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Developmental plasticity affects sexual size dimorphism in an anole lizard

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Summary

1. While developmental plasticity has been shown to contribute to sexual size dimorphism (SSD) in laboratory studies, its role in shaping SSD variation in wild vertebrate populations is unclear.
2. Here we use a field study and a laboratory experiment to show that resource availability influences the degree of SSD among insular populations of *Anolis sagrei* lizards in the Bahamas.
3. Total amounts of food biomass explained variation in male, but not female, body size on six Bahamian islands, giving rise to significant differences in SSD.
4. Laboratory experiments on a captive colony of *A. sagrei* confirmed that variation in SSD was mediated by the effects of prey biomass on developmental plasticity in males, but not females. Indeed, males grew faster and attained larger sizes as adults under high-food treatments than under restricted diets, whereas adult females retained similar body sizes under both conditions.
5. Our results indicate that the amount of food available can influence intersexual variation in body size within a vertebrate species. Sex-specific developmental plasticity may be favoured if it allows individuals to take advantage of varying levels of food opportunities offered by different habitats, by reducing competition between the sexes. As such, plasticity in response to food availability may have played a role in the invasion success of *A. sagrei*.
6. This study adds to our growing understanding of the effect of resource availability in shaping SSD in reptiles and lends further support to the condition-dependent hypothesis, according to which the larger sex should display greater plasticity in growth in response to environmental conditions.

Key-words: *Anolis*, food availability, growth, habitat quality, islands, resources

Introduction

Sexual selection is expected to lead to phenotypic differences between the sexes (Darwin 1871; Andersson 1994). In species where intersexual differences are at least partly expressed as a difference in body size, directional selection on body size should lead to ever increasing (or decreasing) measures of body size and sexual dimorphism. However, larger body sizes are costly to produce and maintain, and under poor environmental conditions, the largest individuals may be at a distinct disadvantage (Wikelski & Thom 2000). Theory suggests that mothers should thus be selected to produce the cheaper (i.e. the smaller) of the two sexes when conditions are poor (Trivers & Willard 1973). However, there is another, less explored possibility that the larger sex is plastic in its growth, such that individuals grow more quickly to achieve large sizes when conditions permit and grow more slowly and to smaller sizes when conditions are disadvantageous (Teder & Tammaru 2005; Stillwell & Fox 2007; Stillwell *et al.* 2010).

Food availability has been shown to affect growth and adult morphology in many species, with often differing

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consequences for males and females (Roughgarden & Fuentes 1977; Post *et al*. 1999; Uhl *et al*. 2004; Le Galliard *et al*. 2006; Bonduriansky 2007). Such sex-specific responses can give rise to within-species variation in sexual size dimorphism (SSD) (Stillwell *et al*. 2010), as demonstrated by laboratory experiments on the hawkmoth *Manduca sexta* (Stillwell & Davidowitz 2010a,b), the fly *Telostylinus angusticollis* (Bonduriansky 2007) and the Mediterranean tarantula *Lycosa tarantula* (Fernandez-Montraveta & Moya-Larano 2007). In all cases, the magnitude of SSD increased under high-quality diet compared to a lower quality one, with sex differences in plasticity to environmental conditions giving rise to variation in SSD. However, we know less about the extent of intraspecific variation in SSD that can be attributed to disparities in food availability in vertebrate populations and in the wild (Krause, Burghardt & Gillingham 2003; Cox 2006; Cox & Calsbeek 2010b; Ceballos & Valenzuela 2011).

Lizards in the *Anolis* genus are particularly appropriate for studies of the links between environmental variation and SSD for two reasons. First, there is a well-established link between morphology and ecological conditions in this group (Losos 1990, 1994; Irschick & Losos 1998; Butler, Sawyer & Losos 2007). For example, longer limbed lizards tend to occupy broad perches because longer limbs increase maximum sprint speed (Losos 1990), whereas lizards with shorter limbs tend to occupy narrow perches because shorter limbs confer greater agility (Losos & Sinervo 1989; Irschick & Losos 1998). While variation in limb morphology influences locomotor performance, variation in male body size influences competitive ability. Larger males are more successful in obtaining mates because they have larger territories that overlap with the territories of more females (Trivers 1976; Jenssen & Nunez 1998), reviewed in Stamps (1983). Secondly, *Anolis* lizards exhibit varying degrees of both inter- and intraspecific SSD (Butler, Schoener & Losos 2000; Butler, Sawyer & Losos 2007; Losos 2009), with among-species variation reflecting differences in habitat types rather than phylogeny (Butler, Schoener & Losos 2000). Although females can be the larger sex in mainland anoles (Fitch 1976), island species exhibit a range of male-biased SSD, with some species being largely non-dimorphic, and others having males that are three times heavier than females (Butler & Losos 2002). In addition, across populations of a single species, males may be 10–40% larger than females (Schoener & Schoener 1980; Stamps 1999). Variation in SSD among and within *Anolis* species is thought to be primarily driven by diverging natural and sexual selection on male and female body size (Andrews & Rand 1974; Trivers 1976; Stamps 1983; Shine 1988; Jenssen & Nunez 1998; Lailvaux & Irschick 2006; Kratochvil & Kubicka 2007).

One method for understanding the broader patterns of SSD among anole species is to examine variation across populations of a single species. Because the same anole species can occur on different islands, we are then able to examine the links between food availability and level of SSD on each island. We combined data collected from such a study of natural populations with laboratory experiments to test the role of food availability in shaping SSD among populations of *Anolis sagrei*, a common anole species that displays nearly the entire range of SSD observed across Caribbean anole species (Schoener & Schoener 1980; Stamps, Losos & Andrews 1997; Stamps 1999; Vanhooydonck *et al*. 2009). First, we gathered field data to test the role of food availability in explaining variation in SSD across six Bahamian populations of *A. sagrei*. Secondly, we used laboratory feeding experiments to test the link between food availability and SSD in *A. sagrei*, as well as whether it is mediated by developmental plasticity in males and/or females.

Specifically, we addressed the following questions. (1) Can differences in food availability on different Bahamian islands explain interpopulation variation in the level of SSD? (2) Can experimental manipulation of the mass of food available give rise to variation in SSD? (3) Is variation in SSD mediated by developmental plasticity in males or in females in response to different food treatments?

Material and methods

FIELD STUDIES

We used field observations to test the role of food availability in explaining variation in SSD across six populations of *A. sagrei*. Adult males ($N = 132$) and adult females ($N = 116$) were captured on six Bahamian islands (Acklins, Andros, Grand Bahamas, Chub Cay, Pigeon Cay and Staniel Cay) over a period of 1 month between April and May 2003 (Table S1, Supporting information) [see (Vanhooydonck *et al*. 2009) for further details]. All lizards were captured by hand or by noose; sexed and snout-to-vent length (SVL) was measured using digital callipers (±0·01 mm). Animals were then released at their site of capture. Sexual size dimorphism (SSD) was calculated as the mean trait value in the larger sex (here: males)/mean trait value in the smaller sex (here: females) + 1 (Lovich & Gibbons 1992; Smith 1999; Cox & Calsbeek 2009).

We used pitfall traps and sweep netting to estimate prey availability at the six different locations where the lizards were caught to ensure that all microhabitats were sufficiently sampled for arboreal species (sampling techniques followed (Herrel *et al*. 2006). At each site, 20 pitfall traps were positioned 2 metres apart over an area of 30–50 m^2; they were set open for a total of 48 h each and emptied both after 24 h and 48 h. Pitfalls had a diameter of 15 cm and a depth of 10 cm, were positioned in known anole habitat and filled with an aqueous formaldehyde (5%) solution with a small amount of soap added to reduce surface tension. After 24 h and 48 h, all invertebrates were removed from the pitfalls and stored in a 70% aqueous ethanol solution. At each site, potential prey residing among the vegetation were sampled ten times for two minutes each using a reinforced sweep net (40 cm diameter, 75 cm long); sweeps were conducted during periods of lizard activity. Sweep samples were transferred to plastic bags and frozen upon return to the field laboratory.

All potential prey were identified to the lowest possible taxonomic level (Order or below) and grouped into morphotypes [for more information, see (Brecko *et al*. 2008)]. Only prey of type and size known to comprise the diet of anoles were included (Herrel *et al*. 2006). Prey were weighed (wet mass) using a digital microbalance (±0·01 mg). For each island, we estimated the total

numbers of prey items and the total amount of prey biomass captured per unit time. We also calculated the diversity of prey taxa per island using Simpson's diversity index, which is a measure of diversity that takes into account both richness and evenness (i.e. relative abundance) of the different taxa.

LABORATORY EXPERIMENT

We conducted a feeding experiment to test the link between food availability and SSD in *A. sagrei*, as well as whether SSD is mediated by developmental plasticity in males and/or females. The experiment took place from August 2005 to July 2007 with laboratory-reared F2 and F3 descendants of wild *A. sagrei* collected in June 2004 on the island of Great Exuma, Bahamas. Offspring were kept on *ad libitum* food supplies for the first 2 weeks of their lives to maximize survival and were then randomly assigned to either high-food (*ad libitum*) or low-food treatment. In the low-food treatment, offspring that weighed 0·5 g or less received one cricket per feeding (14% of *ad lib*), those between 0·6 and 1·1 g received two crickets per feeding (29% of *ad lib*), and those 1·2 g or greater received 3 crickets per feeding (43% of *ad lib*). These amounts were based on a preliminary study of the minimum quantities of crickets required to sustain individuals of each size category. A total of 106 offspring were included in this study, 53 in each treatment (22 males and 31 females *ad lib*; 25 males and 28 females low food). All offspring were housed in 45 L terrariums and provided with a small houseplant and full spectrum lighting on a 12-h:12-h light: dark cycle. Siblings were randomly distributed across food treatments to reduce shared-family effects on growth and morphology, and there were no intrasexual differences in SVL between those allocated to the two treatments (for each sex, initial differences in body size were examined using mixed model with family as a random factor and treatment as the explanatory variable (see Material and methods above); males: $F_{1,25} = 1{\cdot}02$, $P = 0{\cdot}322$; females: $F_{1,29} = 0{\cdot}19$, $P = 0{\cdot}667$). Body size (±0·1 mm) was measured every 14 days following the onset of the experiment until they reached 196 days of age [range in mean age at sexual maturity of female anoles: 57–279 days; (Andrews 1976)].

STATISTICAL ANALYSES

All statistical analyses were performed using SAS software version 9.3 (SAS Inc., Cary, NC, USA). For the field study, we first investigated sex differences in body size (SVL) among the 6 populations of *A. sagrei* using a general linear model (PROC GENMOD) with a normal error structure, and with sex, island and their interaction as fixed effects; in addition, pairwise population comparisons were obtained within the same model using the 'estimate' statement. Effects of food availability on male and female body size in the 6 populations of *A. sagrei* were then analysed using a general linear mixed model (PROC MIXED) with a normal error structure, by specifying sex, total prey biomass ($\log_{10}$-transformed), Simpson's diversity index of prey taxa richness and their interactions with sex as fixed effects, and island as the random effect. The same model was rerun after including total prey numbers and its interaction with sex as fixed effects. Using all three estimates of prey availability (biomass, diversity and number) helps to clarify the precise mediator of variation in SSD among populations, with diversity used to test the opportunity for niche partitioning which could explain population differences in SSD (Schoener 1967; Camilleri & Shine 1990). These three estimates of prey availability were not significantly correlated with each other (Pearson's correlations; total prey numbers and total prey biomass: $r = 0{\cdot}60$, $P = 0{\cdot}210$; total prey numbers and Simpson's diversity index of prey taxa richness: $r = 0{\cdot}63$, $P = 0{\cdot}180$; total prey biomass and Simpson's diversity index of prey taxa richness: $r = 0{\cdot}38$, $P = 0{\cdot}454$). Finally, we used Pearson's correlations (PROC CORR) to analyse correlations between SSD and total prey numbers, total prey biomass ($\log_{10}$-transformed) and Simpson's diversity index of prey taxa richness.

For the laboratory study, we first verified that *A. sagrei* lizards had been randomly allocated with respect to their body size to either of the two food treatments by running two general linear mixed model with normal error structures, for males and females separately; we specified treatment as the fixed effect and family as the random effect (see results in Method section above). We investigated differences in initial body size between males and females using a general linear mixed model with sex as the fixed effect and family as the random effect. We then examined the effects of food treatment on growth and adult body size (i.e. at 196 days of age). The sex-specific effect of laboratory treatments on adult body size was computed using a mixed model with a normal error structure, and by specifying sex, food treatment and their interaction as fixed effects, and family as a random factor. To assess the sex-specific effect of treatments on growth, we ran a mixed model with normal error structures, including sex, treatment, age and their interactions as fixed effects; we also included $(\text{age})^2$ to account for non-linear effects of time. In addition, since measurements were not independent with regard to both the individual and the family, we included random effects by specifying the intercept, and designating family and individual nested within family as subjects. Furthermore, some hatchlings died during the experiment, so we also corrected for right censoring in the data by fitting the age at last observation for each individual within the data set (van de Pol & Verhulst 2006). Within-sex effects of laboratory treatment on growth and adult body size were investigated similarly, but after removing sex from the models; between-treatment differences in adult body sizes for males and females separately were contrasted within the models using the 'estimate' statement. In these analyses of growth, SVL was log10-transformed to fulfil assumptions of normality and homoscedasticity. Finally, we calculated the average growth rate during the primary phase of growth (between days 14 and 126) and tested for sex-specific differences in growth rate between treatments using a mixed model with a normal error structure, and by specifying sex, food treatment and their interaction as fixed effects, and family as a random factor. Among- and within-treatment sex differences in growth rates were obtained within this model by using the 'estimate' statement. Results were qualitatively similar if we considered growth rate over the entire duration of the study (i.e. over 196 days).

Results

FIELD STUDY

The average snout–vent length (SVL) of *A. sagrei* varied significantly across populations (Table S1, Supporting information; GLM, main island effect: $F_{5,226} = 15{\cdot}43$, $P < 0{\cdot}0001$), and males were significantly larger than females (main sex effect: $F_{1,226} = 268{\cdot}99$, $P < 0{\cdot}0001$). Although males were larger than females on all islands (all P values <0·001), the degree to which they were so varied, generating a marginally non-significant island by sex interaction (sex×island interaction: $F_{5,226} = 2{\cdot}18$, $P = 0{\cdot}054$). Overall, males were 19–39% larger than females across the six islands (Fig. 1a). The SVL of both sexes increased as a function of Simpson's diversity index of prey taxa richness (GLMM, main prey taxa diversity effect: $F_{1,229} = 13{\cdot}22$, $P = 0{\cdot}0003$; sex × prey taxa diversity: $F_{1,229} = 0{\cdot}20$,

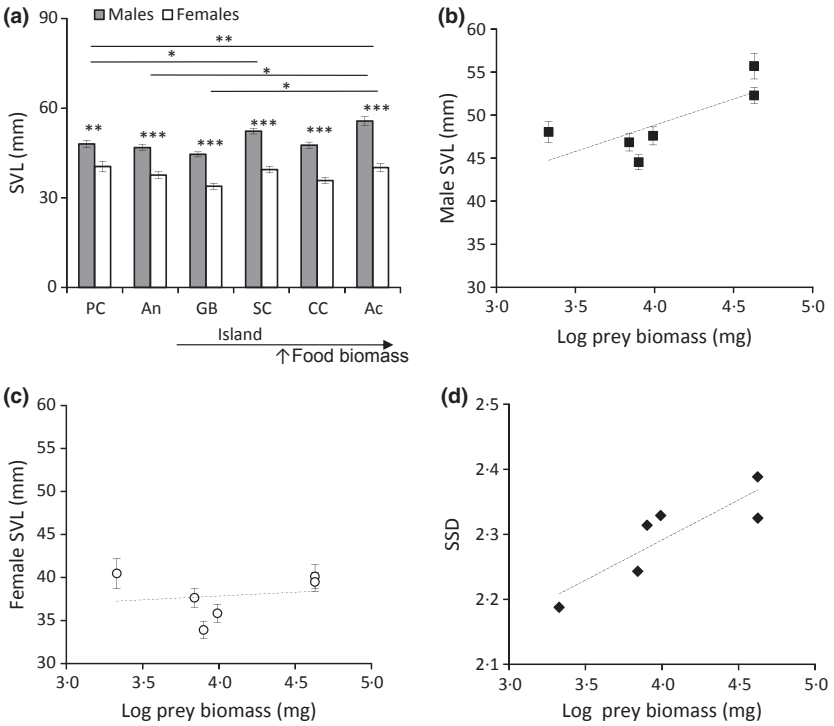

Fig. 1. Male and female snout–vent length (SVL, in mm) and sexual size dimorphism (SSD) in wild-caught *Anolis sagrei* sampled on six Bahamian islands. (a) Male and female adult SVL in the six populations; islands are given in order of increasing mass of food available. Values show predicted means and standard errors. Asterisks above histograms denote significant differences in SVL between sexes within islands, and those above the lines indicate significant differences in SSD between islands (* indicates $P < 0{\cdot}05$, ** indicates $P < 0{\cdot}001$ and *** indicates $P < 0{\cdot}0001$). (b) Male and (c) female SVL, and (d) SSD as a function of total prey biomass (log10-transformed, in mg). Dotted lines are presented to provide visual aid of best fit lines.

$P = 0{\cdot}657$; Table S1, Supporting information). By contrast, although there was no main effect of the total prey biomass on SVL, we found a significant sex by prey biomass interaction (GLMM, main prey biomass effect: $F_{1,229} = 1{\cdot}27$, $P = 0{\cdot}261$, sex × prey biomass interaction: $F_{1,229} = 5{\cdot}71$, $P = 0{\cdot}018$; Table S2, Supporting information). This significant interaction between sex and total prey biomass arose because there was a positive association between total prey biomass and body size in males (GLMM: $F_{1,126} = 4{\cdot}97$, $P = 0{\cdot}028$), but not in females (GLMM: $F_{1,100} = 0{\cdot}14$, $P = 0{\cdot}708$) (Fig. 1b and c). This interaction remained significant when the total number of prey items was included in the model (GLMM, main total number of prey items effect: $F_{1,227} = 0{\cdot}10$, $P = 0{\cdot}757$, sex × total number of prey items: $F_{1,227} = 0{\cdot}77$, $P = 0{\cdot}381$; Table S1, Supporting information).

The effect of total prey biomass on SVL in the two sexes explained interpopulation variation in SSD in *A. sagrei*. The SSD of this species ranged from 2·19 to 2·40 among the six populations (Fig. 2). Overall, islands with low total prey biomass showed low SSD, while those with high total prey biomass showed the greatest SSD ($r = 0{\cdot}87$, $P = 0{\cdot}025$; Fig. 1d). By contrast, we found no evidence to suggest that total prey numbers ($r = 0{\cdot}67$, $P = 0{\cdot}143$) or the diversity of prey taxa ($r = 0{\cdot}26$, $P = 0{\cdot}626$) was significantly associated with SSD across the populations of *A. sagrei*.

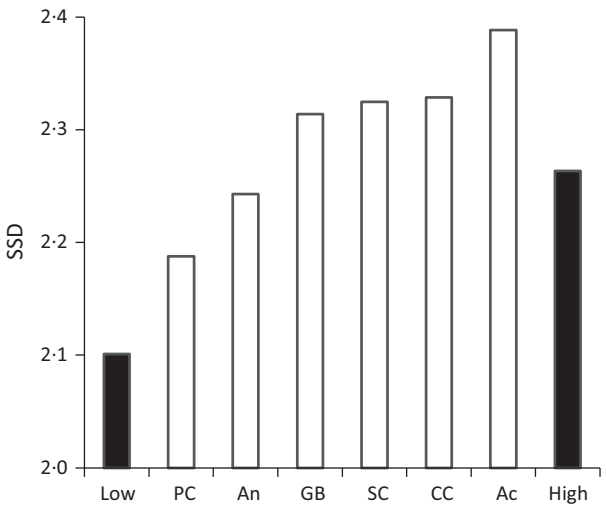

Fig. 2. Sexual size dimorphism (SSD) in laboratory-raised and wild-caught *Anolis sagrei*. SSD is given for laboratory individuals raised on low (restricted)- and high (*ad libitum*)-food treatments and for wild individuals caught on each of the six islands sampled. PC, Pigeon Cay; An, Andros; GB, Grand Bahamas; CC, Chub Cay; Ac, Acklins; SC, Staniel Cay; islands are given in order of increasing food availability.

LABORATORY EXPERIMENT

Our laboratory evidence supports the field-based evidence that prey biomass influences SSD in *A. sagrei* lizards. At the start of the experiment (i.e. when individuals were 14 days old), males were <3% larger than females (GLMM, $F_{1,63} = 4{\cdot}49$, $P = 0{\cdot}038$; males: $N = 35$, mean = 23·31 ± 1·55 mm; females: $N = 40$, mean = 22·68 ± 1·23 mm). Food treatment affected male and female adult body sizes differently (GLMM, diet: $F_{1,38} = 6{\cdot}79$, $P = 0{\cdot}013$; sex: $F_{1,38} = 24{\cdot}75$, $P < 0{\cdot}0001$; diet × sex: $F_{1,38} = 5{\cdot}08$, $P = 0{\cdot}030$). Because food treatment had little

effect on female body size at adulthood (GLMM, $F_{1,17} = 0{\cdot}47$, $P = 0{\cdot}502$), this significant interaction was likely driven entirely by the differential effect of food treatment on the body size of males (GLMM, $F_{1,14} = 6{\cdot}33$, $P = 0{\cdot}025$) (Fig. 3b and c). Under high-food treatments, males were 16% larger than they were under low-food treatment and were 26% larger than females under high-food treatment ($t_{38} = 5{\cdot}67$, $P < 0{\cdot}0001$) versus only 10% under low-food treatment ($t_{38} = 1{\cdot}77$, $P = 0{\cdot}085$) (Fig. 2). Evidence suggests that larger SVL in males under high-food treatment could be generated both through faster growth (Table 1, Fig. 3b, c) and a delay in the reaching of growth asymptotes ($\text{Age}^2 \times$ diet: $P < 0{\cdot}0001$). However, females on high food showed growth asymptotes more comparable to those of males ($\text{Age}^2 \times$ diet $\times$ sex: $P = 0{\cdot}066$) and elevated growth rates only between 42 and 90 days (Fig. 3c), suggesting that the primary effect of high food on SVL is to increase growth rate rather than duration. These results are corroborated by specific analyses of mean growth rates between days 14 and 126 (i.e. the primary linear phase of growth) (GLMM, sex: $F_{1,56} = 8{\cdot}11$, $P = 0{\cdot}006$; diet: $F_{1,56} = 18{\cdot}80$, $P < 0{\cdot}0001$). Males on high-food diets grew significantly faster between days 14 and 126 than females ($t_{55} = 2{\cdot}97$, $P = 0{\cdot}005$; males = $0{\cdot}17 \pm 0{\cdot}09$ mm day^{-1};
females = $0{\cdot}10 \pm 0{\cdot}02$ mm day^{-1}), but this was not true of males on low-food treatments ($t_{55} = 1{\cdot}09$, $P = 0{\cdot}280$; males = $0{\cdot}08 \pm 0{\cdot}09$ mm day^{-1};
females = $0{\cdot}06 \pm 0{\cdot}05$ mm day^{-1}).

Discussion

We combined comparative field and experimental laboratory approaches to show that variation in prey biomass was significantly and positively correlated with the degree of SSD among populations of an anole species. Comparisons of the body sizes of males and females among populations of *A. sagrei* inhabiting six islands in the Bahamas revealed that males were larger in areas of high food biomass availability, a difference that could not be explained by diversity of prey taxa or total number of prey items. Our laboratory data confirmed that males were developmentally more plastic than females and that high food biomass availability allowed males to attain greater larger body sizes than females, which provided a mechanism for different populations achieving higher values of SSD. Overall, our results suggest that the amount of food available might be an important factor shaping SSD in *A. sagrei*, although other factors are also important, as we note below.

Ecological explanations for the evolution of SSD in anoles have received less attention than those involving sexual and/or natural selection (but see Shine 1989; Camilleri & Shine 1990, 1990, 1991; Cox, Barrett & John-Alder 2008), despite the fact that the latter sometimes fail to explain the full spectrum of variation in SSD observed in the wild (Schoener & Schoener 1980; Stamps 1999; Cox & Calsbeek 2010b). For example, while a survival analysis of two wild populations of *A. sagrei* demonstrated directional selection for large male SVL and stabilizing selection for intermediate female SVL that was consistent with observed patterns of SSD (Cox & Calsbeek 2010b), other studies failed to find support for a role of natural selection in explaining differences in male and female SVL in this species (Losos, Schoener & Spiller 2004; Calsbeek & Smith 2007; Calsbeek 2008; Calsbeek & Bonneaud 2008). Indeed, monitoring *A. sagrei* populations in unmanipulated and experimentally altered (predator introduced or density altered) islands revealed either significant directional selection for increased female, but not male, body size, or

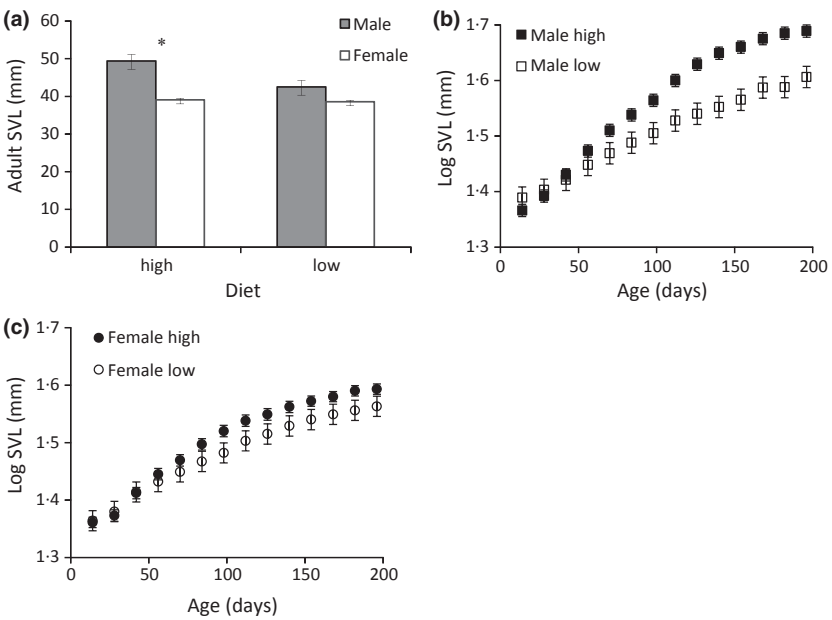

Fig. 3. Male and female snout-vent length (SVL, in mm) in laboratory-raised A. sagrei. (a) Male and female adult SVL under high (ad libitum) and low (restricted) food diets (* indicates $P < 0{\cdot}05$); values shown are the predicted means and standard errors. Changes in SVL with age of (b) male and (c) female *A. sagrei* raised under high (black) and low (white) food diets; sexes are shown separately for illustrative reasons only, but were entered in the same model. Values shown are the log-10 transformed predicted means and standard errors.

Table 1. Sex-specific effects of diet on changes in snout–vent length with age in laboratory-raised *Anolis sagrei*. We ran linear effects mixed models with family and individual nested within family as subjects. All: d.f. = 724, males: d.f. = 368, females: d.f. = 425. (A) Males and females, (B) males only, (C) females only. Estimates and standard errors are provided for main effects only (see figures for interaction effects)

Model	Term	Estimate ± SE	Test statistics (F)	P value
A	intercept	1·310 ± 0·012		
	sex	0·015 ± 0·012	0·77	0·381
	diet	−0·029 ± 0·012	14·74	0·0001
	sex × diet		0·69	0·406
	age	0·025 ± 0·001	1428·22	<0·0001
	sex × age		114·04	<0·0001
	age × diet		96·27	<0·0001
	age × sex × diet		51·86	<0·0001
	age of last observation	0·002 ± 0·001	7·56	0·006
	age^2	−0·001 ± 0·0001	284·46	<0·0001
	age^2 × diet		43·55	<0·0001
B	intercept	1·331 ± 0·018		
	diet	−0·037 ± 0·016	5·28	0·022
	age	0·026 ± 0·004	1843·98	<0·0001
	age × diet		16·00	<0·0001
	age^2	−0·001 ± 0·0002	29·37	<0·0001
	age^2 × diet		6·52	0·011
	age of last observation	0·001 ± 0·001	0·74	0·389
C	intercept	1·296 ± 0·011		
	diet	−0·017 ± 0·009	3·79	0·052
	age	0·029 ± 0·002	492·97	<0·0001
	age × diet		6·62	0·010
	age^2	−0·001 ± 0·0001	113·55	<0·0001
	age^2 × diet		3·91	0·049
	age of last observation	0·002 ± 0·001	15·04	0·0001

analogous selection for longer bodies in both sexes (Losos, Schoener & Spiller 2004; Calsbeek & Smith 2007; Calsbeek 2008; Calsbeek & Bonneaud 2008). Our results are consistent with ecological factors acting as a constraint on phenotypic responses to selection, with reduced levels of SSD occurring under restricted food availability.

The importance of resource availability in shaping SSD is evidenced by the fact that 62% of the variation in SSD that we measured in wild *A. sagrei* was accounted for in the laboratory by rearing individuals under *ad libitum* versus restricted diets. Indeed, in the laboratory, mean male body size varied between 42·5 and 49·4 mm depending on whether individuals were reared in restricted or *ad lib* food availability, while mean male body size varied between 44·5 and 55·7 mm in wild individuals. Thus, variation in male size in the laboratory, under experimentally manipulated food conditions, accounted for 44% of that observed in the wild. On the other hand, mean female body size only varied from 38·6 to 39·1 mm in the laboratory under either food treatments, compared to 33·9–40·5 mm in the wild. Although laboratory conditions only explained 7·5% of the variation in female body size observed in the field, the body sizes of most laboratory females were in the upper third quartile of wild females, a difference that was statistically significant (GLM, $\chi^2 = 5{\cdot}84$, $P = 0{\cdot}016$; wild = 37·3 ± 3·5 mm, laboratory = 38·9 ± 2·4 mm). Decreased sexual differences in growth rate in captivity have been recorded previously in reptiles (John-Alder, Cox & Taylor 2007) and suggest that, while our laboratory conditions were not successful at recreating the full range of female body sizes, captive rearing did not inflate our estimate of difference in SSD between high- and low-food diets. Overall, our results show that laboratory variation resulted from an increase in adult male, but not female, body size under high-food treatment, indicating that the degree of SSD is mainly determined by developmental plasticity in males rather than females.

Although our laboratory studies support a causal role of resource biomass in shaping patterns of SSD in the wild, it is conceivable that this effect could be exacerbated by two factors. First, because anoles continue to grow asymptotically after reaching maturity, patterns of SSD in the wild may also have been shaped by site/island differences in sex-specific survival, which may vary as a function of food availability (Stamps 1983; Stamps, Losos & Andrews 1997). Secondly, on islands large enough to display heterogeneity in food abundance and permit migration, the non-random movement of individuals between habitats of differing resource availability (Cote & Clobert 2010) may also inflate an association between resources and SSD. Indeed, directional migration between habitat patches is likely if small males are at a selective disadvantage in habitats of high food supply, but advantaged under low-food habitats (and *vice versa* for large males). This would be expected if the viability costs of being large outweigh the reproductive advantages when resources are scarce (Blanckenhorn, Preziosi & Fairbairn 1995) and/or if occupying territories in high-food habitats increase the fitness of large males. While such effects of survival and migration do not lessen the importance of food availability *per se*, their contribution to patterns of SSD in the wild should be further evaluated.

The role of sex-specific plasticity in shaping intraspecific variation of SSD between insular populations of *A. sagrei* begs the question of its contribution in driving differences in SSD among different species of anoles. Given the vast radiation of anoles in the Caribbean and the New World mainland (Roughgarden 1995; Irschick *et al.* 1997; Butler, Schoener & Losos 2000; Losos 2009), testing this would require SSD data on multiple anole species as well as measures of prey availability in each of their microhabitats. We currently lack these data, but preliminary data for four Puerto Rican *Anolis* species (*A. cristatellus, A. evermanni, A. pulchellus*, *A. cuvieri*), representing four different ectomorphs (trunk-ground, trunk-crown, grass-bush and crown-giant) show a strong positive association between SSD and the total amount of prey biomass measured in each of their microhabitat (A. Herrel, B. Vanhooydonck, J.J. Meyers & D.J. Irschick, unpublished data). These preliminary data suggest that food abundance may also explain interspecific differences in levels of SSD (Butler, Schoener & Losos 2000; Butler & Losos 2002), although further work involving a wider sampling of anole species and microhabitats is needed to verify this trend.

Sex-specific plasticity is thought to shape the evolution of SSD either through adaptive canalization (Fairbairn 2005; Stillwell *et al.* 2010) or condition-dependent growth (Bonduriansky 2007) of the larger sex. Canalization should occur under strong directional selection for larger body size and has been shown in both water striders [*Aquarius remigis* (Fairbairn 2005)] and Mediterranean tarantulas [*L. tarantula*; (Fernandez-Montraveta & Moya-Larano 2007)], with the smaller sex (males) exhibiting greater plasticity in body size. Condition-dependent growth should, on the other hand, allow the larger sex to take advantage of favourable environmental conditions, a pattern that has been detected in the fly *T. angusticollis*, in which the larger sex (males) has been found to exhibit the greatest sensitivity to diet (Bonduriansky 2007). Studies in invertebrate species show mixed support for the relative roles of the canalization and condition dependence of the larger sex in mediating variation in SSD, and a similar pattern is now emerging from studies of vertebrate species (Taylor & Denardo 2005; Cox 2006; Ceballos & Valenzuela 2011). For instance, in three vertebrate species displaying male-biased SSD, variation in SSD in response to food treatment was found to be mediated either by female plasticity [the Western Diamond-backed rattlesnake *Crotalus atrox*; (Taylor & Denardo 2005)], male plasticity [the snapping turtle *Chelydra serpentine*, (Ceballos & Valenzuela 2011)], or failed to be observed under laboratory conditions [Yarrow's spiny lizard *Sceloporus jarrovii*; (Cox & Calsbeek 2010a)]. Conversely, in two other vertebrate species exhibiting female-biased SSD (the northern water snake *Nerodia sipedon* and the garter snake *Thamnophis sirtalis*), diet-shaped variation in SSD was mediated by greater plasticity in the larger sex (females) (Queral-Regil & King 1998; Krause, Burghardt & Gillingham 2003). Our finding of variation in SSD driven by male plastic growth responses to food availability in a reptile exhibiting male-biased SSD lends further weight to the hypothesis that plasticity in the largest sex shapes SSD. While so far a majority of studies therefore appear to be consistent with the condition-dependent hypothesis, further work is required to understand why this is not always the case (e.g. in water striders, tarantulas and rattlesnakes) and to identify the selective pressures that may instead favour the canalization of body size in the larger sex.

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Data accessibility

Data for this article have been deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.c983b (Bonneaud *et al.* 2015).

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Table S1. Mean body length (SVL, in mm) of wild-caught male and female A. sagrei and sexual size dimorphism (SSD) in each of the six Bahamian islands sampled.

Table S2. Mean body length (SVL) and sexual size dimorphism (SSD) of wild-caught male and female anoles from 4 different species in Puerto Rico.