SEX-SPECIFIC SELECTION AND INTRASPECIFIC VARIATION IN SEXUAL SIZE DIMORPHISM

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Sexual size dimorphism (SSD) is thought to evolve due to sex differences in selection on body size, but it is largely unknown whether intraspecific variation in SSD reflects differences in sex-specific selection among populations. We addressed this question by comparing viability selection between two island populations of the brown anole lizard (*Anolis sagrei*) that differ in the magnitude of male-biased SSD. On both islands, females experienced stabilizing selection favoring intermediate size whereas males experienced directional selection favoring larger size. Thus, sex-specific selection matched the overall pattern of male-biased SSD, but population differences in the magnitude of SSD were not associated with local differences in selection. Rather, population differences in SSD appear to result from underlying differences in the environmental potential for a rapid growth, coupled with sex-specific phenotypic plasticity. Males grew more slowly on the island with low SSD whereas growth of females did not differ between islands. Both sexes had substantially lower mass per unit length on the island with low SSD, suggesting that they were in a relatively poorer energetic condition. We propose that this energetic constraint disproportionately impacts growth of males due to their greater absolute energy requirements, thus driving intraspecific variation in SSD.

KEY WORDS: Body size, directional selection, geographic variation, growth, lizard, stabilizing selection, survival.

Sexual size dimorphism (SSD) occurs when males and females of a species or population differ systematically in body size (Fairbairn et al. 2007). This widespread phenomenon is generally attributed to sex differences in the relationship between body size and survival (i.e., viability selection), fecundity (i.e., fecundity selection), and mating success (i.e., sexual selection). These individual components of fitness are thought to interact such that males and females equilibrate at separate fitness optima for body size (Price 1984; Blanckenhorn 2000, 2007). Sexual and fecundity selection have been shown to drive the evolution of SSD in numerous comparative studies (Cox et al. 2003; Lindenfors et al. 2007; Szekely et al. 2007) and population-level selection analyses (Ward 1988; Badyaev and Martin 2000; Preziosi and Fairbairn 2000). Relatively less is known about the role of viability selection in shaping SSD. Viability selection can constrain the evolution of SSD by favoring similar fitness optima in each sex (Bouteiller-Reuter and Perrin 2005) or by opposing the direction of dimorphism favored by sexual and fecundity selection

(Badyaev and Martin 2000). However, sex differences in viability selection can also drive the evolution of sexual dimorphism (Reimchen and Nosil 2004) or reinforce patterns of dimorphism favored by sexual and fecundity selection (Schulte-Hostedde et al. 2002). Here, we ask whether sex-specific viability selection favors or opposes the extreme male-biased SSD exhibited by the brown anole lizard (*Anolis sagrei*).

Despite its fundamental role in the evolution of SSD, relatively few studies have simultaneously measured sex-specific selection on body size and linked these selection pressures to SSD. Those that have done so yield a range of associations between SSD and current selection (Cox and Calsbeek 2009). In some species, males and females are subject to sex-specific stabilizing selection that maintains each sex at its respective phenotypic optimum (Preziosi and Fairbairn 2000; Fairbairn 2007). In others, stabilizing selection maintains one sex at its current size whereas directional selection on the opposite sex favors SSD (Schulte-Hostedde et al. 2002; Fernandez-Montraveta and Moya-Larano

2007). Directional selection can also favor SSD when it is relatively stronger in one sex (Ward 1988; Harvey 1990; Bouteiller-Reuter and Perrin 2005), or when it acts in opposite directions in each sex (Price 1984; Price and Burley 1994; Badyaev et al. 2000; Badyaev and Martin 2000). Annual shifts in the action of sex-specific selection, variously favoring or opposing sexual dimorphism, have also been shown to correlate with intergenerational changes in the magnitude of sexual dimorphism (Reimchen and Nosil 2004). However, other studies have concluded that patterns of current selection do not correspond to observed patterns of sexual dimorphism (Bjorklund and Linden 1993; Baird et al. 1997; Merila et al. 1997). Thus, our first goal in the present study was to determine whether current selection on body size of males and females matches the pattern of male-biased SSD observed in two island populations of *A. sagrei*.

Our second goal was to determine whether intraspecific variation in the magnitude of SSD corresponds to local variation in sex-specific selection on body size. In many taxa, SSD exhibits considerable intraspecific variation (Fairbairn and Preziosi 1994; Teder and Tammaru 2005; Roitberg 2007; Stillwell et al. 2007), often along predictable environmental or latitudinal clines (Iverson 1985; Lappin and Swinny 1999; Fox et al. 2007). In extreme instances, both the direction (i.e., male- or female-biased) and the relative magnitude of SSD can differ dramatically among populations of a single species (Pearson et al. 2002). Only a handful of studies have quantified intraspecific variation in selection among populations that differ in the expression of sexual dimorphism. Collectively, these studies suggest that the intensity of sex-specific selection is often correlated with the magnitude of dimorphism (Fairbairn and Preziosi 1994; Badyaev et al. 2000; Moller et al. 2006). However, the relationship between current selection and sexual dimorphism is often more complex (Baird et al. 1997). Here, we address this issue by comparing sex-specific selection on body size between two island populations of *A. sagrei* that differ significantly in the relative magnitude of male-biased SSD.

Our first two goals address the hypothesis that intraspecific variation in SSD reflects underlying variation in sex-specific viability selection on body size. However, even in systems in which local differences in selection have been confirmed, sex-specific phenotypic plasticity may provide a better explanation for intraspecific variation in SSD (Fairbairn 2005; Fernandez-Montraveta and Moya-Larano 2007; Stillwell and Fox 2007). Thus, our third goal was to gain insight into the potential for sex-specific phenotypic plasticity by examining the extent to which intraspecific variation in SSD reflects underlying differences in the growth and body condition of males and females from each island. To do this, we use the relationship between body mass and snout-vent length (SVL) as a measure of "body condition" to approximate energetic condition (Cox and John-Alder 2007).

We predict that, if growth is differentially constrained by limitations on the acquisition or allocation of energy, then sex and island differences in growth and body size should be accompanied by underlying differences in body condition. This would suggest that intraspecific variation in SSD arises, at least in part, due to proximate environmental differences among populations, rather than genetic responses to alternative selective regimes. Although common garden breeding studies and reciprocal transplant experiments would be required to directly quantify the environmental and genetic components of phenotypic variation (Madsen and Shine 1993; Niewiarowski and Roosenburg 1993), these approaches are beyond the scope of the present study. Instead, we discuss our selection analyses and measures of growth and body condition within the framework of two nonexclusive hypotheses: that intraspecific variation in SSD reflects (1) local differences in sex-specific selection on body size, and/or (2) local differences in energetic constraints on growth, coupled with sex-specific phenotypic plasticity.

Materials and Methods
SPECIES AND STUDY SITES

The brown anole (*A. sagrei*, Polychrotidae) is a small, semiarboreal lizard native to islands throughout the West Indies. This species always exhibits pronounced male-biased SSD (Butler et al. 2000), but the magnitude of this dimorphism varies considerably across populations (Schoener and Schoener 1980; Stamps 1999). We studied two geographically distinct populations of *A. sagrei* located on separate islands in The Bahamas. The first population is located on Kidd Cay (23°30′N, 75°45′W), a small offshore cay connected to the nearby island of Great Exuma by a narrow causeway. This population has been studied intensively since 2004 and details regarding its ecology and demography are available elsewhere (Calsbeek and Irschick 2007; Calsbeek and Smith 2008; Calsbeek et al. 2008). The second population is located on a small peninsula near The Island School on the island of Eleuthera (24°50′N, 76°19′W). These two study populations are separated by ca. 158 km of ocean and are similar in some general ecological characteristics, but different in many others. One difference that is of particular importance to the present study is that both populations exhibit strong male-biased SSD, but the magnitude of this dimorphism is substantially greater on Exuma than on Eleuthera (see Results).

Both sites include a mixture of native shrubs (e.g., sea grape, *Coccoloba uvifera*; buttonwood, *Conocarpus erectus*) and introduced trees (e.g., Australian pine, *Casuarina equisetifolia*) that comprise the majority of perching habitat used by anoles. Whereas the habitat on Exuma is a relatively heterogeneous mixture of these and other species, the habitat on Eleuthera is dominated by *Casuarina* (e.g., 70% of lizards on Eleuthera in the present study

were captured while perching on *Casuarina*). Both populations share many of the same primary predators (e.g., mockingbirds, *Mimus polyglottos* and *M. gundlachii*, green herons, *Butorides virescens*; Bahamian racers, *Alsophis vudii*) and lizard competitors (e.g., *Anolis smaragdinus, A. distichus, Ameiva auberi*). However, the predatory curly-tailed lizard (*Leiocephalus carinatus*) occurs only on Eleuthera, whereas several introduced mammalian predators (rats, *Rattus norvegicus*; cats, *Felis catus*) have been observed only on Exuma. Higher sighting and capture rates suggest that anoles are more active on Exuma than on Eleuthera (R. Cox and R. Calsbeek, pers. obs.), but this difference has not been rigorously quantified. We also currently lack detailed information on other potential differences between these sites, particularly the diversity and abundance of prey species, seasonal patterns of rainfall and temperature, and detailed comparisons of thermal microhabitats. We have no a priori expectations that the above characteristics are related to the differences in SSD that are the focus of this study. We include them only to give a representative picture of the general ecological similarities and differences between our sites on Exuma and Eleuthera.

MARK–RECAPTURE STUDIES

We conducted mark–recapture studies at both sites in 2007 and 2008. During May and early June of each year, we searched each site thoroughly and captured every visible lizard by hand or hand-held slip noose. We then measured each animal's snout-vent length (SVL, to the nearest 1 mm using a ruler) and body mass (to the nearest 0.1 g using a Pesola spring scale, Pesola AG, Baer, Switzerland). For permanent identification, we gave each individual a unique combination of colored elastomer tags (Nauwelaerts et al. 2000), injected subcutaneously into the underside of each limb so that they were invisible to predators (Calsbeek and Irschick 2007; Calsbeek and Smith 2008; Calsbeek et al. 2008). To avoid immediate recapture of marked animals, we painted a temporary color spot on each animal's dorsum. We then released each animal to its exact location of capture within 24 h of initial capture. In September, we searched each site and recaptured all surviving lizards. Because both sites are bounded primarily by water and because we searched each site exhaustively, recapture success is a reliable estimate of survival. Survivors were measured for SVL and body mass, and growth was estimated from the difference between size measurements in May and September.

We restricted our analyses to the adult portion of each population by excluding individuals that fell below the minimum size of sexual maturity at initial capture in May. We excluded all females below 38 mm SVL because this is the minimum size at which we detected oviductal eggs via abdominal palpation (Exuma and Eleuthera populations) and surgical laparotomy (adjacent populations on Exuma). We excluded all males below 40 mm SVL because this is the minimum size at which males exhibit testic-

ular enlargement (Lee et al. 1989). Males between 40 mm and 50 mm SVL comprise a transitional gradient from juvenile to adult phenotypes. During this maturational stage, males develop sex-specific dorsal coloration, nuchal and dorsal crests, and enlarged dewlaps, all of which are expressed by males larger than 50 mm SVL. Males in this transitional size class may experience different selection pressures than large adult males, so we conducted all selection analyses in two ways: including and excluding these small males. Genetic paternity analyses reveal that males smaller than 50 mm SVL do achieve reproductive success in wild populations of *A. sagrei* (R. Calsbeek, unpubl. data), so the decision to exclude these individuals is somewhat arbitrary. Thus, we focus our analyses and discussion on the more complete dataset including all males above 40 mm SVL.

We used mean adult SVL at initial capture (May) to calculate an index of SSD (Lovich and Gibbons 1992) for each population as: (mean male SVL/mean female SVL) − 1. We calculated growth over the breeding season as change in SVL between capture (May) and recapture (September). Hence, growth was only measured for those animals that survived to September. We measured viability selection on the basis of survival over this same interval. Viability selection arises from variation in survival, as opposed to variation in fecundity (i.e., fecundity selection) or mating success (i.e., sexual selection). *Anolis sagrei* females iteratively lay single eggs at ca. 10-day intervals throughout the reproductive season (March to October, Lee et al. 1989), so fecundity should be closely tied to survival over this interval. Thus, our estimates of viability selection likely capture much of the variance in fitness that is attributable to differential fecundity, although we do not consider them as estimates of fecundity selection per se.

STATISTICAL ANALYSES

Within each island population, we tested for sex differences in SVL using analysis of variance (ANOVA) with factors for sex, year, and their interaction. Within each sex, we tested for island differences in SVL using analysis of covariance (ANCOVA) with factors for island, year, and their interaction. We also analyzed SVL using ANOVA with sex, island, and year as factors with full interaction. We used this full model to determine whether SSD differed between islands by testing for a sex × island interaction. We used analogous models to test for sex, island, and year effects on body mass.

We compared survival over the breeding season (May–September) between islands and sexes using logistic regression with survival (0,1) as a dependent variable and factors for island, sex, and the island × sex interaction. These analyses were conducted separately within each year and also with data pooled across years. For these pooled analyses, year and the island × year and sex × year interactions were included in the final statistical

models. We also compared interannual survival (May 2007–May 2008) with similar logistic regressions.

We quantified natural selection on body size using conventional selection gradient analyses with SVL standardized to the population mean in units of standard deviations (Lande and Arnold 1983; Arnold and Wade 1984). We calculated relative fitness by dividing survival (0,1) by the population mean survival rate. We standardized SVL and calculated relative fitness separately within each sex, island, and year. To estimate overall selection within each sex and island, we pooled data from 2007 and 2008 and then standardized SVL and calculated relative fitness for this pooled dataset. We estimated linear (i.e., directional) selection as the regression coefficient ($\beta \pm 1SE$) for relative fitness as a function of standardized SVL. We estimated quadratic (i.e., stabilizing or disruptive) selection from the regression coefficient for relative fitness as a function of the square of standardized SVL. These quadratic models also included linear terms. Estimates of quadratic selection ($\gamma \pm 1SE$) were calculated by doubling the quadratic regression coefficient and its associated standard error (Phillips and Arnold 1989; Stinchcombe et al. 2008). Because survival is binomially distributed, we report significance values from logistic regressions that account for binomial error variance (Janzen and Stern 1998). We visualized the form of selection using cubic spline analysis (Schluter 1988).

Within each island, we tested for sex differences in the strength and form of selection using a logistic regression with survival as the dependent variable and a sex $\times$ SVL interaction term. To compare overall patterns of viability selection between sexes and islands, we conducted a logistic regression with survival as the dependent variable and standardized SVL, sex, island, and year as independent variables. We assessed overall sex and island differences in selection on the basis of sex $\times$ SVL and island $\times$ SVL interactions. Year $\times$ SVL interactions were never significant and were omitted from these models. Trait values were standardized to mean and unit variance separately within each sex, year, and island before pooling datasets.

To investigate proximate energetic constraints that might differentially impact growth between islands, we plotted $\log_{10}$ body mass as a function of $\log_{10}$ SVL. We tested for interisland differences in this measure of body condition by including a factor for island and the island $\times$ SVL interaction in these models. Because the relationship between mass and SVL differed among years, we conducted these analyses separately for each year and within each sex. For those animals that survived to the end of the reproductive season, we compared growth (change in SVL) between islands and sexes using SVL as a covariate and appropriate interaction terms (i.e., island $\times$ SVL, sex $\times$ SVL). We included initial SVL as a covariate because growth decreases with age and size. We also compared absolute growth between islands and sexes using ANOVA with change in SVL as a dependent variable (i.e., no

covariate for initial SVL). Analyses were conducted separately within each year and also with data pooled across years. For these pooled analyses, year and appropriate two- and three-way interaction terms were included in the final statistical models.

Results

SAMPLE SIZE AND SEX RATIO

On Eleuthera, we measured a total of 245 females (135 in 2007, 110 in 2008) and 209 males (100, 109). On Exuma, we measured 385 females (161, 224) and 264 males (119, 145). The adult sex ratio was biased in favor of females on each island, although this bias was not significant on Eleuthera (54% females; $\chi^2 = 2.86$; $P = 0.091$) and highly significant on Exuma (59% females; $\chi^2 = 22.69$; $P < 0.001$). We used these samples to calculate mean SVL and body mass and derive estimates of SSD and body condition. These samples also comprise the initial pool of individuals for which we measured subsequent survival to estimate viability selection. The exclusion of males smaller than 50 mm SVL from our selection analyses resulted in sample sizes of 151 adult males on Eleuthera (74 in 2007, 77 in 2008) and 223 adult males on Exuma (100, 123). The exclusion of these potentially "subadult" males resulted in highly biased adult sex ratios on both Eleuthera (62% females; $\chi^2 = 22.53$; $P < 0.001$) and Exuma (63% females; $\chi^2 = 43.69$; $P < 0.001$). Comparisons of body size, SSD, survival, demography, natural selection, growth, and body condition between these two islands are described in detail in following paragraphs and summarized in Table 1.

BODY SIZE AND SSD

Males exceeded females by 32% in mean adult SVL on Exuma ($F_{1,645} = 1431.83$; $P < 0.0001$) and by 22% on Eleuthera ($F_{1,450} = 634.33$; $P < 0.0001$; Fig. 1A). This population difference in the magnitude of SSD was highly significant (sex $\times$ island interaction: $F_{1,1095} = 62.56$; $P < 0.0001$) and entirely attributable to interisland variation in male body size. Females did not differ in SVL between islands ($F_{1,626} = 0.54$; $P = 0.46$), but males from Exuma were 8% larger than males from Eleuthera ($F_{1,469} = 61.32$; $P < 0.0001$; Fig. 1). Mean SVL was slightly greater in 2007 than in 2008 ($F_{1,1095} = 3.45$; $P = 0.06$), but this weak year effect was consistent across sexes and islands and did not influence comparisons of SSD ($P > 0.47$ for all statistical interactions with year).

Males exceeded females by 153% in mean adult body mass on Exuma ($F_{1,645} = 1056.55$; $P < 0.0001$) and by 106% on Eleuthera ($F_{1,450} = 528.29$; $P < 0.0001$; Fig. 1B). This population difference was highly significant (sex $\times$ island interaction: $F_{1,1095} = 149.57$; $P < 0.0001$) and was driven by the large interisland difference in body mass of males. Whereas body mass of females on Exuma was only 39% greater than the body mass of

Table 1. Summary of important biological parameters for two island populations of *Anolis sagrei* that differ in the magnitude of male-biased SSD. All data are combined from 2007 and 2008. Estimates of growth and body condition are derived from equations plotting growth and body mass as functions of initial SVL so that comparisons are standardized to animals of average size between populations. See text for further details.

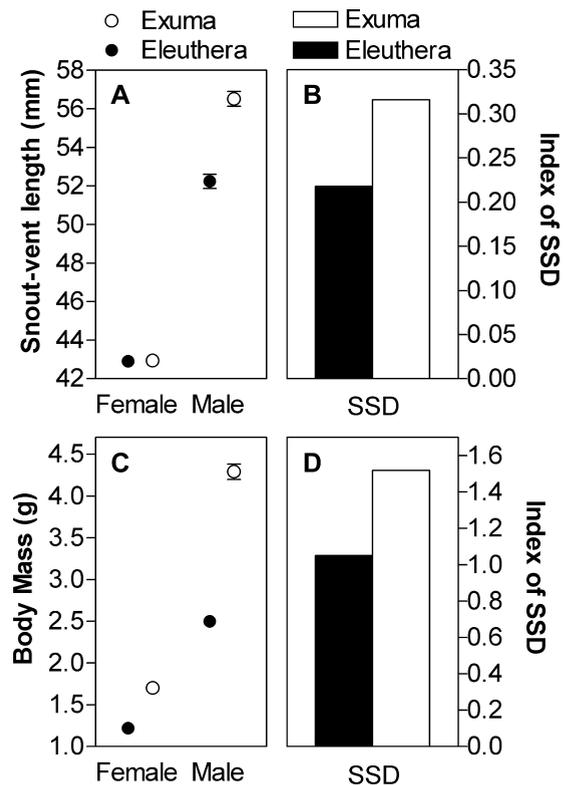|	Eleuthera	Exuma
Body size and SSD		
Mean SVL, females	42.90	42.94
Mean SVL, males	52.24	56.52
Index of SSD	0.22	0.32
Demography		
Proportion of females	0.54	0.59
Proportion of males	0.46	0.41
Proportion of first year adults	0.72	0.91
Proportion of second year adults	0.28	0.09
Survival probability		
Breeding season, females	0.39	0.34
Breeding season, males	0.42	0.31
Interannual, females	0.30	0.10
Interannual, males	0.26	0.08
Selection on body size (SVL)		
Directional (β), females	0.14	0.01
Directional (β), males	0.28	0.18
Quadratic (γ), females	−0.20	−0.24
Quadratic (γ), males	−0.06	−0.01
Growth (mm)		
Predicted growth of 43-mm female	1.16	1.39
Predicted growth of 54-mm male	1.36	4.17
Body condition (g)		
Predicted mass of 43-mm female	1.20	1.65
Predicted mass of 54-mm male	2.76	3.53

Figure 1. Panels on the left report mean (±1 SE) snout-vent length (A) and body mass (C) for adult males and females from Eleuthera and Exuma populations. Panels on the right illustrate population differences in the relative magnitude of sexual size dimorphism, which are driven by differences in body size of males.

females on Eleuthera ($F_{1,626} = 406.23$; $P < 0.0001$), body mass of males on Exuma was 71% greater than the body mass of males on Eleuthera ($F_{1,469} = 234.84$; $P < 0.0001$). Body mass was significantly greater in 2007 than in 2008 ($F_{1,1095} = 9.86$; $P < 0.002$), but this year effect was consistent across sexes and islands ($P > 0.36$ for all statistical interactions with year). Thus, for both body mass and SVL, the degree of male-biased SSD was significantly greater on Exuma than on Eleuthera, and this difference was driven by differences in the size of males, rather than females.

SURVIVAL

Survival over the breeding season (May–September) was higher on Eleuthera than on Exuma ($\chi^2 = 7.21$; $P = 0.007$; Fig. 2). This difference was driven primarily by the higher survival of males on Eleuthera (42% survival) relative to Exuma (31%), which was consistent across both years of the study (island: $\chi^2 = 6.02$; $P = 0.01$; island × year: $\chi^2 = 0.07$; $P = 0.79$). Considering both years combined, survival of females did not differ between

islands (island: $\chi^2 = 1.63$; $P = 0.20$; island × year: $\chi^2 = 3.61$; $P = 0.058$), although survival of Eleuthera females (45%) greatly exceeded that of Exuma females (32%) in 2008 ($\chi^2 = 5.10$; $P = 0.024$). Overall, survival over the breeding season did not differ between males and females ($\chi^2 = 0.06$; $P = 0.81$), although we detected a weak sex × year effect ($\chi^2 = 6.47$; $P = 0.01$). This indicates that survival of males decreased from 2007 to 2008, whereas survival of females tended to remain constant.

Interannual survival (May 2007–May 2008) was also significantly higher on Eleuthera than on Exuma ($\chi^2 = 31.25$; $P < 0.0001$). Interannual survival of females was three times greater on Eleuthera (30%) than on Exuma (10%; $\chi^2 = 18.83$; $P < 0.0001$). Interannual survival of males was also three times greater on Eleuthera (26%) than on Exuma (8%; $\chi^2 = 12.45$; $P = 0.0004$). Consequently, the age structure of the breeding population differed considerably between islands. Whereas 28% of the breeding population consisted of 2-year olds on Eleuthera, only 9% percent of the breeding population consisted of this older age class on Exuma, where *A. sagrei* is effectively an annual species. Interannual survival did not differ between males and females (sex: $\chi^2 = 0.051$; $P = 0.48$) and this pattern was consistent across islands (sex × island: $\chi^2 < 0.01$; $P = 0.99$).
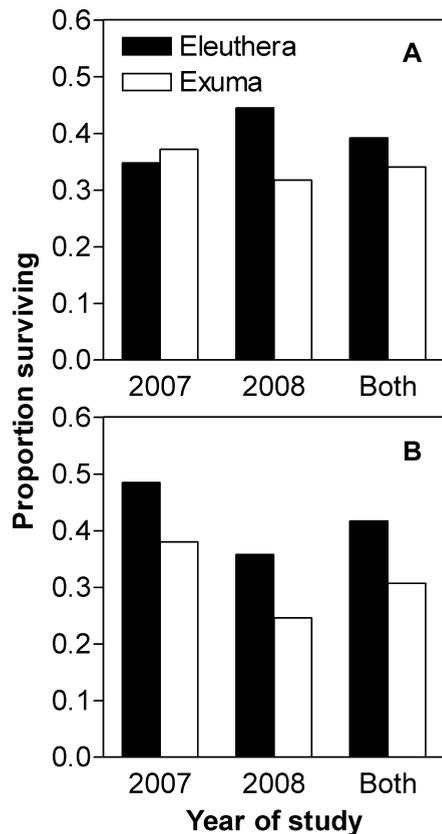
Figure 2. Proportion of marked lizards surviving over the breeding season (May–September) for females (A) and males (B) on Eleuthera and Exuma in 2007, 2008, and both years combined.

Figure 3. Top panels report linear selection differentials (±1 SE) for viability selection on snout-vent length, estimated separately for males and females in (A) 2007, (B) 2008, and (C) both years combined. Bottom panels illustrate sex differences in linear selection differentials in (D) 2007, (B) 2008, and (C) both years combined. Positive values indicate selection consistent with observed patterns of male-biased sexual size dimorphism.

SELECTION ON BODY SIZE

In 2007, directional selection on SVL favored larger males on both Eleuthera ($\beta = 0.246 \pm 0.103$; $P = 0.017$) and Exuma ($\beta = 0.328 \pm 0.115$; $P = 0.004$; Fig. 3). In 2008, directional selection favored larger males on Eleuthera ($\beta = 0.304 \pm 0.127$; $P = 0.015$), but not on Exuma ($\beta = -0.033 \pm 0.147$; $P = 0.82$). By contrast, females did not experience significant directional selection for larger SVL on either island in either year (Table 2; Fig. 3). Size of females was under strong stabilizing selection on Exuma in 2007 ($\gamma = -0.586 \pm 0.182$; $P = 0.002$), although quadratic selection was not significant for any other combination of sex, island, and year (Table 2). The sex difference in directional selection on SVL was marginally significant on Exuma in 2007 (sex $\times$ SVL: $\chi^2 = 2.92$; $P = 0.087$), but we did not detect any other significant sex differences in directional or quadratic selection on SVL within a given year and island.

Combining data from both years revealed a general similarity between islands in the strength and form of viability selection on SVL (Fig. 4; Table 2). Directional selection favored larger males on both Eleuthera ($\beta = 0.279 \pm 0.081$; $P < 0.001$) and Exuma ($\beta = 0.183 \pm 0.049$; $P = 0.045$). By contrast, directional selection for larger female size was weak on Eleuthera ($\beta = 0.143 \pm 0.080$;
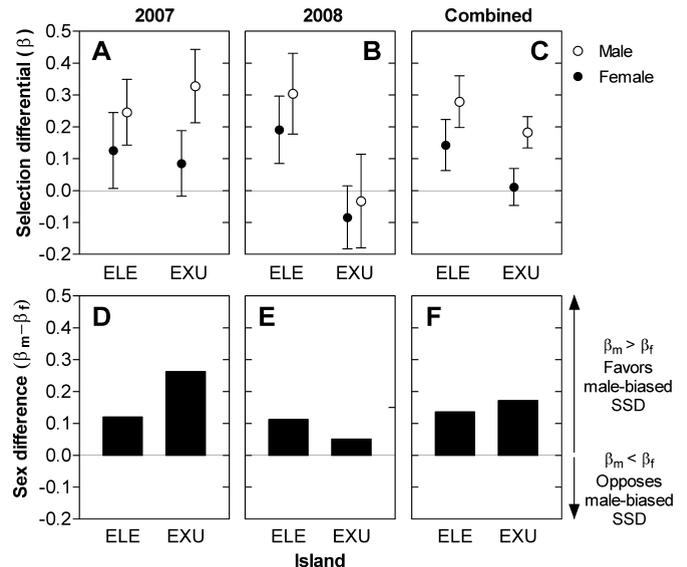
$P = 0.070$) and entirely absent on Exuma ($\beta = 0.011 \pm 0.058$; $P = 0.85$). However, females on Exuma experienced negative quadratic selection on SVL ($\gamma = -0.241 \pm 0.094$; $P = 0.008$) and a similar trend was evident on Eleuthera ($\gamma = -0.202 \pm 0.202$; $P = 0.080$). By contrast, we never observed significant quadratic selection acting on males (Table 2). Thus, males generally experienced purely directional selection favoring larger body size, whereas females tended to experience stabilizing selection favoring intermediate body size (Fig. 4). Patterns of viability selection on body mass (Table 3) were qualitatively similar to those observed for SVL, which is not surprising given that SVL and mass are highly correlated. Males experienced directional selection favoring larger body mass on both islands, whereas females experienced stabilizing selection favoring intermediate body mass on both islands (Table 3).

Combining selection data from both sexes and both islands into a single statistical model revealed a strong positive relationship between SVL (standardized separately within each sex and island) and survival ($\chi^2 = 14.49$; $P < 0.0001$). Although viability selection generally favored larger SVL, this positive directional selection was relatively stronger in males than in females (sex $\times$ SVL: $\chi^2 = 3.63$; $P = 0.057$) and on Eleuthera relative to Exuma (island $\times$ SVL: $\chi^2 = 4.15$; $P = 0.042$). Viability selection also favored larger body mass ($\chi^2 = 19.10$; $P < 0.0001$), but this overall trend did not differ as a function of sex (sex $\times$ mass: $\chi^2 = 1.94$; $P = 0.16$) or island (island $\times$ mass: $\chi^2 = 0.07$; $P = 0.79$). Overall,

Table 2. Linear (β) and quadratic (γ) selection differentials for viability selection on standardized snout-vent length (SVL). Asterisks (*) indicate significant selection (*P*<0.05), as determined by a logistic regression. Selection estimates are reported for all females above the minimum size of sexual maturity (38 mm), for all males above the minimum size of physiological maturity (40 mm), and for the subset of larger males above the size at which adult secondary sexual characteristics are fully developed (50 mm).

| Year	Island	Sex (min. SVL)	*N*	Linear selection β±1 SE	Quadratic selection γ±1 SE
2007	Eleuthera	F≥38	135	0.126±0.119	−0.148±0.192
		M≥40	97	0.246±0.103*	−0.104±0.176
		M≥50	74	0.099±0.109	0.019±0.246
	Exuma	F≥38	161	0.085±0.103	−0.586±0.182*
		M≥40	119	0.328±0.115*	−0.202±0.222
		M≥50	100	0.096±0.116	−0.016±0.200
2008	Eleuthera	F≥38	101	0.191±0.106	−0.206±0.182
		M≥40	109	0.304±0.127*	0.036±0.278
		M≥50	77	0.293±0.141*	0.126±0.236
	Exuma	F≥38	222	−0.084±0.099	−0.186±0.146
		M≥40	146	−0.033±0.147	0.104±0.262
		M≥50	123	0.007±0.162	0.200±0.254
Both	Eleuthera	F≥38	245	0.143±0.080	−0.202±0.202
		M≥40	206	0.279±0.081*	−0.064±0.156
		M≥50	151	0.182±0.087	0.069±0.164
	Exuma	F≥38	383	0.011±0.058	−0.241±0.094*
		M≥40	264	0.183±0.049*	−0.006±0.170
		M≥50	223	0.056±0.097	0.082±0.158
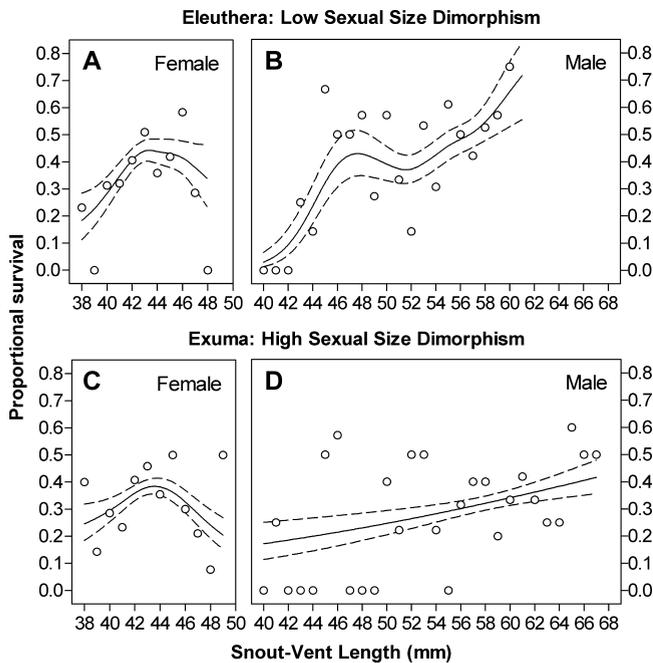
Figure 4. Fitness surfaces for survival as a function of body size in females (left) and males (right) on Eleuthera (top) and Exuma (bottom). Datapoints show the probability of survival at each size increment and are weighted in the analysis by the number of observations contributing to each estimate. Fitness functions show the best-fit cubic spline (solid line) with 95% confidence intervals (dashed lines) generated from 500 bootstrap replicates (Schluter 1988). Data from 2007 and 2008 are combined.

quadratic selection was significantly negative (i.e., stabilizing) on SVL ($\chi^2 = 11.11$; $P < 0.001$) and body mass ($\chi^2 = 6.19$; $P = 0.013$), but these patterns did not differ by sex or island.

Omitting males smaller than 50 mm SVL (see Methods) generally weakened the strength of directional selection on SVL, although selection remained significantly positive on Eleuthera in 2008 and when combining data from both years (Table 2). Quadratic selection remained weak and nonsignificant when these small males were excluded (Table 2). The exclusion of small males eliminated any overlap in body size between males and females, but it also removed most evidence of sexually antagonistic selection on standardized body size (sex × SVL: $\chi^2 = 0.42$; $P = 0.53$; data combined for both years and both islands). Thus, sex differences in selection on body size occur in part because of the low survival of small males with body sizes similar to those of females (Fig. 4). The exclusion of small males did not influence comparisons of selection between islands, which never revealed any significant difference in selection on SVL or body mass between Eleuthera and Exuma.

GROWTH AND BODY CONDITION

Males grew substantially more than did females on both Exuma ($F_{1,213} = 399.17$; $P < 0.0001$) and Eleuthera ($F_{1,199} = 681.04$; $P < 0.0001$) when including initial SVL as a covariate. Even without correcting for the negative scaling of growth and the inherent sex difference in body size, males grew absolutely more

Table 3. Linear (β) and quadratic (γ) selection differentials for viability selection on standardized body mass. Asterisks (*) indicate significant selection (*P*<0.05), as determined by a logistic regression. Selection estimates are reported for all females above the minimum size of sexual maturity (38 mm), for all males above the minimum size of physiological maturity (40 mm), and for the subset of larger males above the size at which adult secondary sexual characteristics are fully developed (50 mm).

Year	Island	Sex (min. SVL)	N	Linear selection β±1 SE	Quadratic selection γ±1 SE
2007	Eleuthera	F≥38	135	0.148±0.118	−0.148±0.180
		M≥40	97	0.239±0.103*	−0.124±0.208
		M≥50	74	0.119±0.109	0.064±0.234
	Exuma	F≥38	161	0.140±0.103	−0.540±0.166*
		M≥40	119	0.325±0.115*	−0.188±0.206
		M≥50	100	0.128±0.116	0.092±0.180
2008	Eleuthera	F≥38	101	0.202±0.106	−0.230±0.202
		M≥40	109	0.226±0.128	0.032±0.244
		M≥50	77	0.126±0.116	−0.430±0.272
	Exuma	F≥38	222	0.122±0.098	−0.210±0.168
		M≥40	146	0.075±0.145	0.112±0.278
		M≥50	123	0.114±0.165	0.238±0.246
Both	Eleuthera	F≥38	245	0.160±0.081*	−0.216±0.112*
		M≥40	206	0.227±0.083*	−0.180±0.160
		M≥50	151	0.121±0.088	−0.172±0.176
	Exuma	F≥38	383	0.128±0.071	−0.208±0.112*
		M≥40	264	0.189±0.095*	0.088±0.164
		M≥50	223	0.120±0.098	0.162±0.148

than females on both Exuma ($F_{1,215} = 16.70$; $P < 0.001$) and Eleuthera ($F_{1,202} = 11.42$; $P < 0.001$). Thus, sex differences in adult growth contribute to male-biased SSD on both islands, although earlier sex differences in juvenile growth are known to account for the extreme SSD that is observed in *A. sagrei* prior to maturation (Cox et al. 2009).

When including initial SVL as a covariate, males from Exuma grew significantly more than did males from Eleuthera ($F_{1,172} = 102.77$; $P < 0.0001$; Fig. 5). This difference in growth was observed in both 2007 ($F_{1,92} = 56.17$; $P < 0.0001$) and 2008 ($F_{1,76} = 47.33$; $P < 0.0001$). By contrast, growth of females did not differ between islands (2007: $F_{1,116} = 0.17$; $P = 0.68$; 2008: $F_{1,121} = 3.42$; $P = 0.067$; years combined: $F_{1,240} = 2.55$; $P = 0.11$). On the basis of these regressions, a male of average SVL for both populations (54 mm) would grow 4.17 mm during the breeding season on Exuma, but only 1.36 mm on Eleuthera, a threefold difference in growth. A female of average SVL (43 mm) would grow 1.39 mm on Exuma and 1.16 mm on Eleuthera, a difference of only 20%. Thus, the difference in magnitude of SSD between Eleuthera and Exuma is accompanied by a dramatic difference in growth of adult males, but not of adult females.

For any given SVL, adult lizards from Exuma weighed significantly more than adults from Eleuthera ($F_{1,1025} = 2012.80$; $P < 0.0001$; Fig. 6). This population difference in body condition was evident in both 2007 ($F_{1,611} = 790.02$; $P < 0.0001$) and 2008 ($F_{1,584} = 1458.32$; $P < 0.0001$) and within both males

($F_{1,626} = 1340.22$; $P < 0.0001$) and females ($F_{1,469} = 587.06$; $P < 0.0001$). On the basis of these regressions, a male of average SVL for both populations (54 mm) would weigh 3.53 g on Exuma and only 2.76 g on Eleuthera, a relative difference of 28%. Similarly, a female of average SVL (43 mm) would weigh 1.65 g on Exuma and only 1.20 g on Eleuthera, a relative difference of 38%. These analyses suggest that both sexes are in a substantially poorer energetic condition on Eleuthera, relative to Exuma. Despite this inferred energetic constraint on Eleuthera, differences in growth between islands are only apparent for males (Fig. 5).

Discussion

The brown anole (*A. sagrei*) is a geographically widespread species that occurs on most major islands in the West Indies. Even within smaller portions of this broad distribution, *A. sagrei* exhibits considerable geographic variation in SSD, ranging from modest dimorphism in which adult males average only 11% larger than females to extremes in which males exceed females by 34% in length (Schoener and Schoener 1980; Stamps 1999). Our two Bahamian populations span a large portion of this variation: males exceed females by 32% in mean adult SVL on Exuma, but only by 22% on Eleuthera. This difference in SSD is entirely attributable to variation in male size (Fig. 1A), a pattern that is observed in other lizards (Zamudio 1998) and which gives rise to allometry known as Rensch's Rule (Abouheif and Fairbairn 1997; Fairbairn
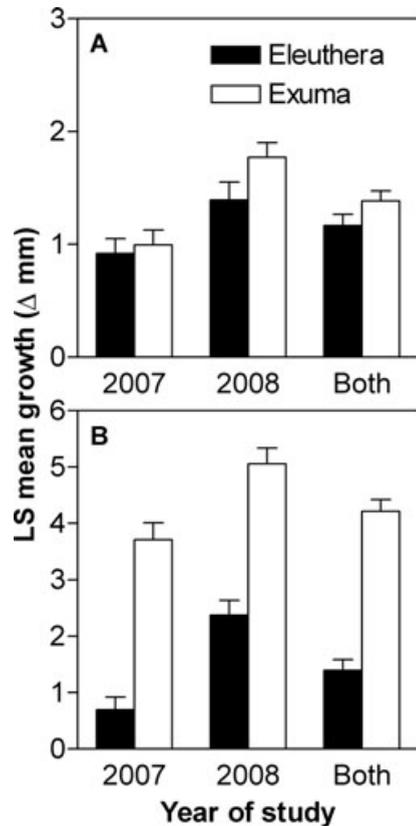
Figure 5. Growth over the breeding season (May to Sept.) for females (A) and males (B) on Eleuthera and Exuma in 2007, 2008, and both years combined. Data are least square means (+1SE) from within-sex analyses including initial SVL as a covariate. Hence, values are comparable between islands within each sex, but not between males and females. See text for statistical comparisons between males and females.

Figure 6. Log_{10} body mass as a function of log_{10} snout-vent length (SVL) for adults from Eleuthera and Exuma. Lizards from Exuma weighed significantly more per unit body length than did lizards from Eleuthera. This interisland difference in body condition was significant within each sex. Males and females are pooled here for illustrative purposes.

1997, 2005; Blanckenhorn et al. 2006). Rensch's Rule occurs when the magnitude of male-biased SSD increases with body size and/or the magnitude of female-biased SSD decreases with body size across related species or populations (Blanckenhorn et al. 2006). This pattern reflects a greater underlying variation in male size within a particular clade or species, as we observed between island populations of *A. sagrei*.

Given that variation in SSD between Exuma and Eleuthera arises almost exclusively due to variation in male size, we predicted that the strength of selection on males in particular should differ between islands. Two years of data quantifying viability selection on adult body size failed to support this prediction. In general, the strength of selection on body size was highly congruent between islands, with males experiencing directional selection for larger size and females experiencing stabilizing selection for intermediate size (Tables 2 and 3, Figs. 3 and 4). Thus, current selection favored the observed pattern of SSD in each population, similar to other dimorphic species (Price 1984; Ward 1988; Harvey 1990; Price and Burley 1994; Badyaev and Martin
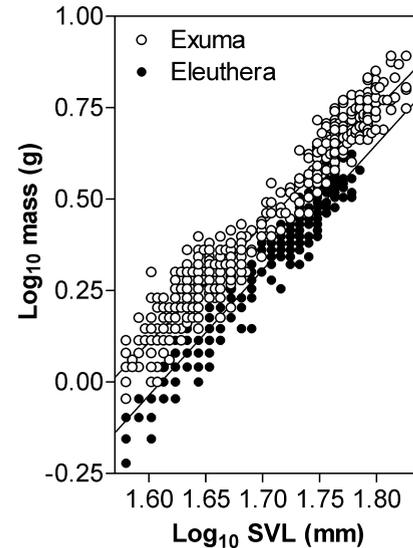
2000; Ferguson and Fairbairn 2000; Preziosi and Fairbairn 2000; Schulte-Hostedde et al. 2002; Bouteiller-Reuter and Perrin 2005; Fernandez-Montraveta and Moya-Larano 2007). However, differences in SSD between populations were not accompanied by predicted differences in selection on male body size, which is contrary to results from previous studies of intraspecific variation in selection on dimorphic traits (Fairbairn and Preziosi 1994; Badyaev et al. 2000; Moller et al. 2006). On Eleuthera, patterns of selection were highly congruent between years, with male body size consistently subject to positive directional selection. On Exuma, where males are larger and SSD is more pronounced, directional selection favored large male size in 2007, but male size was unrelated to survival in 2008. To the extent that two years of data can be considered representative of annual variation in selection, our results suggest that selection for large male body size is actually somewhat stronger and more consistent on Eleuthera, where males are nonetheless smaller and SSD is less pronounced.

Although sex-specific selection on body size was congruent between islands, we have not directly assessed the extent to which selection is acting on phenotypic variation arising from underlying genetic variation for body size. In *A. sagrei*, body size is known to be heritable within sexes (Calsbeek and Bonneaud 2008), but it is also subject to considerable ontogenetic variation due to the indeterminate growth pattern that characterizes this species (Schoener and Schoener 1978; Stamps 1999). Although males between 40 mm and 50 mm SVL are physiologically mature, they typically comprise a transitional gradient of juvenile to adult phenotypes with respect to other sexually dimorphic traits (e.g.,

coloration, dewlaps, dorsal and nuchal crests). The positive directional selection on male size that we documented is driven in part by the low survival of this size class (Fig. 4). This suggests that selection is acting on phenotypic variation that reflects both ontogenetic and genetic variation in body size. When selection acts primarily on the nonheritable component of phenotypic variation, estimates of sex-specific selection can lead to unrealistic predictions regarding the evolution of SSD (Merila et al. 1997; Kruuk et al. 2001). Nonetheless, the low viability of this transitional class implies that males of small sizes are under strong selective pressure to attain the larger sizes characteristic of adult males.

Although viability selection favors male-biased SSD in *A. sagrei* (Fig. 3), our analysis of adult survival captures only a portion of the total variation in lifetime fitness. Because female anoles iteratively produce single eggs at ca. 10-day intervals throughout the breeding season, our measure of survival encompasses a substantial amount of the variation in both adult viability and fecundity. However, we have not considered sex-specific selection arising from variation in juvenile survival or mating success of males. Indeed, comparative meta-analyses suggest that sex differences in the strength and direction of selection are typically greatest with respect to sexual selection, rather than viability or fecundity selection (Cox and Calsbeek 2009). Moreover, the evolution of SSD in lizards is due in part to the effects of sexual selection for large male size (Cox et al. 2003), which we did not quantify. Patterns of sex-specific selection arising from variation in total lifetime fitness often differ from those related to the individual contributions of viability, fecundity, and mating success (Badyaev and Martin 2000; Ferguson and Fairbairn 2000; Preziosi and Fairbairn 2000; Bouteiller-Reuter and Perrin 2005; McGlothlin et al. 2005). The relative importance of various selective episodes in generating overall sex differences in selection on total lifetime fitness could also potentially differ among populations (Badyaev et al. 2000). Therefore, it is possible that other components of fitness, particularly mating success, are related to the difference in SSD between Eleuthera and Exuma. Previous comparative studies have shown that female density, a proxy for the intensity of sexual selection (Stamps 1983), explains a significant portion of the variation in SSD across *Anolis* species (Stamps et al. 1997). However, this measure does not correlate with variation in SSD across Bahamian populations of *A. sagrei* (Stamps 1999). Either female density is a poor predictor of the intensity of sexual selection within this species, or intraspecific variation in SSD is unrelated to the intensity of sexual selection (Stamps 1999).

Our results provide no evidence that sex-specific selection on body size differs between islands, but they strongly support the alternative hypothesis that proximate environmental factors drive geographic variation in SSD. Males and females on Eleuthera weighed substantially less per unit body length than males and fe-

males on Exuma (Fig. 6), suggesting that they were in a relatively poorer energetic condition. Consistent with this interpretation, males grew substantially more on Exuma than on Eleuthera, but growth of females did not differ between islands (Fig. 5). This is precisely the pattern that would be expected if variation in SSD results from a combination of sex-specific phenotypic plasticity and geographic variation in the extent to which environmental conditions permit rapid growth. In many reptiles, growth is highly plastic and dependent upon proximate environmental conditions (Sinervo and Adolph 1989; Niewiarowski and Roosenburg 1993; Sinervo and Adolph 1994), as are the sex differences in growth that give rise to SSD (Taylor and DeNardo 2005; Cox et al. 2006, 2008). Because *A. sagrei* males are larger and grow at higher rates than females, their absolute energy requirements are greater. Hence, we predict that male growth should be relatively more sensitive to environmental variation, thus exhibiting a greater degree of phenotypic plasticity. This prediction could be tested by reciprocal transplant of anoles between Exuma and Eleuthera (Niewiarowski and Roosenburg 1993), or by raising males and females from each population in a common garden environment (Sinervo and Adolph 1989).

Sex-specific phenotypic plasticity could also reflect sex-specific developmental canalization. If body size is subject to stabilizing selection in one sex and directional selection in the other sex (e.g., Schulte-Hostedde et al. 2002; this study, Fig. 4), body size is expected to become developmentally canalized near its optimum value in the sex experiencing stabilizing selection, while remaining developmentally plastic in the sex subject to directional selection (Fernandez-Montraveta and Moya-Larano 2007). This pattern of sex-specific developmental canalization has been proposed as an explanation for intraspecific vartiation in SSD of water striders and is potentially general to other systems (Fairbairn 2005). A growing body of research supports the conclusion that variation in SSD, both intra- and interspecific, is often attributable to local variation in environmental conditions coupled with underlying sex differences in phenotypic responses to these conditions (Blanckenhorn et al. 2006; Fernandez-Montraveta and Moya-Larano 2007; Fox et al. 2007; Stillwell and Fox 2007). Our results are consistent with this "differential plasticity hypothesis" (Fairbairn 2005) for variation in SSD among island populations of the brown anole. Future work should focus on experimentally verifying sex-specific phenotypic plasticity and confirming that anoles from Exuma and Eleuthera share similar genetic potentials for growth. To elucidate the ecological context for intraspecific variation in body size, future studies should also quantify the environmental factors (e.g., energy availability, thermal opportunity, activity time) that give rise to population differences in growth and, ultimately, SSD.

In summary, we have shown that the magnitude of SSD differs substantially between two island populations of *A. sagrei*.

This difference is driven entirely by variation in the size of males. Viability selection favored male-biased SSD on both islands, with females subject to stabilizing selection and males experiencing directional selection for larger size. However, selection did not differ between islands, and thus failed to explain the observed variation in SSD. Instead, this variation apparently reflects the fact that adult males grow more slowly on Eleuthera than on Exuma. Although both sexes exhibited markedly poorer body condition on Eleuthera, relative to Exuma, the growth of females did not differ between islands. Thus, our results suggest that intraspecific variation in SSD in *A. sagrei* reflects a combination of (1) environmental variation in the energetic potential for rapid growth, and (2) sex-specific phenotypic plasticity in growth and body size. This conclusion supports a growing body of research showing that geographic variation in SSD is often attributable to local variation in environmental conditions, coupled with underlying sex differences in phenotypic responses to these conditions. This also suggests that the selective forces responsible for interspecific patterns in SSD (e.g., viability selection, sexual selection, fecundity selection; Cox et al. 2003) may be less important than alternative processes (e.g., environmental variation coupled with sex-specific phenotypic plasticity) when attempting to explain intraspecific variation in SSD. As with other complex biological phenomena, the study of SSD is best approached from an integrative framework that simultaneously addresses multiple causal explanations from both inter- and intraspecific perspectives.

ACKNOWLEDGMENTS

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