	149	8.34	0.84	Stamina (s)	F	165	63.83	1.53	39.25	0.0001	M	148	77.77	1.62	Stamina residuals	F	165	0.06	1.47	0.004	0.95	M	148	-0.06	1.55	Sprint speed narrow ( $\text{m} \cdot \text{s}^{-1}$ )	F	161	1.73	0.38	8.51	0.004	M	131	1.9	0.43	Speed narrow residuals	F	161	-0.064	0.039	6.13	0.01	M	131	0.079	0.043	Sprint speed broad ( $\text{m} \cdot \text{s}^{-1}$ )	F	160	2.02	0.04	54.23	0.0001	M	133	2.43	0.04	Speed broad residuals	F	160	-0.72	0.04	7.72	0.006	M	133	0.87	0.042	Sprint sensitivity ( $\Delta\text{speed}$ )	F	160	-0.29	0.047	12.25	0.0005	M	131	-0.54	0.052	Sensitivity residuals	F	160	0.005	0.047	0.04	0.98	M
Perch diameter (mm)	F	163	4.69	0.81	9.79	0.002																																																																																																
	M	149	8.34	0.84			Stamina (s)	F	165	63.83	1.53	39.25	0.0001	M	148	77.77	1.62	Stamina residuals	F	165	0.06	1.47	0.004	0.95	M	148	-0.06	1.55	Sprint speed narrow ( $\text{m} \cdot \text{s}^{-1}$ )	F	161	1.73	0.38	8.51	0.004	M	131	1.9	0.43	Speed narrow residuals	F	161	-0.064	0.039	6.13	0.01	M	131	0.079	0.043	Sprint speed broad ( $\text{m} \cdot \text{s}^{-1}$ )	F	160	2.02	0.04	54.23	0.0001	M	133	2.43	0.04	Speed broad residuals	F	160	-0.72	0.04	7.72	0.006	M	133	0.87	0.042	Sprint sensitivity ( $\Delta\text{speed}$ )	F	160	-0.29	0.047	12.25	0.0005	M	131	-0.54	0.052	Sensitivity residuals	F	160	0.005	0.047	0.04	0.98	M	131	-0.006	0.051								
Stamina (s)	F	165	63.83	1.53	39.25	0.0001																																																																																																
	M	148	77.77	1.62			Stamina residuals	F	165	0.06	1.47	0.004	0.95	M	148	-0.06	1.55	Sprint speed narrow ( $\text{m} \cdot \text{s}^{-1}$ )	F	161	1.73	0.38	8.51	0.004	M	131	1.9	0.43	Speed narrow residuals	F	161	-0.064	0.039	6.13	0.01	M	131	0.079	0.043	Sprint speed broad ( $\text{m} \cdot \text{s}^{-1}$ )	F	160	2.02	0.04	54.23	0.0001	M	133	2.43	0.04	Speed broad residuals	F	160	-0.72	0.04	7.72	0.006	M	133	0.87	0.042	Sprint sensitivity ( $\Delta\text{speed}$ )	F	160	-0.29	0.047	12.25	0.0005	M	131	-0.54	0.052	Sensitivity residuals	F	160	0.005	0.047	0.04	0.98	M	131	-0.006	0.051																			
Stamina residuals	F	165	0.06	1.47	0.004	0.95																																																																																																
	M	148	-0.06	1.55			Sprint speed narrow ( $\text{m} \cdot \text{s}^{-1}$ )	F	161	1.73	0.38	8.51	0.004	M	131	1.9	0.43	Speed narrow residuals	F	161	-0.064	0.039	6.13	0.01	M	131	0.079	0.043	Sprint speed broad ( $\text{m} \cdot \text{s}^{-1}$ )	F	160	2.02	0.04	54.23	0.0001	M	133	2.43	0.04	Speed broad residuals	F	160	-0.72	0.04	7.72	0.006	M	133	0.87	0.042	Sprint sensitivity ( $\Delta\text{speed}$ )	F	160	-0.29	0.047	12.25	0.0005	M	131	-0.54	0.052	Sensitivity residuals	F	160	0.005	0.047	0.04	0.98	M	131	-0.006	0.051																														
Sprint speed narrow ( $\text{m} \cdot \text{s}^{-1}$ )	F	161	1.73	0.38	8.51	0.004																																																																																																
	M	131	1.9	0.43			Speed narrow residuals	F	161	-0.064	0.039	6.13	0.01	M	131	0.079	0.043	Sprint speed broad ( $\text{m} \cdot \text{s}^{-1}$ )	F	160	2.02	0.04	54.23	0.0001	M	133	2.43	0.04	Speed broad residuals	F	160	-0.72	0.04	7.72	0.006	M	133	0.87	0.042	Sprint sensitivity ( $\Delta\text{speed}$ )	F	160	-0.29	0.047	12.25	0.0005	M	131	-0.54	0.052	Sensitivity residuals	F	160	0.005	0.047	0.04	0.98	M	131	-0.006	0.051																																									
Speed narrow residuals	F	161	-0.064	0.039	6.13	0.01																																																																																																
	M	131	0.079	0.043			Sprint speed broad ( $\text{m} \cdot \text{s}^{-1}$ )	F	160	2.02	0.04	54.23	0.0001	M	133	2.43	0.04	Speed broad residuals	F	160	-0.72	0.04	7.72	0.006	M	133	0.87	0.042	Sprint sensitivity ( $\Delta\text{speed}$ )	F	160	-0.29	0.047	12.25	0.0005	M	131	-0.54	0.052	Sensitivity residuals	F	160	0.005	0.047	0.04	0.98	M	131	-0.006	0.051																																																				
Sprint speed broad ( $\text{m} \cdot \text{s}^{-1}$ )	F	160	2.02	0.04	54.23	0.0001																																																																																																
	M	133	2.43	0.04			Speed broad residuals	F	160	-0.72	0.04	7.72	0.006	M	133	0.87	0.042	Sprint sensitivity ( $\Delta\text{speed}$ )	F	160	-0.29	0.047	12.25	0.0005	M	131	-0.54	0.052	Sensitivity residuals	F	160	0.005	0.047	0.04	0.98	M	131	-0.006	0.051																																																															
Speed broad residuals	F	160	-0.72	0.04	7.72	0.006																																																																																																
	M	133	0.87	0.042			Sprint sensitivity ( $\Delta\text{speed}$ )	F	160	-0.29	0.047	12.25	0.0005	M	131	-0.54	0.052	Sensitivity residuals	F	160	0.005	0.047	0.04	0.98	M	131	-0.006	0.051																																																																										
Sprint sensitivity ( $\Delta\text{speed}$ )	F	160	-0.29	0.047	12.25	0.0005																																																																																																
	M	131	-0.54	0.052			Sensitivity residuals	F	160	0.005	0.047	0.04	0.98	M	131	-0.006	0.051																																																																																					
Sensitivity residuals	F	160	0.005	0.047	0.04	0.98																																																																																																
	M	131	-0.006	0.051																																																																																																		

negatively correlated with female body size (SVL,  $r = 0.14$ ,  $P = 0.02$ ). Sprint sensitivity ( $\Delta\text{speed}$ ), also negatively correlated with hindlimb length in males ( $r = 0.17$ ,  $P < 0.04$ ) (Calsbeek and Irschick, 2007), was not significantly correlated with limb length in females ( $r = 0.00$ ,  $P = 0.95$ ,  $n = 158$ ). Similarly, endurance was positively correlated with hindlimb length in males ( $r = 0.26$ ,  $P < 0.001$ ) (Calsbeek and Irschick, 2007) but was not significant in females ( $r = 0.04$ ,  $P = 0.33$ ,  $n = 163$ ). In summary, although all of the correlations between locomotor performance and morphology were significant when tested in males, only body size and sprinting speed were correlated in females.

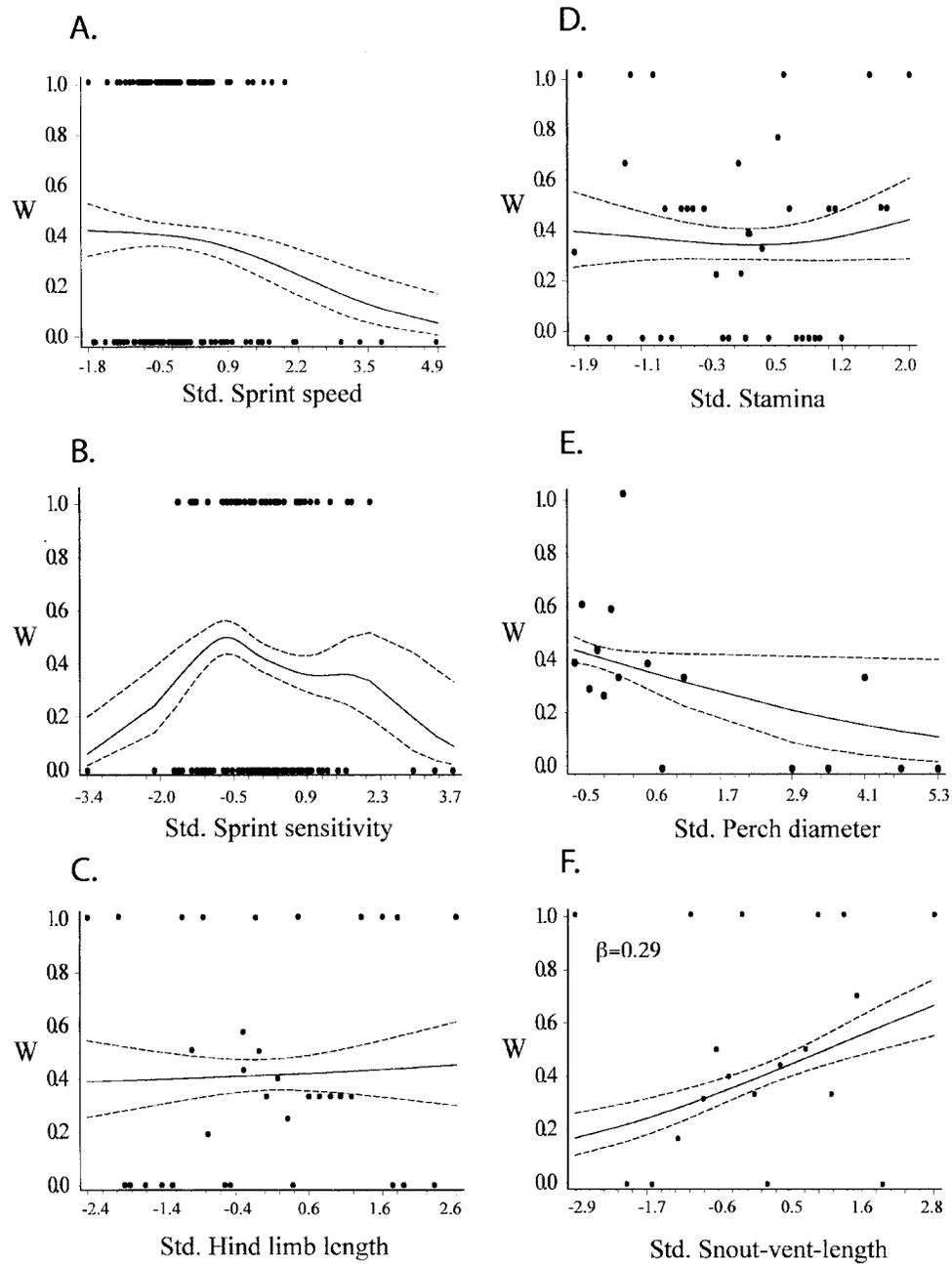
### Effects of individual traits on survival

There was only a single significant selection gradient that I detected in males, namely a negative effect of maximum sprint speed on male viability ( $\beta = -0.27 \pm 0.10$ ,  $\chi^2 = 6.81$ ,  $P = 0.009$ ; Fig. 1A). None of the quadratic (i.e. non-linear) gradients were significant for males. However, there was a significant polynomial effect related to stamina (stamina<sup>4</sup>; Fig. 1D), representing selection that would affect kurtosis in this trait. However, this higher-order moment is rarely considered in selection studies and will not be discussed further here.

Similarly, in females, there was a single significant linear selection gradient (Fig. 2), but in females this gradient was positive and favoured larger female body size ( $\beta = 0.29 \pm 0.13$ ,



**Fig. 1.** Univariate fitness surfaces (non-parametric cubic splines) demonstrating the form of selection acting on males in this study. Panels show the best-fit cubic spline (solid line) and 95% confidence intervals (dashed lines). In each panel, W represents survival (live/die). All traits were standardized before analysis (mean zero, unit variance). The significant linear gradient on sprint speed is indicated in panel (A). No other linear or quadratic gradients were significant in males, although I did detect a significant fourth-order effect on stamina (see text).



**Fig. 2.** Univariate fitness surfaces (non-parametric cubic splines) demonstrating the form of selection acting on females in this study. Panels show the best-fit cubic spline (solid line) and 95% confidence intervals (dashed lines). In each panel, W represents survival (live/die). All traits were standardized before analysis (mean zero, unit variance). The only significant linear selection gradient in females was that measured on snout-to-vent length (panel F). As was the case for males, no quadratic gradients were significant. However, I did detect a significant cubic effect on sprint sensitivity in females (see text).

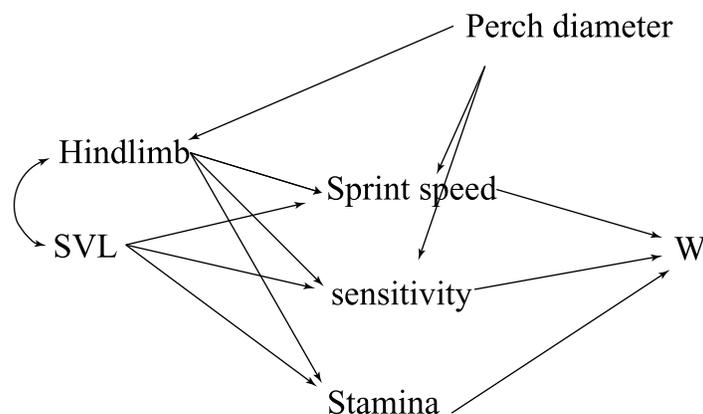
$\chi^2 = 4.95$ ,  $P = 0.02$ ; Fig. 2F). Again, none of the quadratic gradients was significant in females. The non-linear selection gradient acting on sprint sensitivity (Fig. 2B) represents a significant cubic gradient (sigmoidal), which may indicate selection affecting the skewness of this trait. It appears that selection may favour two optima for this trait in females, stabilizing sprint sensitivity at values near the mean in one case, and for larger values in the second case. However, as noted above, these higher moments will not be discussed further.

### Path analysis

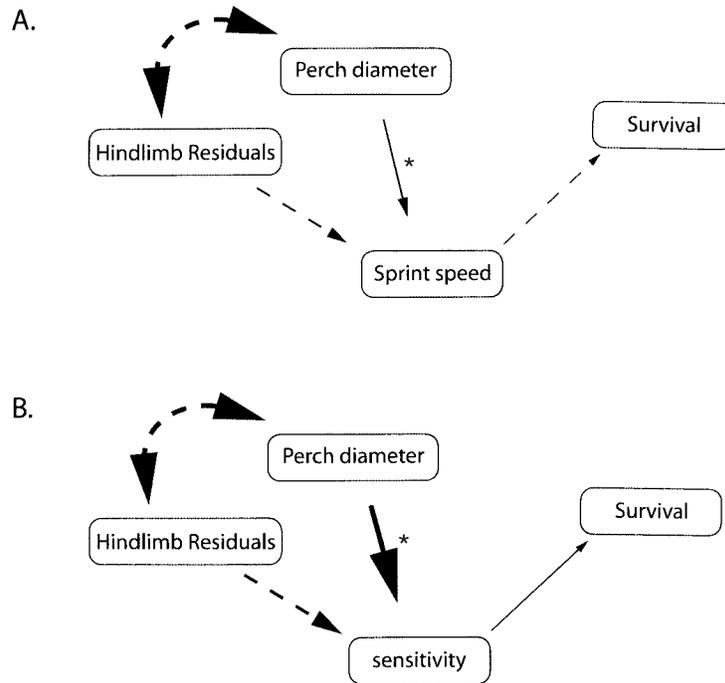
None of the direct effects in the full (hypothetical) path model (Fig. 3) was significant for males or females. Based on AIC scores, the only significant path models were extremely simple and involved only hindlimb length (residuals correcting for body size), sprint speed or sensitivity, and perch diameter. I present only the two simplest path models with the lowest chi-square scores (i.e. those that were not significantly deviant) and the most degrees of freedom. These models were assigned unambiguously with AIC criteria as the only significant models in the analysis (Fig. 4A:  $\chi^2 = 4.38$ ,  $P = 0.35$ ; Fig. 4B:  $\chi^2 = 4.18$ ,  $P = 0.38$ ). Paths largely conformed to *a priori* predictions regarding the importance of morphology and ecology; however, the paths failed to capture interactive effects of these variables on fitness (Calsbeek and Irschick, 2007). Overall, the paths illustrate very weak effects of individual traits or ecological values on fitness and further emphasize the importance of considering interactions among these variables (i.e. correlational selection).

### Correlational selection

Although univariate tests were nearly all non-significant, Calsbeek and Irschick (2007) previously demonstrated significant interactive effects of several of these variables on survival. For example, limb length, sprint speed, sprint sensitivity, and perch diameter were under strong correlational selection in males (e.g. hindlimb length  $\times$  sprint speed:  $\gamma_{1,2} = 0.14 \pm 0.05$ ,  $P = 0.01$ ; perch diameter  $\times$  sprint sensitivity:  $\gamma_{1,2} = -0.09 \pm 0.05$ ,  $P = 0.04$ )



**Fig. 3.** Hypothetical path model constructed based on previous studies (Schoener, 1969; Losos, 1990; Losos and Irschick, 1996; Irschick and Losos, 1999) illustrating the hypothesized causal roles of morphology and habitat use in determining variation in locomotor performance and subsequently variation in viability.



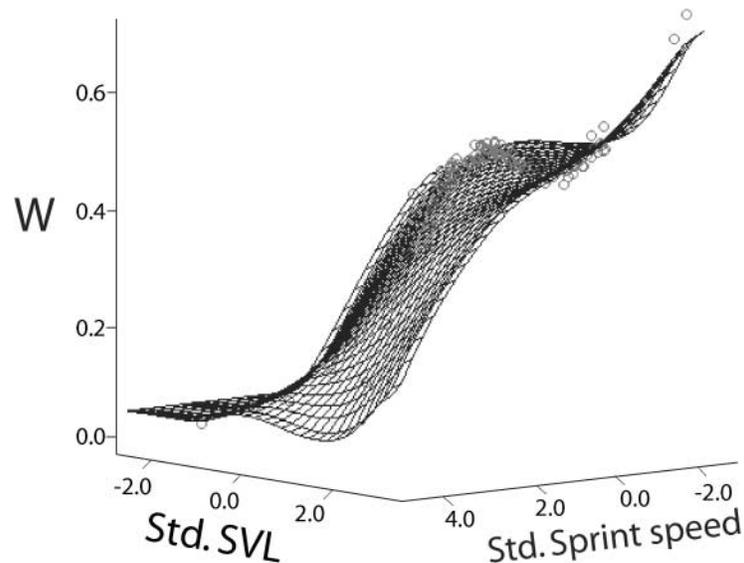
**Fig. 4.** Model subsets showing effects of hindlimb length (residuals correcting for variation due to body size) and perch diameter on viability mediated through the effects of (A) sprint speed and (B) sprint sensitivity. While these are the two best fit models to come out of the analysis, only one individual path was significant (highlighted with an asterisk). Positive path coefficients are illustrated with solid arrows, negative coefficients with dashed arrows. For clarity, all residual terms ( $U$ 's) were omitted.

(Calsbeek and Irschick, 2007). These results suggested that while individual traits did not have direct effects on fitness, interactions with other traits and with the environment had important consequences for male survival.

I tested whether these same interactions were important for viability in females. Body size was under weak correlational selection with sprint speed, although this effect was non-significant for females ( $\gamma_{1,2} = 0.11 \pm 0.09$ , Wald  $\chi^2 = 6.97$ ,  $P = 0.06$ ; Fig. 5), and none of the other morphological, performance, or ecological variables had interactive effects on female survival.

## DISCUSSION

Understanding the ties that bind performance, morphology, and fitness remains an important goal in studies of evolutionary ecology (Arnold, 1983; Irschick and Losos, 1999; Kingsolver and Huey, 2003). Although many studies have linked performance with morphology or morphology with fitness (Ghalambor *et al.*, 2004; Irschick *et al.*, 2005; Husak *et al.*, 2006), relatively few studies have illustrated the full causal pathways that connect variation in morphology with variation in performance and how these interact to influence fitness. I have provided evidence for causal relationships between morphology, running performance, and an



**Fig. 5.** Multivariate cubic spline showing the correlational selection acting on female body size and sprint speed. In the figure, *W* represents survival (live/die). Traits were standardized before analysis (mean zero, unit variance). Overall, selection favoured large, fast females.

important component of male fitness (survival) in the wild. However, these relationships were largely non-significant in females. It is difficult to determine if this is a general trend in nature. Most studies of performance variation are conducted on males, with relatively little attention thus far having been paid to females in the literature. In males, variation in limb length was negatively correlated with sprinting speed on the narrow surface and with sprinting sensitivity. These correlations also had significant impacts on male survival, but the effects of selection were mediated only through differences in habitat use (e.g. survival was enhanced when males that sprinted well on narrow surfaces also lived in habitats with narrow diameter twigs). The importance of the relationships between morphology, locomotor performance, and habitat use is one of the hallmarks of the adaptive radiation of *Anolis* lizards in the Greater Antilles, and is, in essence, the key distinction by which ecomorphs (different anole species) are characterized (Williams, 1983).

Because path models failed to capture the interactive effects of morphology, performance, and ecology on survival, Calsbeek and Irschick (2007) plotted multivariate fitness surfaces using the methods of Schluter and Nychka (1994). I have added to that here by presenting the fitness surface that describes interactions between body size and sprint speed in females (Fig. 5). This surface illustrates the weak correlational selection between traits in the form of moderate curvature to what is otherwise a plane, favouring larger-bodied females with high maximum sprint speeds. This surface stands in striking contrast to the magnitude of curvature in both surfaces pertaining to male survival (Calsbeek and Irschick, 2007).

The adaptive radiation of anoles is thought to have progressed owing to selection favouring long-limbed lizards that live on broad diameter perching surfaces and short-limbed individuals living in more scrubby habitats (Moermond, 1979; Williams, 1983; Losos, 1990). Results presented by Calsbeek and Irschick (2007) provide some of the first empirical evidence that

patterns of natural selection acting on males may underlie patterns of interspecific variation in these same traits. However, the analyses presented here underscore the differences in both the morphology–performance correlations and the ways in which these correlations translate into viability differences between the sexes.

Results from this study also provide evidence that sex-specific differences in the morphology–performance–fitness relationships could have retarded rates of *Anolis* diversification. That is, results were non-significant in females, and since the traits measured in this study are likely to have a genetic basis, and one which is shared by both males and females, any response to the selection pressures reported here would be slowed owing to between-sex genetic correlations in these traits (Lande, 1980). Similar ideas have recently been explored in detail by Butler *et al.* (2007), who showed that variation in sexual dimorphism among species of anoles may play an important role in diversification rates (Schoener, 1967). Butler and colleagues (2007) suggest that increases in sexual dimorphism may further facilitate diversification within and between species by increasing the degree of resource partitioning (Schoener, 1967). Although the processes leading to divergent use of the habitat have been investigated in depth for males of different species of anole (Stamps, 1977; Schoener, 1983; Losos, 1990; Ogden and Thorpe, 2002; Thorpe *et al.*, 2005), differences in resource use between males and females of a single species may similarly lead to ecological diversification (Butler *et al.*, 2007). The implications of this idea, together with results presented here, are that the extraordinary dimorphism exhibited by *A. sagrei* may be the cause of divergent selection pressures as well as the consequence. Dimorphism may be the cause of divergent selection because size dimorphism puts males and females on alternative adaptive peaks in terms of performance variation. It may be a consequence if increasing morphological differences between the sexes can alleviate conflicting selection pressures. Further studies of performance variation and the consequent selection pressures acting on females are clearly warranted.

There are several possible explanations for the difference in morphology–performance correlations in males and females. Sexual dimorphism in size may play a significant role in setting up performance variation. Males are significantly larger than females in most anole species (Butler *et al.*, 2000; Butler and Losos, 2002), including *A. sagrei*. In addition to being larger, males are also more variable in body size than females. This difference in size and variability could form the basis for performance variation (and/or its detection) in males which is absent (or reduced/undetected) in females. The morphological traits measured here are known to have a heritable basis (Calsbeek *et al.*, 2007; Calsbeek and Bonneaud, in press), although others have also demonstrated a significant effect of phenotypic plasticity on variation in limb length (Losos *et al.*, 2000).

Similarly, differences in morphology and habitat use might explain why patterns of selection were only significant in males. Because females generally spend more time on the ground, particularly in the leaf litter, they may be subject to weaker performance-driven selection pressures overall (Butler *et al.*, 2000). By contrast, males are nearly always observed perched on vegetation, defending territories from rival males and signalling to females. Differences in activity and total time spent in the vegetation are likely to impose more severe locomotor constraints on males, and this may explain the importance of selection acting together on sprinting performance and habitat use in males but not in females.

Together, these observations underscore the importance of considering ecology in studies of the relationships among morphology, performance, and fitness. They also provide an example of correlational selection measured in a group for which we could make *a priori* predictions about these patterns based on the ecology of the group (Schoener, 1969; Losos, 1990;

Losos and Irschick, 1996). Although path analysis has been the tool of choice in many studies of the morphology–performance–fitness axis, the correlational (i.e. interactive) nature of selection in this study detracted from the utility of a path analytic framework. Results based on measures of correlational selection, however, suggest that processes operating within populations parallel the patterns of diversity measured among species, and therefore may provide at least part of the mechanism for eco-morphological divergence.

### ACKNOWLEDGEMENTS

I thank D. Irschick for many helpful discussions that improved this paper. B. Calsbeek provided valuable assistance in the field, digitized video clips, and made helpful suggestions that improved the paper. Thanks to R. Irwin and B. Taylor for help with path analyses. Special thanks go to Nancy Bottomley for logistical support in the field and for permission to conduct work on her property. Research was funded by a National Geographic Research grant.

### REFERENCES

- Akaike, H. 1987. Factor-analysis and AIC. *Psychometrika*, **52**: 317–332.
- Arnold, S.J. 1983. Morphology, performance and fitness. *Am. Zool.*, **23**: 347–361.
- Bartholomew, G.A. 1964. The roles of physiology and behavior in the maintenance of homeostasis in the desert environment. *Symp. Soc. Exp. Biol.*, **8**: 7–29.
- Benkman, C.W. and Lindholm, A.K. 1991. The advantages and evolution of a morphological novelty. *Nature*, **349**: 519–520.
- Bennett, A.F. 1980. The thermal dependence of lizard behaviour. *Anim. Behav.*, **28**: 752–762.
- Bennett, A.F., Huey, R.B. and John-Alder, H.B. 1984. Physiological correlates of natural activity and locomotor capacity in two species of lacertid lizards. *J. Comp. Physiol. B*, **154**: 113–118.
- Blows, M.W. and Brooks, R. 2003. Measuring nonlinear selection. *Am. Nat.*, **162**: 815–820.
- Brodie, E.D. 1992. Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. *Evolution*, **46**: 1284–1298.
- Brodie, E.D.I. 1993. Homogeneity of the genetic variance–covariance matrix for antipredator traits in two natural populations of the garter snake *Thamnophis ordinoides*. *Evolution*, **47**: 844–854.
- Brodie, E.D.I., Moore, A.J. and Janzen, F.J. 1995. Visualizing and quantifying natural selection. *Trends Ecol. Evol.*, **10**: 313–318.
- Butler, M.A. and Losos, J.B. 2002. Multivariate sexual dimorphism, sexual selection, and adaptation in Greater Antillean *Anolis* lizards. *Ecol. Monogr.*, **72**: 541–559.
- Butler, M.A., Schoener, T.W. and Losos, J.B. 2000. The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution*, **54**: 259–272.
- Butler, M.A., Sawyer, S.A. and Losos, J.B. 2007. Sexual dimorphism and adaptive radiation in *Anolis* lizards. *Nature*, **447**: 202–205.
- Calsbeek, R. and Bonneaud, C. in press. Post-copulatory sperm sorting as an adaptive form of mate choice in the brown anole, *Anolis sagrei*. *Evolution*.
- Calsbeek, R. and Irschick, D.J. 2007. The quick and the dead: correlational selection on morphology, performance, and habitat use in island lizards. *Evolution*, **61**: 2493–2503.
- Calsbeek, R. and Smith, T.B. 2003. Ocean currents mediate evolution in island lizards. *Nature*, **426**: 552–555.
- Calsbeek, R., Smith, T.B. and Bardeleben, C. 2007. Intraspecific variation in *Anolis sagrei* mirrors the adaptive radiation of Caribbean anoles. *Biol. J. Linn. Soc.*, **90**: 189–199.
- Charlesworth, D. and Charlesworth, B. 1975. Sexual selection and polymorphism. *Am. Nat.*, **109**: 465–470.

- Christian, K.A. and Tracy, C.R. 1981. The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. *Oecologia (Berl.)*, **49**: 218–223.
- Garland, T. 1984. Physiological correlates of locomotory performance in a lizard – an allometric approach. *Am. J. Physiol.*, **247**: R806–R815.
- Garland, T., Jr. 1985. Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *J. Zool. (Lond.)*, **207**: 425–439.
- Ghalambor, C.K., Reznick, D.N. and Walker, J.A. 2004. Constraints on adaptive evolution: the functional trade-off between reproduction and fast-start swimming performance in the Trinidadian guppy (*Poecilia reticulata*). *Am. Nat.*, **164**: 38–50.
- Gomez, J.M. and Zamora, R. 2000. Spatial variation in the selective scenarios of *Hormatophylla spinosa* (Cruciferae). *Am. Nat.*, **155**: 630–648.
- Grant, B.W. 1990. Trade-offs in activity time and physiological performance for thermoregulating desert lizards, *Sceloporus merriami*. *Ecology*, **71**: 2323–2333.
- Grant, P.R. 1968. Bill size, body size and the ecological adaptations of bird species to competitive situations on islands. *Syst. Zool.*, **17**: 319–333.
- Hereford, J., Hansen, T.F. and Houle, D. 2004. Comparing strengths of directional selection: how strong is strong? *Evolution*, **58**: 2133–2143.
- Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hoang, A., Hill, C.E. *et al.* 2001. Strength and tempo of directional selection in the wild. *Proc. Natl. Acad. Sci. USA*, **98**: 9157–9160.
- Huey, R.B. 1983. Natural variation in body temperature and physiological performance in a lizard (*Anolis cristatellus*). In *Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams* (A.G.J. Rhodin and K. Miyata, eds.), pp. 485–490. Cambridge, MA: Harvard University Press.
- Husak, J.F., Fox, S.F., Lovern, M.B. and Van den Bussche, R.A. 2006. Faster lizards sire more offspring: sexual selection on whole-animal performance. *Evolution*, **60**: 2122–2130.
- 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.
- Irschick, D.J. and Losos, J.B. 1999. Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean anoles. *Am. Nat.*, **154**: 293–305.
- Irschick, D.J., Carlisle, E., Elstrott, J., Ramos, M., Buckley, C., Vanhooydonck, B. *et al.* 2005. A comparison of habitat use, morphology, clinging performance and escape behaviour among two divergent green anole lizard (*Anolis carolinensis*) populations. *Biol. J. Linn. Soc.*, **85**: 223–234.
- Janzen, F.J. and Stern, H.S. 1998. Logistic regression for empirical studies of multivariate selection. *Evolution*, **52**: 1564–1571.
- Jones, A.G., Arnold, S.J. and Borger, R. 2003. Stability of the G-matrix in a population experiencing pleiotropic mutation, stabilizing selection, and genetic drift. *Evolution*, **57**: 1747–1760.
- Kingsolver, J.G. and Huey, R.B. 2003. Introduction: the evolution of morphology, performance, and fitness. *Integr. Comp. Biol.*, **43**: 361–366.
- Kingsolver, J.G.H., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hill, C.E. *et al.* 2001. The strength of phenotypic selection in natural populations. *Am. Nat.*, **157**: 245–261.
- Lailvaux, S.P., Herrel, A., VanHooydonck, B., Meyers, J.J. and Irschick, D.J. 2004. Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proc. R. Soc. Lond. B*, **271**: 2501–2508.
- Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, **34**: 292–305.
- Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proc. Natl. Acad. Sci. USA*, **78**: 3721–3725.

- Lande, R. and Arnold, S.J. 1983. The measurement of selection on correlated characters. *Evolution*, **37**: 1210–1226.
- Langerhans, R.B., Chapman, L.J. and DeWitt, T.J. 2007. Complex phenotypic–environment associations revealed in an East African cyprinid. *J. Evol. Biol.*, **20**: 1171–1181.
- Le Galliard, J.F., Clobert, J. and Ferrière, R. 2004. Physical performance and Darwinian fitness in lizards. *Nature*, **432**: 502–505.
- Li, C.C. 1975. *Path Analysis – A Primer*. Pacific Grove, CA: Boxwood Press.
- Losos, J.B. 1990. The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution*, **44**: 1189–1203.
- Losos, J.B. and Irschick, D.J. 1996. The effect of perch diameter on escape behaviour of *Anolis* lizards: laboratory predictions and field tests. *Anim. Behav.*, **51**: 593–602.
- Losos, J.B. and Sinervo, B. 1989. The effect of morphology and perch diameter on sprint performance of *Anolis* lizards. *J. Exp. Biol.*, **145**: 23–30.
- Losos, J.B., Irschick, D.J. and Schoener, T.W. 1994. Adaptation and constraint in the evolution of specialization of Bahamian *Anolis* lizards. *Evolution*, **48**: 1786–1798.
- Losos, J.B., Warheit, K.I. and Schoener, T.W. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature (Lond.)*, **387**: 70–73.
- Losos, J.B., Jackman, T.R., Larson, A., DeQueiroz, K. and Rodriguez-Shettino, L. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science*, **279**: 2115–2118.
- Losos, J.B., Creer, D.A., Glossip, D., Goellner, R., Hampton, A., Roberts, G. *et al.* 2000. Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. *Evolution*, **54**: 301–305.
- Losos, J.B., Leal, M., Glor, R.E., de Queiroz, K., Hertz, P.E., Schettino, L.R. *et al.* 2003. Niche lability in the evolution of a Caribbean lizard community. *Nature*, **424**: 542–545.
- McHenry, M.J. and Lauder, G.V. 2003. How do ontogenetic changes in morphology, behavior, and hydrodynamics affect the performance of gliding in zebrafish? *Integr. Comp. Biol.*, **43**: 907.
- Miles, D.B. 2004. The race goes to the swift: fitness consequences of variation in sprint performance in juvenile lizards. *Evol. Ecol. Res.*, **6**: 63–75.
- Moermond, T.C. 1979. The influence of habitat structure on *Anolis* foraging behavior. *Behaviour*, **70**: 147–168.
- Nauwelaerts, S., Coeck, J. and Aerts, P. 2000. Visible implant elastomers as a method for marking adult anurans. *Herpetol. Rev.*, **31**: 154–155.
- Ogden, R. and Thorpe, R.S. 2002. Molecular evidence for ecological speciation in tropical habitats. *Proc. Natl. Acad. Sci. USA*, **99**: 13612–13615.
- Perry, G., Levering, K., Girard, I. and Garland, T., Jr. 2004. Locomotor performance and social dominance in male *Anolis cristatellus*. *Anim. Behav.*, **67**: 37–47.
- Phillips, P.C. and Arnold, D.J. 1989. Visualizing multivariate selection. *Evolution*, **43**: 1209–1222.
- Roff, D.A. and Fairbairn, D.J. 2007. The evolution of trade-offs: where are we? *J. Evol. Biol.*, **20**: 433–447.
- Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. *Evolution*, **42**: 849–861.
- Schluter, D. 1995. Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth. *Ecology*, **76**: 82–90.
- Schluter, D. 1996. Ecological causes of adaptive radiation. *Am. Nat.*, **148**: s40–s64.
- Schluter, D. 2000. *The Ecology of Adaptive Radiation*. New York: Oxford University Press.
- Schluter, D. and Nychka, D. 1994. Exploring fitness surfaces. *Am. Nat.*, **143**: 597–616.
- Schoener, T.W. 1967. Ecological significance of sexual dimorphism in size in the lizard *Anolis cospersus*. *Science*, **155**: 474–477.
- Schoener, T.W. 1969. Size patterns in West Indian *Anolis* lizards. I. Size and species diversity. *Syst. Zool.*, **18**: 386–401.

- Schoener, T.W. 1983. Field experiments in interspecific competition. *Am. Nat.*, **122**: 240–285.
- Seehausen, O. and Schluter, D. 2004. Male–male competition and nuptial-colour displacement as a diversifying force in Lake Victoria cichlid fishes. *Proc. R. Soc. Lond. B*, **271**: 1345–1353.
- Shuster, M. and Wade, M.J. 1992. Equal mating success among male reproductive strategies in a marine isopod. *Nature*, **350**: 606–661.
- Sinervo, B. and Lively, C.M. 1996. The rock–paper–scissors game and the evolution of alternative male reproductive strategies. *Nature*, **380**: 240–243.
- Sinervo, B. and Losos, J.B. 1991. Walking the tight rope: a comparison of arboreal sprint performance among populations of *Sceloporus occidentalis*. *Ecology*, **72**: 1225–1237.
- Sinervo, B. and Svensson, E. 2002. Correlational selection and the evolution of genomic architecture. *Heredity*, **89**: 329–338.
- Smith, T.B. 1997. Adaptive significance of the mega-billed form in the polymorphic black-bellied seedcracker *Pyrenestes ostrinus*. *Ibis*, **139**: 382–387.
- Stamps, J.A. 1977. The relationship between resource competition, risk and aggression in a tropical lizard. *Ecology*, **58**: 349–358.
- Svensson, E.I., Eroukhmanoff, F. and Friberg, M. 2006. Effects of natural and sexual selection on adaptive population divergence and premating isolation in a damselfly. *Evolution*, **60**: 1242–1253.
- Temeles, E.J., Pan, I.L., Brennan, J.L. and Horwitt, J.N. 2000. Evidence for ecological causation of sexual dimorphism in a hummingbird. *Science*, **289**: 441–443.
- Thorpe, R.S., Reardon, J.T. and Malhotra, A. 2005. Common garden and natural selection experiments support ecotypic differentiation in the Dominican anole (*Anolis oculatus*). *Am. Nat.*, **165**: 495–504.
- Van Berkum, F.H. 1983. Evolutionary interaction of thermal physiology and field body temperatures of *Anolis* lizards. *Am. Zool.*, **23**: 889.
- Van Buskirk, J. and Schmidt, B.R. 2000. Predator-induced phenotypic plasticity in larval newts: trade-offs, selection, and variation in nature. *Ecology*, **81**: 3009–3028.
- Williams, E.E. 1983. Ecomorphs, faunas, island size, and diverse endpoints in island radiations of *Anolis*. In *Lizard Ecology: Studies of a Model Organism* (R.B. Huey, E.R. Pianka and T.W. Schoener, eds.), pp. 326–370. Cambridge, MA: Harvard University Press.
- Wright, S. 1934. The method of path coefficients. *Ann. Math. Stats.*, **5**: 161–215.