

EXPERIMENTALLY REPLICATED DISRUPTIVE SELECTION ON PERFORMANCE TRAITS IN A CARIBBEAN LIZARD

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A central theme underlying studies of adaptive radiation is that ecologically mediated selection drives diversification. However, demonstrating the ecological basis of natural selection and linking this process to patterns of morphological diversity represents a formidable challenge. This is because selection experiments that test correlations between an organism's phenotype and its ecology are difficult to perform in the wild. Previous studies of *Anolis* lizards have shown that divergent morphologies are correlated with habitat use and have evolved repeatedly on islands throughout the Greater Antilles. Here, we show that the forms of selection acting within a species support an ecological mechanism for diversification. In natural populations, performance-related traits such as limb length are subject to correlational and disruptive selection driven by differences in habitat use. Experimental manipulations in the wild verify the same pattern of selection and indicate that both the targets and forms of selection are consistent through time. Elsewhere, we have demonstrated that these traits are heritable and should therefore evolve in response to selection. Our results provide evidence for the short-term repeatability of selection and its potency in the diversification of anoles.

KEY WORDS: *Anolis* lizard, disruptive selection, island, performance, selection gradient.

Disruptive selection occurs when the extremes of a phenotypic distribution experience a fitness advantage over intermediate forms (Thoday 1958). Disruptive selection can occur when extreme phenotypes are specialized to highly divergent resource types (Smith 1993; Schluter 1995,1996) or when frequency-dependent competition for a single resource causes a depression in the fitness of the population's mean phenotype. Interest in disruptive selection has a long history (Rueffler et al. 2006) owing to its potential for generating and maintaining biological diversity (Mather 1955; Smith 1962), including polymorphism (Smith 1993; Van Doorn and Dieckmann 2006) and for potentially driving speciation. However, there have been relatively few empirical demonstrations of disruptive selection in nature (Smith 1993; Bolnick 2004), especially compared to linear (e.g., directional) forms (Kingsolver et al. 2001).

There are several potential explanations for why studies of disruptive selection have lagged behind directional or stabilizing forms of selection. First, measuring nonlinear selection generally requires larger sample sizes compared with measures of linear selection (Brodie et al. 1995) and may therefore be logistically more difficult to measure. Second, many quantitative genetic models of evolution are built on a framework of weak stabilizing selection, under the assumption that chronic natural selection should move most populations toward their selective optima (Lande 1980; Hoekstra et al. 2001) and hold them there. Thus, it is possible that few studies begin with the a priori hypothesis that disruptive selection should be operating. However, it is still unclear how frequently stabilizing selection actually operates in natural populations (Kingsolver et al. 2001) as experimental tests of the assumption are lacking.

Finally, it may be that disruptive selection is simply rare in natural populations.

Anolis lizards in the Greater Antilles provide an exceptional opportunity to test for the action of disruptive selection in nature, because the well-documented correlations between morphology, performance, and habitat use among species of anoles (Williams 1983; Losos 1990; Losos et al. 1994, 2001; Losos and Miles 2002; Langerhans et al. 2006), suggest the action of disruptive selection in driving species level diversification. The adaptive radiation of *Anolis* lizards is one of the most extraordinary vertebrate radiations known (Schluter 2000). Nearly 150 species of anole have speciated on Caribbean islands and comprise roughly six morphospecies termed as “ecomorphs” (Williams 1983). The diversification of ecomorphs is correlated with habitat use; relatively longer limbed lizards occupy habitats characterized by broad perching surfaces, whereas relatively shorter limbed lizards occupy more narrow perches.

Performance differences on alternative perching diameters have been well documented (Calsbeek and Irschick 2007). Long-limbed lizards on broad perches run faster than do short-limbed lizards, but short limbs enhance agility on narrow perches (Losos 1990; Losos et al. 1998). Performance differences on alternative perching surfaces may be important in both foraging and escape from predators (Losos et al. 2004). Although phenotypic variation in limb length might arise from genetic variation (Thorpe et al. 2005) and/or phenotypic plasticity (Losos et al. 2000), both may be adaptive and subject to natural selection (West-Eberhard 2003; Le Galliard et al. 2004). The repeated evolution of similar ecomorphs on different islands has thus been widely attributed to natural selection on habitat use (Losos et al. 1997; Schluter 2000), and different performance optima on broad and narrow perches are thought to drive selection for long and short limbs, respectively.

Whereas natural selection has long been espoused as the principle agent of diversification in the Greater Antilles *Anolis* radiation (Williams 1983; Losos 1990; Losos et al. 1994, 2001; Losos and Miles 2002; Langerhans et al. 2006), less is known about natural selection at the population level (Ogden and Thorpe 2002; Thorpe et al. 2005; Calsbeek and Smith 2007). Here, we capitalize on the fact that performance differences on alternative perching surfaces allow us to make specific predictions regarding the form of selection on phenotypic variation in different habitats. We test the hypothesis that intraspecific variation in limb length is shaped by disruptive selection with selective optima for long-limbed lizards on broad perches and short-limbed lizards on narrow perches, ultimately leading to adaptive differences on alternative perching surfaces.

Methods

Anolis sagrei is a small (40–70 mm snout-vent-length; SVL) semi-arboreal lizard with a broad tropical and subtropical distribution.

It is the most common anole in the Bahamas and a member of the “trunk-ground” ecomorph in the Greater Antilles adaptive radiation. We studied wild populations of *A. sagrei* during 2003 and 2004 on a small island in the Bahamas. Initial lizard captures took place each spring during May and June on Kidd cay, an offshore island connected to the mainland by a > 80 m cement causeway supporting no lizard habitat. All lizards were sexed, weighed with a Pesola spring scale (nearest gram) and measured for SVL (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. All measurements were made by one observer (RC), without prior knowledge of habitat use. Lizards were marked with unique combinations of colored elastomer dye, injected in the ventral side of the hind and forelimbs (information available at www.nmt-inc.com). Tags serve as permanent identification in the wild, allowing us to track the fate of every individual over the course of the study.

SELECTION STUDIES

During spring 2003, we captured 133 male and 100 female subadult *A. sagrei* that were naturally present on Kidd cay, a small (~0.084 km²) island near Great Exuma, Bahamas. Kidd cay contains both broad diameter vegetation like palm trees (*Pseudophoenix* spp.) and Australian pine trees (*Casuarina equisetifolia*) (mean perch diameter = 230 mm), and narrow diameter vegetation such as sea-grape (*Coccoloba wifera*), sea hibiscus (*Hibiscus tiliaceus*), and buttonwood (*Conocarpus erectus*) (mean perch diameter = 25 mm). We chose this site because broad and narrow perches are thought to be the ecological force driving the diversification of anoles (Losos et al. 1997; Schluter 2000). All lizards from Kidd cay were uniquely marked with elastomer dye, measured, and were released at their original point of capture. We also measured characteristics of the habitat (i.e., perching diameter, nearest mm) 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 and Irschick 2007).

During 2004, we repeated our study as in 2003, but all ($N = 104$) male *A. sagrei* lizards were removed from Kidd cay and replaced with males ($N = 97$) from an adjacent study island. None of the other *Anolis* species (*A. angusticeps*, *A. distichus*, and *A. carolinensis*) were removed from the island, nor were any female *A. sagrei*. Thus, the presence of interspecific competitors and the density of females were left unchanged. This manipulation introduced naive lizards to the island, and was performed to control for potential effects of prior local adaptation to the habitat on Kidd Cay.

We measured viability selection on 330 lizards over the four-month period from first capture in spring to our population censuses conducted in autumn. This time frame encompasses survival to sexual maturity and the end of the lizards' first breeding

season, and is an estimate of one component of fitness (survival). Each day we walked multiple transects over our entire study site and captured surviving lizards. Lizards were marked with a small spot of white paint to prevent recapture. Censuses can be considered exhaustive because although the majority of surviving lizards were captured within the first two days at each plot, censuses continued for two to three weeks, or until three consecutive days of searching turned up no new marked lizards. Lizards that were not recovered during our censuses were considered dead; a reasonable assumption given that emigration from islands is rare, except during hurricanes (Calsbeek and Smith 2003), none of which affected our study islands during this study.

We measured the strength of linear (i.e., directional, β) and quadratic (i.e., stabilizing/disruptive $\gamma_{1,1}$ or correlational $\gamma_{1,2}$) selection in each population using separate regressions of limb length against survival to each fall census. We calculated relative fitness (standardized by the population mean) separately for each sex. All trait distributions were standardized to mean zero and unit standard deviation. Because the dependent variable "survival" was binomially distributed (live/die), we report significance values of each selection gradient from a logistic regression that accounts for binomial error variance (Janzen and Stern 1998). In our initial analyses, we also estimated selection on residual limb-length (SVL) to control for body size (Table 1).

Selection surfaces were computed using projection pursuit regression and were fitted using the cubic spline (Schluter 1988), a nonparametric technique for visualizing multivariate selection (Phillips and Arnold 1989; Schluter and Nychka 1994; Brodie et al. 1995; Blows et al. 2003; McGlothlin et al. 2005). This method makes no a priori assumptions about data distribution. To find the best-fit cubic spline, we searched a range of possible smoothing parameters (λ) to find the value of λ that minimized the generalized cross validation (GCV) score. We then used this λ to plot the best-fit cubic spline to survival data separately for each year.

Results

VIABILITY SELECTION ON MORPHOLOGY

We recaptured 44 of the 133 males (33%) and 38 of the 100 females (38%) that we marked during 2003. Based on differences in individual survival on broad and narrow perches, we found nonlinear natural selection on morphology of males but not females. We measured significant disruptive (i.e., concave) selection on male hind limb length ($\gamma_{1,1} = 0.22$ SE = 0.10; logistic regression $\chi^2 = 4.84$, $P < 0.03$; covariate for SVL $P = 0.61$; Table 1, Fig. 1) and nearly significant disruptive selection on male forelimb length ($\gamma_{2,2} = 0.17$ SE = 0.10; logistic regression $\chi^2 = 2.95$, $P = 0.08$; covariate for SVL $P = 0.84$; Table 1, Fig. 1). Selection did not operate on male or female body size during 2003 (males: logistic regression SVL $\chi^2 = 0.73$, $P = 0.38$; females $\chi^2 = 0.87$,

Table 1. Selection coefficients for linear (β) and nonlinear (γ) forms of natural selection acting on males during (A) 2003 and (B) 2004 and females during (C) 2003. Tables show results from standardized (mean zero, unit variance) traits including body size (standardized SVL) as a covariate. Linear and quadratic gradients were calculated from separate analyses. Note that all analyses from 2003 were robust whether we used raw or residual trait values, but residuals were not significant for 2004 (see discussion). Total sample sizes are 133 males in 2003, 97 males in 2004, and 99 females in 2003.

A				
Source for W 2003 (males)	β/γ	SE	χ^2	P
HL	0.29	0.31	0.66	0.22
FL	0.04	0.23	0.31	0.65
HL ²	0.22	0.10	4.84	0.03*
FL ²	0.17	0.10	2.95	0.09
HL × FL	0.24	0.11	5.63	0.02*
SVL	-0.11	0.33	0.73	0.75
B.				
Source for W 2004 (males)	β/γ	SE	χ^2	P
HL	-0.13	0.18	0.09	0.40
FL	-0.13	0.18	0.08	0.72
HL ²	0.29	0.08	10.35	0.001*
FL ²	0.21	0.09	5.49	0.01*
HL × FL	0.28	0.10	7.92	0.005*
SVL	0.39	0.20	7.37	0.05*
C				
Source for W 2003 (females)	β/γ	SE	χ^2	P
HL	0.13	0.17	1.27	0.43
FL	-0.04	0.18	0.27	0.82
HL ²	-0.06	0.13	0.37	0.56
FL ²	0.04	0.09	0.14	0.62
HL × FL	0.02	0.14	0.00	0.91
SVL	0.08	0.19	0.87	0.63

HL, hind limb; FL, forelimb; SVL, snout-vent-length.
Significant results are highlighted with an asterisk.

$P = 0.34$; Calsbeek and Smith 2007) indicating that we were not simply measuring disruptive selection on overall size variation. Moreover, the patterns of selection remained identical, although not significant, when we examined limb length after correcting for body size (i.e., using residuals from the regression of log-transformed limb length on log-transformed SVL; $\gamma_{1,1} = -0.17$ SE = 0.11; logistic regression $\chi^2 = 3.19$, $P = 0.07$). We did not detect any significant selection on female limb morphology, or any linear (i.e., directional) component to selection on males. The difference in selection on males and females was also significant (hindlimb × sex ANCOVA $F_{1,227} = 2.27$; $P = 0.02$). When we combined limb traits in a multivariate analysis, we found significant correlational selection on male hind and forelimb length ($\gamma_{1,2} = 0.24$ SE = 0.11; logistic regression $\chi^2 = 5.63$, $P < 0.02$; Covariate for SVL $P = 0.75$; Table 1, Fig. 1). Results remained

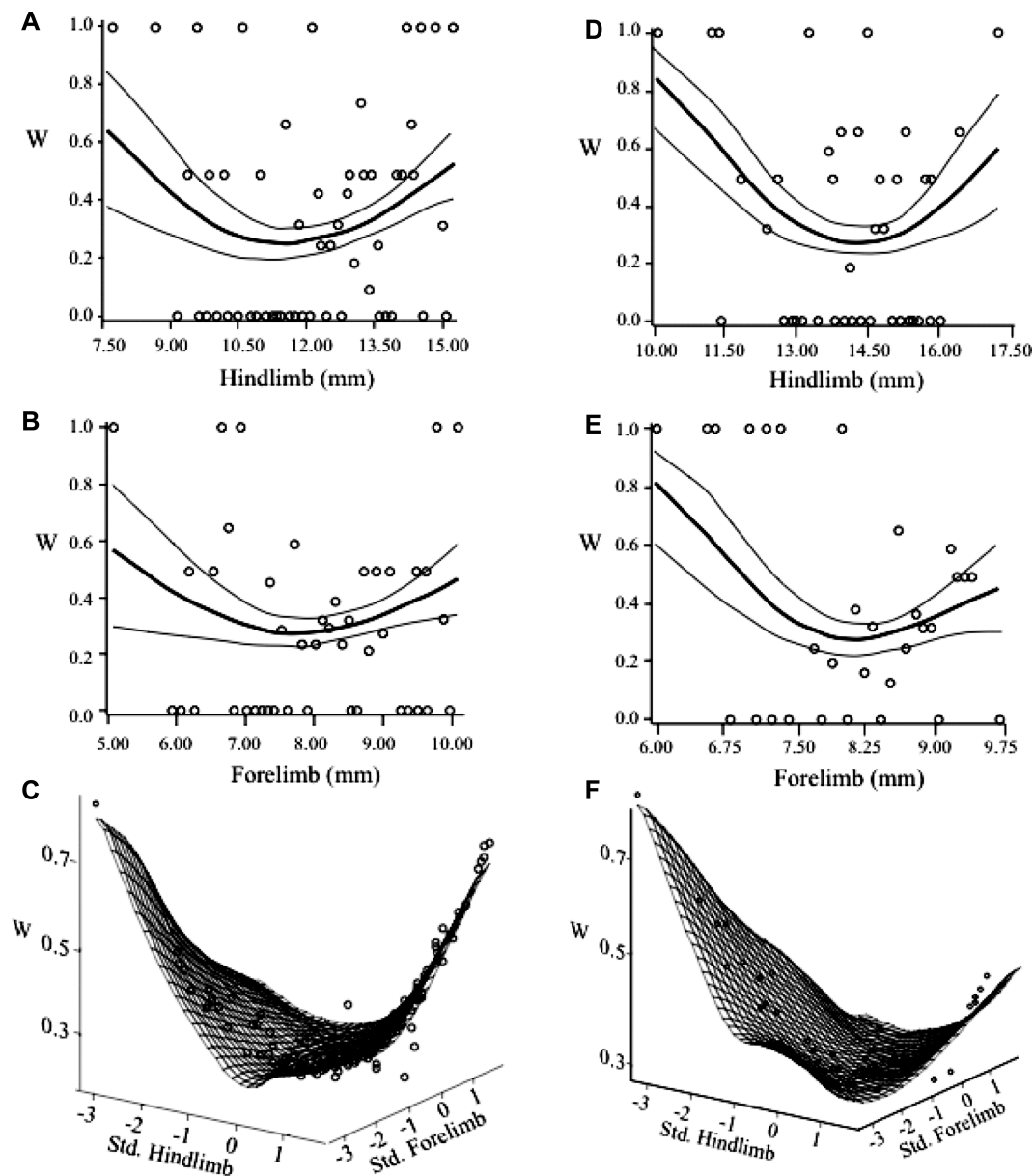


Figure 1. Panels (A–C) show fitness surfaces for individuals (males only) captured from natural populations and censused four months later during 2003. Panel A shows disruptive selection on hindlimb length, (B) disruptive selection on forelimb length, and (C) correlational selection on standardized hind and forelimb lengths in natural populations. Panels D–F show congruent fitness surfaces for male lizard experimentally introduced to Kidd cay during 2004 following the removal of the natural population. No linear terms were significant in either year of our analyses. Note the congruence in all aspects of the fitness surfaces between years, showing that the action of selection is consistent (repeatable) across time. Fitness surfaces were estimated using the nonparametric regression methods of Schluter and Nychka (1994), the cubic spline, and are graphical representations of the selection gradients reported in the text. W represents fitness (probability of survival to maturity) and datapoints were estimated by resampling using the cubic spline approach. Standard hind- and forelimb lengths are standardized limb length (mean zero, unit standard deviation). Univariate surfaces show the spline (heavy line) computed using raw trait values with 95% confidence intervals (light lines) generated from 1000 bootstrap replicates.

significant when we used size-corrected measures of limb length (i.e., residuals ($\gamma_{1,2} = 0.29$ SE = 0.16; logistic regression $\chi^2 = 4.14$, $P < 0.04$).

Both the targets and forms of selection acting on limb length during our experiment in 2004 were remarkably similar to mea-

surements made in natural variation during 2003. We recaptured 32 of the 97 males (33%) in our experiment, and again measured significant disruptive selection on hind limb length ($\gamma_{1,1} = 0.29$ SE = 0.08; logistic regression $\chi^2 = 10.35$, $P < 0.001$; covariate for SVL $P = 0.04$ Table 1, Fig. 1) and significant disruptive

selection on male forelimb length ($\gamma_{2,2} = 0.21$ SE = 0.09; logistic regression $\chi^2 = 5.49$, $P = 0.01$; covariate for SVL $P = 0.11$; Table 1, Fig. 1). Results were not significant for size residual values of limb length (e.g., $\gamma_{1,1} = 0.07$ SE = 0.10; logistic regression $\chi^2 = 0.49$, $P = 0.48$). During 2004, we measured disruptive selection on male body size ($\gamma_{1,1} = 0.108$ SE = 0.035; logistic regression $\chi^2 = 7.37$, $P < 0.007$; Calsbeek and Smith 2007). In addition, correlational selection again acted on the covariance between male hind and forelimb lengths (although not the residuals), favoring the same successful trait combinations in our experiment as we measured in natural variation during 2003 ($\gamma_{1,2} = 0.28$ SE = 0.10; logistic regression $\chi^2 = 7.92$, $P < 0.005$; covariate for SVL $P = 0.05$; Table 1, Fig. 1; residual limb-lengths $\gamma_{1,2} = 0.01$ SE = 0.17; logistic regression $\chi^2 = 0.01$, $P = 0.95$).

The distribution of perch diameters used by lizards in our study was nonnormal with a few extreme values representing large perch diameters. We log transformed the data to test whether morphology was correlated with habitat use. Following transformation, we detected a positive relationship between body size and perch diameter, although this relationship was not statistically significant (log perch diameter vs. SVL $r^2 = 0.02$, $F_{1,191} = 3.51$, $P = 0.06$).

Discussion

We have demonstrated several important elements of selection operating in *A. sagrei* from the Bahamas. In both years of our study, the action of disruptive and correlation selection was consistent with long-standing predictions based on eco-morphological correlations among species of anole. Results based on residual limb-lengths were only significant during 2003, suggesting that selection was likely acting on limb length and body size together during 2004. However, this should not detract from the general conclusion that limb length, and in some cases body size per se, are important to fitness. The same was not true for females however. We did not detect any selection on female morphology, a result that is consistent with previous work (Calsbeek and Irschick 2007) showing that locomotor performance is under very weak selection in females compared with males.

Differences between males and females likely arise owing to sex-specific differences in habitat use (Butler and Losos 2002; Butler et al. 2007), males being more likely to occupy elevated perching sites, whereas females are more often found on the ground. Differences in selection between years, particularly the difference pertaining to selection acting only on limb length versus selection acting on both body size and limb length, may be related to a variety of causes. Previous studies have shown strong selection on body size arising due to competitive interactions at high density (Calsbeek and Smith 2007). Densities on the island used in this study were similar during 2003 and 2004 and thus

competition is not likely to explain this difference. Another possibility is that there was some intrinsic difference in morphology in the two years. Because animals were experimentally introduced during 2004, this may have changed the nature of selection in that year. Indeed, the lizards introduced to our study site in 2004 were from an interior portion of Great Exuma, where habitats were uniquely comprised of narrow diameter vegetation. Although not significantly different in body size, the 2004 cohort was slightly smaller compared to lizards from 2003, but had slightly longer limbs (data not shown). This difference may partially explain the higher adaptive peak during 2004 that favored lizards on narrow perches (Fig. 1F). Finally, precipitation levels during 2004 were extremely low relative to 2003 and may have changed the nature of selection owing to differences in vegetation structure, prey availability, water balance, or a combination of these factors (Calsbeek et al., unpubl. ms.).

Correlational selection represents selection on the covariance between traits (Brodie 1992), and acts to bundle together successful trait combinations and cull unsuccessful trait combinations from the population. In this case, correlational selection was disruptive and had two optima, one favoring male lizards with both long hind and forelimbs and another favoring lizards with short hind and forelimbs. These selective optima correspond to alternative broad and narrow perching diameters, respectively, and are consistent with our predictions regarding the role of ecological natural selection on lizard morphology that are based on performance studies (Losos 1990; Calsbeek and Irschick 2007).

Congruence in the fitness surfaces between years is consistent with the hypothesis that the adaptive landscape of *A. sagrei* is sculpted by the action of natural selection on traits important for habitat use, and illustrates both the mechanism of ecological diversification and the consistent action of natural selection over the two years of our study. However, chronic natural selection will only lead to an evolutionary response if the traits under selection have a genetic basis (Endler 1986). The variation in body size we report here may have both ontogenetic and genetic sources. Laboratory-based estimates of narrow sense heritability from *A. sagrei* captured on Great Exuma during 2004 and bred under common garden conditions, have shown significant additive genetic variance in limb length (e.g., data for hindlimb $h^2 = 0.77 \pm 0.23$; Calsbeek and Bonneaud, unpubl. ms.). Moreover, hind and forelimb lengths were genetically correlated ($G = 0.64 \pm 0.32$, $P < 0.08$; Calsbeek, unpubl. data), possibly the result of correlational selection acting on these traits (as illustrated in Fig. 1C, F). We also know, based on recapture rates from 2003 to 2004, that a low percentage of individuals survived between years (< 5%) and that selection was measured on separate cohorts of lizards. It is likely that continuous egg laying by anoles results in a range of hatching dates that may span several months. However, the size range of individuals in our study (~ 7 mm; Fig. 1) was equivalent to that of

individuals raised in the laboratory and that hatched on the same day. Although previous studies have shown that variation in these traits may also have a plastic component (Losos et al. 2000), plasticity is also subject to selection and could reflect an adaptive response to differences in habitat use. The role of plasticity in speciation is still not well understood (West-Eberhard 1989; Schlichting and Pigliucci 1998). However, our results clearly implicate disruptive selection on heritable fitness variation as an important part of the diversification of anoles.

Recent meta-analyses of natural selection (Hoekstra et al. 2001; Kingsolver et al. 2001; Hereford et al. 2004) suggested that linear selection is reported far more often than nonlinear and/or correlational forms of selection, owing to both publication bias and the inherent difficulty in measuring complex fitness surfaces (Blows and Brooks 2003). However, the potential importance of disruptive and correlational selection to speciation (Kondrashov and Kondrashov 1999) underscores the need for additional studies of both forms of selection in the wild (Sinervo and Svensson 2002; Blows et al. 2003). It is unclear whether the patterns of disruptive and correlational selection reported here are sufficient to eventually cause speciation. Nonlinear forms of selection act on the variance and covariance among traits, but do not necessarily alter mean phenotypic values (Sinervo and Svensson 2002). Thus, divergence will only lead to speciation when accompanied by reproductive isolation, a process for which we currently have no evidence in *A. sagrei*. It is apparent that the continuous phenotypic distribution in limb length is maintained in our study populations owing to recombination of selected genotypes in each generation.

We have previously demonstrated a surprisingly high level of gene flow among island populations of *A. sagrei* in the Bahamas (Calsbeek and Smith 2003), a result that could also potentially slow the diversification of these lizards. However, divergence in fitness-related morphology among islands in the Bahamas (Losos et al. 1994; Calsbeek and Smith 2003) and elsewhere in the Caribbean (Ogden and Thorpe 2002), suggests that the strength of natural selection acting on these lizards is sufficient to eventually overcome the homogenizing effects of gene flow. Future work will need to incorporate studies of incipient reproductive isolation to better understand processes of divergence acting within populations of these lizards and its relevance to the adaptive radiation in *Anolis* lizards.

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