Experimental evidence that competition and habitat use shape the individual fitness surface

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Abstract

A key prediction made by theories of density-dependent competition is that resource overlap should increase the intensity of competition. By extension, we can predict that competition should lead to density-dependent natural selection. I studied natural selection on limb length and body size in a total of seven populations of *Anolis sagrei* over 3 years in the Bahamas. Experimental manipulations of population density on small off-shore cays revealed that the strength of natural selection on body size increased with density, suggesting that density-dependent intraspecific competition drives natural selection. At low density, reduced competition revealed significant selection on limb length driven by changes in perch diameter, indicating that selection favoured a match between morphology and habitat. The role habitat played in shaping selection was further illuminated by inter-annual changes in vegetation structure stemming from variation in precipitation among years. Thus, changes in both the intensity of competition across spatial replicates, and in resource availability through time, revealed changes in the targets of natural selection. Results provide empirical support for the long-standing hypothesis that density-dependent natural selection shapes the fitness surface of Greater Antilles anoles.

Introduction

After more than 75 years of study, competition remains a fundamentally important topic in community ecology (Lotka, 1932; Schoener, 1974; Tilman, 1994, 2004; Svensson & Sinervo, 2000). This is due in part to the fact that competition and, by extension, density dependence, are central to our understanding of community structure (e.g. concepts of the niche; Hutchinson, 1959), and the evolution of life-history tradeoffs (e.g. r vs. K selection; MacArthur & Wilson, 1967). More recently, studies have further demonstrated an important role for density-dependent competition in shaping species level diversification (Bolnick, 2004).

One of the primary predictions derived from theories of density-dependent competition is that the intensity of interspecific competition should vary with the degree of

resource partitioning, such that greater overlap in resource use between species should intensify the strength of competition (MacArthur & Levins, 1967; Schoener, 1974). This idea has received both theoretical (Doebeli, 1996) and empirical support (Pacala & Rough-garden, 1982; Schoener, 1983; Swanson *et al.*, 2003; Grant & Grant, 2006). However, an important question that remains is how variation in density-dependent competition among populations changes the strength and form of natural selection acting on single species, and whether these patterns may have cascading effects on species level diversity (Emerson & Arnold, 1989).

Anolis lizards provide an excellent opportunity to study variation in population level evolutionary processes, and also to link the action of selection acting within species to patterns of diversity seen among species (Calsbeek *et al.*, 2007). Correlations between morphology and ecology have arisen repeatedly on different islands in the Greater Antilles (Losos *et al.*, 1998; Jackman *et al.*, 1999). Lizards with relatively long limbs are most often found perching on broad diameter substrates where long limbs are advantageous for fast running (Irschick & Losos, 1998).

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Shorter-limbed lizards are most often found on narrow perching surfaces where they are agile and more suited to move through complex vegetation (Losos & Sinervo, 1989). Habitat specialists on different islands have been grouped into categories called 'ecomorphs' (Williams, 1983) based on these divergent ecomorphological correlations, and competition among ecomorphs has led to niche partitioning along habitat and climatological axes (Pacala & Roughgarden, 1982; Williams, 1983; Schluter & McPhail, 1992; Losos, 1994).

Correlations between morphology and performance in different habitat types present testable hypotheses about the action of natural selection: viability selection should favour long-limbed lizards on broad perches and short-limbed lizards on narrow perches. Natural selection arising as a result of competition for habitat use (Roughgarden, 1971; Pacala & Roughgarden, 1982; Schoener, 1983; Williams, 1983; Schluter & McPhail, 1992; Losos, 1994) and variation in locomotor performance (Losos & Sinervo, 1989; Calsbeek & Smith, 2003; Dayan & Simberloff, 2005; Harmon et al., 2005; Irschick et al., 2005a,b; Calsbeek & Irschick, 2007) has long been postulated as the primary mechanism behind the diversification of ecomorphs (i.e. species) in the Greater Antilles. However, despite decades of studying this important example of adaptive radiation, relatively little is known about how ecology influences natural selection at the population level, owing to a paucity of direct estimates of selection in this group (but see Ogden & Thorpe, 2002; Thorpe et al., 2005; Thorpe & Stenson, 2003). Here I present an experimental study of natural selection on lizard morphology in the context of two relevant ecological variables: population density and habitat use. Population density is a useful proxy for the strength of intraspecific competition. Habitat use, in particular perch diameter used by lizards in nature, affects locomotor abilities of lizards with different morphologies (Calsbeek & Irschick, 2007). Using 3 years of data on natural selection, I test the hypothesis that variation in competition and habitat use underlies natural selection on limb and body morphology. Although an explicit link to speciation is beyond the scope of this study, the action of natural selection at the population level may be useful for making inferences about the processes that gave rise to species (Emerson & Arnold, 1989; Emerson, 1991; Moreno et al., 1997).

Methods

General study system and organism

Anolis sagrei is the most common anole on the Great Bahamas Bank and is a member of the trunk-ground ecomorph in the Greater Antilles adaptive radiation. *Anolis sagrei* is a habitat generalist and is commonly found perching on the trunks of trees, in bushes or on the ground. I conducted field studies of natural selection from 2003 to 2005 on three small, off-shore cays near the island of Great Exuma, Bahamas (Kidd cay, Flamingo Bay cay, Nightmare cay) and in one population on Great Exuma. All of the cays chosen for this study were small (< 1500 m^2) and capable of supporting populations of 100–300 *A. sagrei* individuals (Spiller et al., 1998; Schoener et al., 2000). The fourth population was on a similarly-sized study plot on Great Exuma that was bounded on three sides by water, and on the fourth side by a busy highway. Lizards in the study populations nearly all (> 85%) mature and die in a single year, allowing me to track the fate of each individual lizard in the population to estimate survival.

Experimental design

I studied selection on male lizards in all years and on all islands, but owing to time constraints in the field, I measured selection on females only during 2003 (Kidd Cay) and 2005 (Flamingo bay and Kidd cay) (Table 1). I captured all lizards for the selection study during spring (May–June) from 2003 to 2005. Upon capture, all lizards were sexed (males have enlarged post-anal scales), weighed with a Pesola spring scale (to the nearest 0.1 g) and measured snout-vent-length (SVL; to the nearest mm). Hind and forelimb lengths were measured with dial calipers from the point of insertion into the abdomen to the femoral-tibial and humero-radio-ulnar joints. I made all measurements later during the day of capture, with no knowledge of habitat use. Lizards were marked with unique combinations of coloured elastomer dye, injected in the ventral side of the hind and forelimbs (Nauwelaerts et al., 2000). Tags were not visible to predators and served as permanent and unique identification in the wild, allowing me to track the fate of every individual over the course of the study. Lizards were released to natural plots at their original point of capture within 4 h. On experimental plots (see below), lizards were transplanted to nearby study islands and released

Table 1 Experimental design listing density treatments and the sexes measured on each study island for 2003–2005.

Year	Island	Treatment	Sex measured	n before selection	n recaptured
2003	GE	NL	M	171M	21M
2003	KC	NL	M, F	133M, 99F	44M, 35F
2004	KC	EL	M	98M	32M
2004	FBC	EH	M	93M	27M
2005	KC	NL	M, F	111M, 130F	47M, 37F
2005	FBC	EH	M, F	106M, 93F	31M, 14F
2005	NC	EH	M	98M	26M

The final two columns show sample sizes for each sex prior to and after selection.
FBC, Flamingo bay cay; NC, Nightmare cay; KC, Kidd cay; GE, Great Exuma; NL, natural low density; EL, experimental low density; EH, experimental high density; M, male; F, female.

randomly with respect to body size (lizards from both natural and experimental plots were held for the same amount of time in plastic buckets to control for any unforeseen effects of containment).

In addition to measuring lizards, I also surveyed variation in habitat type on each island. A drought occurred during 2004 and naturally accentuated this variation. Although obviously not an *a priori* expectation of this study, I present data from this natural experiment to show the effects of climate variation on habitat use by lizards. I recorded inter-annual variation in the diameter of perches used by each lizard at the point of capture from 2002 to 2005. Following Rand (1964, 1967), habitat-use by lizards that were in motion when first sited was not recorded. Because lizards were experimentally introduced from Great Exuma to Flamingo bay and Nightmare cays, potential perch diameters used by lizards on these two cays were measured before experimental introduction, based on *c.* 500 randomly chosen perch sites across 15 randomly selected 1 m^2 plots on each cay. Although these quadrat-based estimates provided descriptive information about the vegetation potentially available to lizards, they failed to capture variation in habitat actually used by study animals. Perch data recorded during lizard capture are more representative of the actual range of habitat used by individuals during this study and are reported here to document changes in habitat use among years.

Study sites were carefully selected based on habitat type. Exuma and Kidd cay contain both broad diameter trees (e.g. palms *Pseudophoenix* spp. and Australian Pine *Casuarina equisetifolia*), and narrow-diameter scrub (e.g. sea-grape *Coccoloba uvifera* and buttonwood *Conocarpus erectus*). By contrast, Nightmare and Flamingo bay cays are dominated by scrubby vegetation with fewer trees. Consequently the mean and variance in available perches on Exuma and Kidd cay were higher than on the other cays [mean (SE): Exuma 2.57 mm (0.82), Kidd cay 6.9 mm (0.58), Flamingo bay 0.92 mm (0.14) and Nightmare cay 0.57 mm (0.06)]. Previous reports from these cays indicate that they are capable of sustaining large numbers of *A. sagrei* (Spiller *et al.*, 1998; Schoener *et al.*, 2000; Losos *et al.*, 2001), and are similar in both their general ecology (e.g. precipitation, temperature) and their proximity to the main island of Great Exuma (*c.* 500 m offshore).

Not all study sites were included in each year of the study (Table 1). During 2003, I studied selection on the main island of Great Exuma and the near-shore Kidd cay. Studies on Kidd cay continued in 2004 and 2005, but in 2004 I replaced the Exuma site with a second off-shore cay (Flamingo bay cay) because of ongoing real estate development on Exuma. During 2005, I measured selection on a third off-shore cay (Nightmare cay). I report estimates of natural selection on lizard limb morphology (corrected for body size) from these seven separate selection studies. Univariate estimates of den-

sity-dependent selection on body size (SVL) are reported by (Calsbeek & Smith, 2007) but that study did not account for the differences in habitat use or limb length studied here.

Natural selection

I estimated selection on lizards naturally present at all study sites during 2003 and on Kidd cay during 2005. However, I manipulated population densities on Kidd cay and Flamingo bay cay during 2004, and on Flamingo bay cay and Nightmare cay during 2005 (Table 1), by removing all lizards naturally present on those islands and replacing them with lizards captured from an adjacent site on Great Exuma. Complete details regarding density manipulations are provided elsewhere (Calsbeek & Smith, 2007). Briefly, I introduced $n = 93$–170 lizards to each of the different cays to produce four low-density ($\bar{X} = 0.135 \pm 0.01$ SE lizards/m^2) and three high-density ($\bar{X} = 0.361 \pm 0.11$ SE lizards/m^2) populations. Calsbeek & Smith (2007) described an intermediate 'medium' density treatment that is pooled here with the high-density category. I make this distinction here to simplify the present analyses comparing habitat and density categories, whereas Calsbeek & Smith (2007) were concerned with the effects of continuous variation in population density on natural selection. Density treatments were designed to mimic the natural range in densities experienced by *A. sagrei* in the Bahamas. Total sample size over the course of this study was 1132 lizards, of which 322 were females and 810 were males.

I estimated viability selection each fall, 4 months after the initial lizard captures, by recapturing all surviving lizards on each island. I conducted censuses of surviving lizards each day by walking multiple transects over the entire study site. Lizards were recaptured by hand or using a silk noose tied on the end of a fishing pole. Most surviving lizards at each site were recaptured within 2 or 3 days. To maximize recapture efficiency of surviving lizards, censuses continued for 2 weeks or until three consecutive days of searching failed to turn up new individuals. Lizards not recaptured during the censuses were considered to have died. This is a reasonable assumption since conducting the study on small islands likely limited any potential for dispersal off the study sites.

I measured the strength of selection on limb length after controlling for variation in body size using parametric statistics on standardized traits. I used mixed-model analyses of variance with population density, perch diameter, limb length, SVL, island, and year effects, with island as a random factor. All statistical models were checked for significant overdispersion of data; none was detected. The degree of multi-colinearity among traits was assessed by estimating variance inflation factors (Petraitis *et al.*, 1996). All tests were two-tailed and were

performed using JMP v6.0.2 for the Macintosh. Analyses were conducted separately for males and females.

I accounted for the effects of body size in selection analyses in several different ways. First, SVL was included in statistical models as a covariate. Second, I computed residuals from the regression of limb length on body size and use residual variation rather than raw limb length in a separate model. Although this topic is still debated, results from ANCOVAs are generally preferred over residuals (Darlington & Smulders, 2001; Garcia-Berthou, 2001; Freckleton, 2002). For completeness and to facilitate comparison with previous studies, I present results from both analyses here. Finally, to better account for potential colinearity among traits, I also reduced the dimensionality of these data into their first two principle components (PC), and then repeated the selection analyses on these summary variables (Lande & Arnold, 1983).

Selection differentials and gradients were calculated from the regression coefficients of standardized fitness (individual fitness standardized by the population mean) and standardized traits (mean zero, unit variance) (Lande & Arnold, 1983). Linear (β) and quadratic (γ_{ii} and γ_{ij}) terms were estimated from separate models (Brodie et al., 1995). Linear and correlational selection gradients are reported as equivalent to their respective partial regression coefficients, whereas stabilizing and disruptive gradients (and associated standard errors) were doubled (Phillips & Arnold, 1989). Because survival has a binomial distribution (live/die), I calculated significance values for selection differentials and gradients using logistic regression (Janzen & Stern, 1998). I performed selection analyses on the pooled data set across all years and study islands, and then investigated significant effects by performing separate analyses for high and low density plots, and for lizards living on broad and narrow perches. Statistical models were compared by checking all possible model subsets and choosing parameters that minimized the Akaike information criterion (AIC) score (Akaike, 1987). Models that reduced that AIC score by at least two points were considered superior to other models. Variation in perch diameters on Nightmare and Flamingo bay cays was too low to make estimates separately for these high-density sites compared with low density sites. To account for this and at the same time control for potential island effects, I analysed the role of density, perch diameter and hind limb length separately for Kidd cay, the study island for which sample sizes were largest, and which also had a higher variation in available perching diameters.

Visualizing fitness surfaces has proven a useful tool for understanding how variation in phenotypes influence survival (Phillips & Arnold, 1989; Schluter & Nychka, 1994; Brodie et al., 1995; Svensson & Sinervo, 2000). Traditionally, fitness surfaces are plotted as a component of fitness (e.g. survival, reproductive success) on the vertical axis with covarying phenotypic traits on hori-

zontal axes. I extended this method slightly by visualizing interactions between limb length and environmental variables (i.e. population density and perch diameter) against survival. Methods used here to plot individual fitness surfaces are identical to methods used when considering only fitness and phenotypic traits (Schluter & Nychka, 1994). All morphological and environmental variables were first standardized to have a mean of zero and unit variance. I then used projection pursuit regression to estimate nonparametric fitness surfaces. The best-fit cubic spline was found by first performing a grid search over a range of possible values for the smoothing parameter λ, and selecting the value of λ that minimized the generalized cross-validation score (Schluter & Nychka, 1994).

Results

Lizards showed significant variation in habitat use over the course of this study. Perching diameters used by lizards living in scrubby vegetation (i.e. perches < 10 mm diameter) decreased from 2002 to 2004 and then began to increase again during 2005 (ANOVA $F_{2,154} = 5.39$, $P = 0.005$; Fig. 1). By contrast, the diameter of mature vegetation (i.e. perches > 10 mm diameter) used by lizards did not change significantly during the study (ANOVA $F_{2,61} = 1.61$, $P = 0.18$; Fig. 1). Differences in
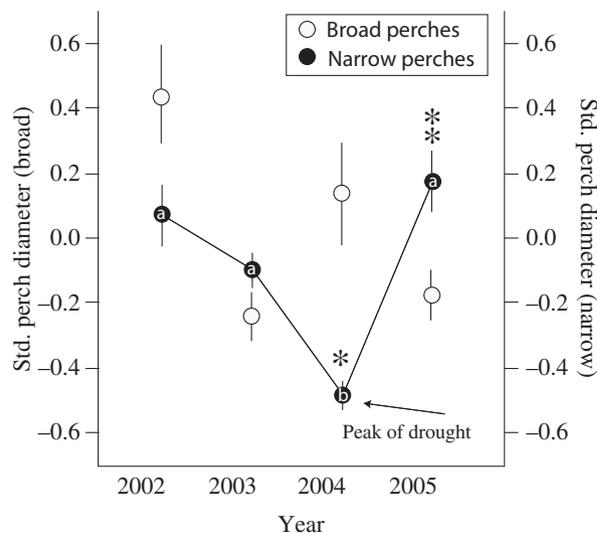
Fig. 1 Variation in broad (> 10 mm) and narrow (< 10 mm) perches used by lizards among years. Inter-annual variation in narrow perches was significant in *post hoc* tests, and perch diameters attained a minimum during 2004, when a severe drought affected the islands of the Bahamas. Broad diameter vegetation (characteristic of mature trees etc…) was not significantly affected. Points show mean values (+ SE) and significant differences are indicated by an *. Lower case letter denote significant differences from Tukey–Kramer *post hoc* tests.

narrow diameter vegetation used during 2004 remained significantly different from other years in *post hoc* tests.

Average survivorship each year from the time I marked sub-adult lizards in spring to the fall censuses was approximately 28%. I analysed linear and quadratic forms of selection on hind and forelimb lengths separately for each island and for each year and subsequently examined the overall patterns of variation with population density, and population (Table 2). These hierarchical analyses revealed strong interaction effects between selection and density, but no affects of the category for year and only a weak effect of island (which was likely an indirect effect of density). I subsequently pooled the data across years, including island and year as factors. The full statistical model including sex, hind limb length, forelimb length, SVL, island, year, density and perch diameter revealed significant effects of selection on all variables or combinations of variables except forelimb length (Table 3). Moreover, AIC scores (Akaike, 1987) were not improved by including forelimb length or interactions with forelimb length in the models. I therefore excluded forelimb length from all subsequent selection analyses. The resulting model again revealed that the strength of natural selection was tied to interactions between hind limb length and density and between the quadratic effect of hind limb length and perch diameter in males. Selection on females was only

significant for SVL (Table 4). For this reason, descriptions of natural selection on limb length deal hereafter only with males.

To understand the relative importance of population density and perch diameter, I repeated the above analysis separately for high and low-density treatments and for lizards on broad and narrow perches. At high density, there were no significant differences among years in selection on hind limb length (Fig. 2a; $P = 0.75$). The selection differential for hind limb length was strong and directional, favouring lizards with longer hind limbs ($s = 0.29 \pm 0.09$, $\chi^2 = 10.10$, $P < 0.001$); however, the selection gradient (β) on hind limb length was not significant when I accounted for variation in body size by including SVL as a covariate ($\beta = 0.18 \pm 0.19$, $\chi^2 = 0.98$, $P = 0.32$). Results were qualitatively similar when I estimated selection on size corrected values (residuals) of limb length ($s = 0.09 \pm 0.09$, $\chi^2 = 0.86$, $P = 0.35$). There was no significant quadratic selection on raw limb length at high density, but I detected stabilizing selection on size corrected residual values ($\gamma_{1,1} = -0.27 \pm 0.14$, $\chi^2 = 4.07$, $P = 0.04$). In low density populations, there were highly significant between-year differences in the quadratic selection gradient for hind limb length (ANCOVA hind limb^2 × year $F_{2,501} = 4.78$, $P = 0.009$), and there was no difference in the effect of SVL among years ($P = 0.97$). Selection on limb length was disruptive

Table 2 Selection differentials (*s*; first line) and gradients (β/γ; second line) calculated separately for each island and year (island abbreviations as in Table 1).

Population (year)	Hind limb (s_1/β_1)	Forelimb (s_2/β_2)	($\gamma_{1,1}$)	($\gamma_{2,2}$)	($\gamma_{1,2}$)	SVL
GE 2003	0.004 (0.09)	0.01 (0.09)	−0.24 (0.14)	−0.08 (0.16)	**−0.32 (0.16)***	−0.01 (0.87)
	0.03 (0.15)	0.04 (0.12)	−0.20 (0.12)	−0.08 (0.14)	**−0.32 (0.15)***	−0.07 (0.15)
KC 2003	0.11 (0.15)	0.06 (0.15)	**0.56 (0.22)****	**0.38 (0.22)***	**1.16 (0.62)**+	0.04 (0.15)
	0.35 (0.37)	0.05 (0.28)	0.50 (0.39)	**0.05 (0.32)**+	**1.16 (0.65)**+	−0.34 (0.38)
FBC 2004	0.28 (0.17)	0.18 (0.17)	0.06 (0.21)	−0.02 (0.22)	−0.34 (0.54)	0.03 (0.17)
	0.52 (0.28)	0.19 (0.28)	−0.24 (0.26)	0.10 (0.28)	−0.43 (0.54)	−0.50 (0.29)
KC 2004	−0.16 (0.18)	−0.11 (0.17)	**0.62 (0.22)****	**0.56 (0.22)****	0.04 (0.37)	−0.04 (0.17)
	−0.32 (0.29)	−0.18 (0.29)	0.66 (0.32)	0.08 (0.32)	0.13 (0.37)	0.36 (0.35)
FBC 2005	**0.55 (0.15)*****	**0.45 (0.16)*****	−0.04 (0.26)	−0.01 (0.26)	0.71 (0.86)	**0.59 (0.15)*****
	0.03 (0.51)	−0.22 (0.32)	0.28 (0.44)	0.21 (0.36)	0.94 (0.86)	0.75 (0.49)
KC 2005	−0.21 (0.17)	−0.19 (0.17)	−0.30 (0.26)	0.08 (0.22)	**−1.17 (0.72)**+	**−0.28 (0.16)**+
	−0.02 (0.37)	0.02 (029)	−0.62 (0.36)	0.38 (0.32)	−1.13 (0.72)	**−0.29 (0.35)**+
NC 2005	0.14 (0.16)	0.17 (0.16)	0.12 (0.24)	0.02 (0.22)	**−2.32 (1.27)**	0.21 (0.16)
	−0.37 (0.48)	0.09 (0.37)	0.38 (0.46)	−0.24 (0.42)	**−2.30 (1.27)***	0.47 (0.43)
Interaction effects						
Island	***	*	+	NS	NS	
Year	NS	NS	NS	NS	NS	
Density	***	***	+	*	*	

Standard errors of each estimate are shown in parentheses. Linear and quadratic terms were calculated from separate models. Differentials correspond to the regression coefficient of survival against the standardized trait of interest, whereas gradients are partial regression coefficients from models that also included the remaining limb character as well as snout-vent-length (SVL). Coefficients (and standard errors) for stabilizing ($\gamma_{1,1}$) and disruptive selection ($\gamma_{2,2}$) were doubled (Phillips & Arnold, 1989). Interactions between each estimate of selection with island, study year and population density are shown at the bottom of the column. Relevant cells are highlighted in bold.
+, 0.09–0.06, *, 0.05–0.01, **, 0.009–0.001, ***, < 0.001.

Table 3 Full model test of selection on standardized traits as a function of standardized perch diameter and population density.

Source	d.f.	Sum of squares	F-value	P-value
Hind	1	0.45	0.18	0.67
Fore	1	0.19	0.08	0.78
SVL	1	8.32	3.35	0.06
Year	2	24.01	4.84	0.008
Density	1	21.40	8.63	0.003
Sex	1	3.71	1.49	0.22
Perch	1	28.99	11.69	0.0007
Hind × Fore	1	0.95	0.38	0.54
Hind × Island	3	5.62	0.76	0.52
Hind × Year	2	7.11	1.43	0.24
Hind × Density	1	0.47	0.19	0.66
Hind × Perch	1	0.27	0.11	0.74
Hind × SVL	1	6.25	2.52	0.11
Hind^2	1	8.02	3.23	0.07
Hind^2 × Density	1	9.41	3.79	0.05
Hind^2 × Year	2	22.10	4.45	0.01
Hind^2 × Island	3	26.39	3.55	0.01
Fore × Island	3	2.50	0.33	0.80
Fore × Year	2	2.42	0.49	0.61
Fore × Density	1	1.01	0.41	0.52
Fore × Perch	1	1.65	0.67	0.41
Fore × SVL	1	0.91	0.37	0.54
Fore^2	1	0.27	0.11	0.74
Fore^2 × Perch	1	0.08	0.03	0.86
Fore^2 × Year	2	0.20	0.04	0.96
Fore^2 × Density	1	0.17	0.07	0.80
Fore^2 × Island	3	4.10	0.55	0.65
Perch × Density	1	30.53	12.31	0.0005
Perch^2	1	27.61	11.13	0.0009
Perch^2 × Density	1	27.08	10.92	0.0010

Total sample size was 1132 lizards.
hind, hind limb length (mm); fore, forelimb length (mm); SVL, snout-vent-length (mm); perch, perch diameter (mm). The random factor island had a variance component of 0.01 and was not significant. Note the highly significant effects of perch diameter, density, and their interactions.

Table 4 Linear (β) and nonlinear (γ) selection coefficients from (a) male ($n = 810$) and (b) female ($n = 322$) survival on standardized morphology, population density and perch diameter pooled across all sites and years.

Source	β/γ	SE	F-value	P-value
(a) Males				
Intercept	1.45	0.15	9.64	< 0.0001
Hind limb	0.15	0.11	1.48	0.14
Density	0.78	0.22	3.55	0.0004
Perch diameter	0.83	0.24	3.48	0.0005
SVL	−0.04	0.11	−0.40	0.69
Perch × Density	1.32	0.38	3.48	0.0005
Hind × Density	0.18	0.07	2.73	0.0064
Hind × Perch	−0.04	0.07	−0.67	0.50
Hind^2	0.019	0.04	0.44	0.66
Hind^2 × Perch	−0.087	0.05	−1.72	0.09
Hind^2 × Density	−0.045	0.05	−0.88	0.34
(b) Females				
Intercept	2.20	1.71	1.29	0.20
Hind limb	0.07	0.10	0.72	0.47
Density	0.55	1.58	0.35	0.73
Perch diameter	2.14	4.08	0.52	0.60
SVL	0.18	0.08	2.39	0.02
Perch × Density	3.28	5.52	0.59	0.55
Hind × Density	0.05	0.08	0.60	0.55
Hind × Perch	−0.18	0.14	−1.35	0.18
Hind^2	−0.06	0.07	−0.87	0.39
Hind^2 × Perch	0.09	0.13	0.69	0.49
Hind^2 × Density	0.047	0.06	0.73	0.47

Linear and nonlinear gradients were calculated from separate model. Note that selection on females was only significant for body size, and only at high density. Abbreviations as in Table 1.

during 2003 and 2004, but became weakly stabilizing during 2005 (Fig. 2b–d). Together, these results generated a significant interaction between the selection gradient on limb length and population density ($\gamma_{1,2} = 1.32 \pm 0.32$, $\chi^2 = 15.98$, $P = 0.0001$; Fig. 3) indicating that directional selection on limb length increased with increasing population density. These relationships were not significant on size corrected values.

To reduce the dimensionality among these traits, and to account for potential confounds arising as a result of multicolinearity, I computed PC of the morphological traits used in selection analyses (Table 5). Body size, hind- and forelimb lengths all loaded positively on the first principal component, indicating that PC1 was largely a size axis. By contrast, whereas body size loaded positively on PC2, both limb traits loaded negatively, indicating that PC2 described limb length relative to body

size. In a result consistent with the above analyses, I detected directional selection favouring larger values of PC1 at high density ($\beta = 0.25 \pm 0.08$; $\chi^2 = 8.88$, $P = 0.003$), but not at low density ($\beta = 0.01 \pm 0.08$; $\chi^2 = 0.03$, $P = 0.87$), and this difference was significant (PC1 × Density $F_{1,800} = 3.98$, $P = 0.04$). Similarly, I detected quadratic selection on PC2 at both high and low density, but the form of selection differed. At high density, selection on PC2 was stabilizing ($\gamma_{2,2} = -0.32 \pm 0.14$; $\chi^2 = 7.02$, $P = 0.008$) and at low density selection was disruptive ($\gamma_{2,2} = 0.28 \pm 0.10$; $\chi^2 = 6.83$, $P = 0.009$). This difference was again significant (PC2^2 × Density, $F_{1,798} = 14.99$, $P = 0.0001$).

To understand the importance of perch diameter apart from density, I analysed the role of perch diameter and hind limb length separately for low-density Kidd cay, the study island for which sample sizes were largest, and which also had higher variation in available perch diameters (see the Methods). Lizards experienced nearly significant inter-annual variation in linear and significant inter-annual variation in quadratic selection on hind limb length (year × hind limb $F_{2,315} = 2.74$, $P = 0.06$; year × hind limb^2 $F_{2,315} = 4.49$, $P = 0.01$; covariate for SVL $P = 0.89$). Lizards perching in narrow diameter
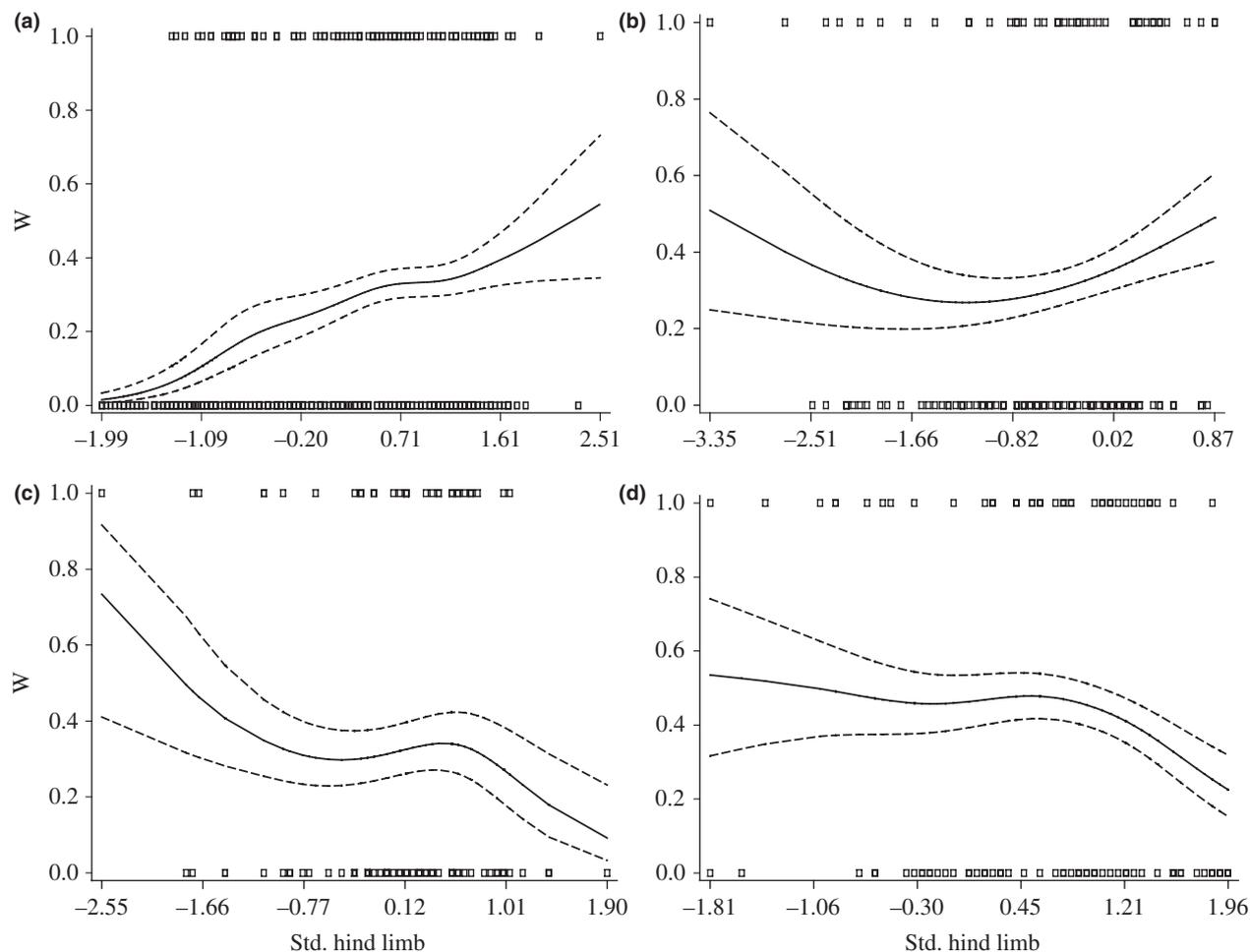
Fig. 2 Panels shows univariate fitness functions for viability selection on standardized hindlimb length (mean zero, unit variance) on (a) high density plots, and year effects on low density plots during (b) 2003 (c) 2004 and (d) 2005. All panels show the best-fit cubic-spline (solid line) and 95% confidence intervals (hatched lines) from 500 bootstrap replicates. At high density, selection favoured longer limbs on all plots and there was no variation between years, and at low density, significant fitness minima for intermediate length hind limbs reveals the action of disruptive selection during 2003 and 2004, but not during 2005.

vegetation experienced significant disruptive selection on hind limb length during both 2003 and 2004 ($\gamma_{1,1} = 0.58 \pm 0.22$, $\chi^2 = 7.02$, $P = 0.007$; covariate for SVL $P = 0.31$) and nonsignificant stabilizing selection during 2005 ($\gamma_{1,1} = 0.34 \pm 0.28$, $\chi^2 = 1.73$, $P = 0.18$; covariate for SVL $P = 0.76$). Similar to effects measured in the pooled data set, year effects were significant when analysed separately for lizards perching on narrow diameter vegetation (year × hind limb $F_{2,257} = 3.57$, $P = 0.02$; covariate for SVL $P = 0.99$), but there was no significant effect of year itself ($P = 0.16$), nor of any interaction between year and hind limb length for lizards on broad perching surfaces ($P = 0.4$). None of the gradients was significant on size corrected residuals, but results were significant and again indicated disruptive selection when analysed using the second principle component (PC2 $\gamma_{2,2} = 0.35 \pm 0.13$; $\chi^2 = 5.92$, $P = 0.02$).

Finally, I measured a weak but significant correlational selection gradient between hind limb length and perch diameter. The gradient revealed one selective optimum on broad perching surfaces for hind limb lengths near the population mean, and a second optimum that favoured lizards with shorter limbs on more narrow diameter perches ($\gamma_{1,2} = -0.18 \pm 0.09$, $F_{1,319} = 3.69$, $P = 0.05$; Fig. 4).

Finally, I compared the strength of linear (beta) and quadratic (gamma; stabilizing and disruptive) selection as a function of population density across all study islands. This analysis considers individual selection gradients as the unit of observation. Results of selection on body size were reported previously (Calsbeek & Smith 2007) and so here I report only the selection differentials on body size. The strength of directional selection on body size increased with increasing population density
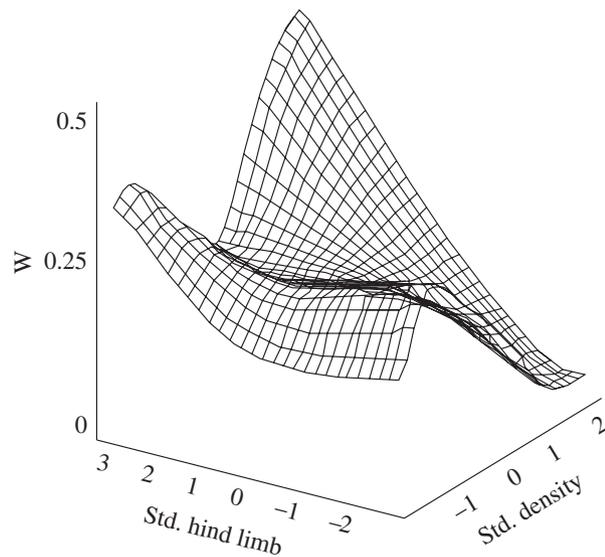
Fig. 3 The nonparametric fitness surface shows survival (W) as a function of hind limb and density. Similar to the panels in Fig. 1, note the presence of disruptive selection at low density, favouring lizards with long and short limb lengths, while at high density, selection became directional and favoured only long limbs. The surface was generated using projection pursuit regression and was fitted with a cubic spline (Schluter & Nychka, 1994).
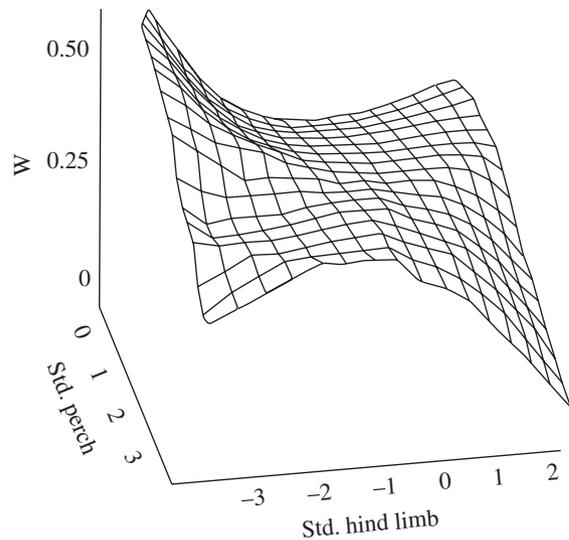

Fig. 4 The nonparametric fitness surface shows correlational selection between limb length and perch diameter and was generated using the cubic spline. The surface was generated using survival data from Kidd Cay only to avoid the confounding effects of experimental density treatments on other islands. Selection on narrow perches tended to favour lizards with relatively short hind limbs, but on broader perches, selection was stabilizing and favoured limb lengths close to the population mean.

Table 5 Factor loadings for the first two principle components revealed that PC1 was largely a size axis while PC2 described limb length relative to body size (SVL).

Factor loadings	PC1	PC2
SVL	0.57	0.73
Hind limb	0.59	−0.05
Forelimb	0.57	−0.67
Eigenvalue	2.54	0.26
Per cent	84.80	8.96
Cum per cent	84.80	93.76

($F_{1,8} = 13.43$, $P = 0.006$). There was no relationship between linear or nonlinear selection on limb length and population density ($P > 0.71$). However, the non-linear gradients calculated using size-corrected limb length residuals showed a significant relationship with density ($F_{1,8} = 12.80$, $P = 0.007$). The relationship was negative indicating disruptive selection on relative limb length at low density and stabilizing selection on relative limb length at high density.

Discussion

I have shown that population density and habitat use play central roles in driving natural selection on body and limb morphology in *Anolis* lizards. Selection on limb length was only significant for males. Selection on female morphology was limited to directional selection for larger

female body size at high population density, an effect I interpret as evidence for competition among females in high-density populations (Calsbeek & Smith, 2007; Calsbeek, 2008). In addition, selection on male morphology was variable among years, but most of this variation occurred in low-density populations. At low population density, selection on hind limb length ranged from disruptive to stabilizing over the 3-year course of this study. At high density, directional selection for larger male body size overwhelmed the pattern of selection on hind limb length (a pattern I also observed using size corrected residuals). Selection on hind limb length was directional at high density, tending to favour males with longer limbs (i.e. there was a highly significant selection differential for limb length), but the gradient (i.e. partial regression coefficient) fell short of what is conventionally considered statistically significant ($P = 0.07$). In contrast to selection at low density, patterns of selection at high density were invariable among years.

These patterns suggest that natural selection may act on at least two discrete axes of morphological variation in this system. Selection on limb morphology acts to increase the fit between an individual and the habitat that it occupies, but the importance of this effect appears to be context dependent. At high population density, selection arising from competitive interactions (Calsbeek & Smith, 2007) increased the intensity of selection for larger body size, and this swamped the effects of habitat

use that may otherwise have contributed to selection on limb length. However, at low population density, the strength of competitive interactions was reduced, effects of density-dependent selection were ameliorated, and I was able to observe natural selection on limb length as a function of habitat use. The lack of between-year variation in the selection gradient at high density indicates that effects of density-dependent competition are relatively stable, at least over short-time scales.

By contrast, annual variation in selection at low density suggests the possibility that changes in habitat structure and use (Fig. 1) alter the strength and form of selection arising from habitat use. Great Exuma experienced drought conditions and a die back of vegetation during the second year of this study (2004), but during 2005, a return to more normal rainfall levels appears to have altered the structure of lizard habitat (R. Calsbeek, W. Buermann & T. B. Smith, unpublished). This natural experiment, arising out of inter-annual variation in rainfall, allowed me to test the importance of habitat differences to selection. Changes in the form of selection appear to be congruent with observed differences in vegetation structure among years that were likely linked to changes in precipitation. The fact that between-year differences in the strength of selection were most evident in narrow diameter vegetation is consistent with this interpretation, as changes in rainfall would likely have greater impacts on scrubby vegetation like shrubs and grasses, than it would have on broad diameter vegetation like tree trunks and branches.

One caveat to this study is that although I measured selection across a range of population densities, these manipulations could not be replicated *within* islands. This is because performing low-density manipulations on Nightmare and Flamingo bay cays would have compromised sample sizes and rendered estimates of the selection gradient useless (Phillips & Arnold, 1989; Brodie et al., 1995). Although I included 'island' as an effect in statistical models, it is impossible to rule out the possibility that the patterns reported here arise because of some property of island that is as yet unaccounted for. One example of such an affect is the greater diversity of habitat types available on Kidd cay (see island descriptions in the Methods). The greater variation in perch diameters may have reduced competition for habitat and led to relaxed selection on body size. The additional variation in perch diameters would further explain the stronger selection on limb length, a trait known to underlie variation in locomotor performance on broad vs. narrow perches (Losos, 1990; Losos et al., 1994; Calsbeek & Irschick, 2007). This supports the hypothesis that resource overlap drives competition and hence density-dependent natural selection.

The lack of significant selection on female morphology provides further support for these interpretations. Like males, female anoles exhibit intrasexual aggression and defend home-ranges (Andrews & Summers, 1996), but

they are more furtive than males, and perch lower down, nearer the ground (Butler et al., 2000). This has led others to the conclusion that habitat-driven diversification has been sex-specific (Butler et al., 2000). Our results support this assertion and suggest a possible mechanism: competition among females at high density favours larger female body sizes, but increased use of perch sites nearer the ground alleviates selection on limb morphology that is experienced only by males.

Few tools better illustrate the outcome of natural selection acting on phenotypes than the adaptive landscape (Lande, 1977, 1979; Arnold et al., 2001). Wright's conception of the adaptive landscape (Wright, 1932) depicted fitness variation in terms of potential combinations of genotypes, with peaks on the surface corresponding to high fitness gene combinations, and valleys corresponding to maladaptive combinations (e.g. hybrids). An alternative version of this surface, replacing combinations of genotypes with phenotypes (the individual fitness surface) has proven exceptionally useful for understanding adaptation in natural populations (Phillips & Arnold, 1989; Schluter & Nychka, 1994; Brodie et al., 1995). Rather than illustrate selection in terms of interacting morphological traits, here I showed fitness variation in terms of the interactions between limb length and two important environmental variables, population density and perch diameter. Although perch diameter is clearly part of the lizards' environment, it may also be considered a behavioural character in the sense that perch diameter could reflect habitat choice by lizards (Johnson et al., 2006). If habitat preference is heritable, then the selective landscape depicted in Fig. 4 could have evolutionary consequences for perch use. The conceptual link connecting population density with the lizard phenotype may be more complex, although relationships between morphology and density have been demonstrated in a variety of taxa (Both et al., 1999; Sinervo et al., 2000; Donohue et al., 2001; Bolnick, 2004), and covariance between density and phenotypes would lead to fitness variation similar to that illustrated in Fig. 3 (Sinervo et al., 2000).

The correlational selection gradient illustrated in Fig. 4 demonstrates that lizards with different limb lengths are adapted to different perch diameters (Johnson et al., 2006; Calsbeek & Irschick, 2007). Lizards on narrow diameter perches are selected to have relatively short limbs, whereas lizards on broad diameter perches are selected to have intermediate limb lengths closer to the population mean. These patterns are roughly congruent with patterns observed among species in the adaptive radiation of anoles in the Greater Antilles, where long-limbed species occupy broader diameter perches compared with shorter-limbed species (Williams, 1983; Losos, 1990; Losos et al., 1994, 2001; Losos & Miles, 2002; Langerhans et al., 2006). One difference between this and previous studies is that some of the results here include the influence of size *per se* (i.e. size corrected analyses using residual limb lengths were, in most cases,

nonsignificant). However, the analyses using principal components account for this effect and still reveal the importance of selection on limb length relative to body size. The fitness surface in Fig. 3 suggests that the importance of habitat use in driving selection on limb morphology may be limited to conditions of low population densities, since at high density, competition almost completely overwhelmed selection on limb length.

Theoretical models have suggested that competition may limit diversity on small islands (Buckley & Roughgarden, 2006), thus high population density and intense competition may, in some scenarios, limit diversification rates once populations on newly colonized islands reach a threshold size. New lizard colonists on small cays could experience high rates of morphological diversification that might facilitate expansion into novel habitats (a process analogous to ecological release; Cox & Ricklefs, 1977; Kohn, 1978; Terborgh & Faaborg, 1973). However, as population sizes increased, an increase in density-dependent selection on body size would constrain further adaptive change on this island. Such a scenario may have partially influenced the current diversity of ecomorphs in the Greater Antilles.

Variation in fitness, whether arising from competition or differences in habitat use, may help to explain the adaptive radiation of anoles if traits under selection contribute to the evolution of reproductive isolation (e.g. ecological speciation (Doebeli & Dieckmann, 2003; Orr & Smith, 1998; Rundle & Nosil, 2005; Schluter, 2000)). There is currently no evidence to either support or reject the hypothesis that such a process is occurring on islands in the Bahamas. However, congruence between the agents of selection measured here, and the eco-morphological correlations in anoles, suggests the strong possibility that traits like limb-length and body size are involved in speciation. Differences in habitat type or population density on different islands may result in selection for alternative morphologies, particularly if the alternative selection regimes are stable through time. Other work in these study populations has shown that limb length and body size are also subject to strong sexual selection (Calsbeek & Bonneaud, 2008), which may further contribute to isolation. Future studies should aim to resolve the contributions of ecology and selection, both natural and sexual, to reproductive isolation.

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