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Camille Bonneaud, Erin Marnocha, Anthony Herrel, Bieke Vanhooydonck, Duncan Irschick, et al..
Developmental plasticity affects sexual size dimorphism in an anole lizard. *Functional Ecology*, 2016,
30 (2), pp.235-243. 10.1111/1365-2435.12468 . hal-02145265

HAL Id: hal-02145265

<https://hal.science/hal-02145265v1>

Submitted on 6 Jan 2025

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Developmental plasticity affects sexual size dimorphism in an anole lizard

AUTHORS

Bonneaud, Camille; Marnocha, Erin; Herrel, Anthony; et al.

JOURNAL

Functional Ecology

DEPOSITED IN ORE

17 February 2016

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1 **DEVELOPMENTAL PLASTICITY AFFECTS SEXUAL SIZE DIMORPHISM IN**
2 **AN ANOLE LIZARD**

3
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6
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21 **Running title:** Plasticity in sexual size dimorphism

22

23 **Summary**

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

45 hypothesis, according to which the larger sex should display greater plasticity in
46 growth in response to environmental conditions.

47

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

49

50 **Introduction**

51 Sexual selection is expected to lead to phenotypic differences between the sexes (Darwin
52 1871; Andersson 1994). In species where inter-sexual differences are at least partly
53 expressed as a difference in body size, directional selection on body size should lead to
54 ever increasing (or decreasing) measures of body size and sexual dimorphism. However,
55 larger body sizes are costly to produce and maintain, and under poor environmental
56 conditions, the largest individuals may be at a distinct disadvantage (Wikelski & Thom
57 2000). Theory suggests that mothers should thus be selected to produce the cheaper (i.e.,
58 the smaller) of the two sexes when conditions are poor (Trivers & Willard 1973).
59 However, there is another, less explored possibility that the larger sex is plastic in its
60 growth, such that individuals grow more quickly to achieve large sizes when conditions
61 permit and grow more slowly and to smaller sizes when conditions are disadvantageous
62 (Teder & Tammaru 2005; Stillwell & Fox 2007; Stillwell *et al.* 2010).

63

64 Food availability has been shown to affect growth and adult morphology in many species,
65 with often differing consequences for males and females (Roughgarden & Fuentes 1977;
66 Post *et al.* 1999; Uhl *et al.* 2004; Le Galliard *et al.* 2006; Bonduriansky 2007). Such sex-
67 specific responses can give rise to within-species variation in sexual size dimorphism
68 (SSD) (Stillwell *et al.* 2010), as demonstrated by laboratory experiments on the
69 hawkmoth *Manduca sexta* (Stillwell & Davidowitz 2010b; Stillwell & Davidowitz
70 2010a), the fly *Telostylinus angusticollis* (Bonduriansky 2007) and the Mediterranean
71 tarantula *Lycosa tarantula* (Fernandez-Montraveta & Moya-Larano 2007). In all cases,
72 the magnitude of SSD increased under high quality diet compared to a lower quality one,

73 with sex differences in plasticity to environmental conditions giving rise to variation in
74 SSD. However, we know less about the extent of intra-specific variation in SSD that can
75 be attributed to disparities in food availability in vertebrate populations and in the wild
76 (Krause, Burghardt & Gillingham 2003; Cox 2006; Cox & Calsbeek 2010; Ceballos &
77 Valenzuela 2011).

78

79 Lizards in the *Anolis* genus are particularly appropriate for studies of the links between
80 environmental variation and SSD for two reasons. First, there is a well-established link
81 between morphology and ecological conditions in this group (Losos 1990; Losos 1994;
82 Irschick & Losos 1998; Butler, Sawyer & Losos 2007). For example, longer limbed
83 lizards tend to occupy broad perches because longer limbs increase maximum sprint
84 speed (Losos 1990), whereas lizards with shorter limbs tend to occupy narrow perches
85 because shorter limbs confer greater agility (Losos & Sinervo 1989; Irschick & Losos
86 1998). While variation in limb morphology influences locomotor performance, variation
87 in male body size influences competitive ability. Larger males are more successful in
88 obtaining mates because they have larger territories that overlap with the territories of
89 more females (Trivers 1976; Jenssen & Nunez 1998); reviewed in (Stamps 1983).
90 Second, *Anolis* lizards exhibit varying degrees of both inter- and intra-specific SSD
91 (Butler, Schoener & Losos 2000; Butler, Sawyer & Losos 2007; Losos 2009), with
92 among species variation reflecting differences in habitat types rather than phylogeny
93 (Butler et al. 2000). Although females can be the larger sex in mainland anoles (Fitch
94 1976), island species exhibit a range of male-biased SSD, with some species being
95 largely non-dimorphic, and others having males that are three-times heavier than females

96 (Butler & Losos 2002). In addition, across populations of a single species, males may be
97 10-40% larger than females (Schoener & Schoener 1980; Stamps 1999). Variation in
98 SSD among and within *Anolis* species is thought to be primarily driven by diverging
99 natural and sexual selection on male and female body size (Andrews & Rand 1974;
100 Trivers 1976; Stamps 1983; Shine 1988; Jenssen & Nunez 1998; Lailvaux & Irschick
101 2006; Kratochvil & Kubicka 2007).

102

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

116

117 Specifically, we addressed the following questions. (1) Can differences in food
118 availability on different Bahamian islands explain inter-population variation in the level

119 of SSD? (2) Can experimental manipulation of the mass of food available give rise to
120 variation in SSD? (3) Is variation in SSD mediated by developmental plasticity in males
121 or in females in response to different food treatments?

122

123 **Material and methods**

124 FIELD STUDIES

125 We used field observations to test the role of food availability in explaining variation in
126 SSD across six populations of *A. sagrei*. Adult males (N=132) and adult females (N=116)
127 were captured on six Bahamian islands (Acklins, Andros, Grand Bahamas, Chub Cay,
128 Pidgeon Cay and Staniel Cay) over a period of one month between April and May 2003
129 (Table S1) (see (Vanhooydonck *et al.* 2009) for further details). All lizards were captured
130 by hand or by noose, sexed and snout-to-vent length (SVL) was measured using digital
131 calipers ($\pm 0.01\text{mm}$). Animals were then released at their site of capture. Sexual size
132 dimorphism (SSD) was calculated as the mean trait value in the larger sex (here:
133 males)/mean trait value in the smaller sex (here: females) + 1 (Lovich & Gibbons 1992;
134 Smith 1999; Cox & Calsbeek 2009).

135

136 We used pitfall traps and sweep netting to estimate prey availability at the six different
137 locations where the lizards were caught to ensure that all micro-habitats were sufficiently
138 sampled for arboreal species (sampling techniques followed (Herrel *et al.* 2006). At each
139 site, 20 pitfall traps were positioned 2 meters apart over an area of 30-50m²; they were set
140 open for a total of 48h each and emptied both after 24h and 48h. Pitfalls had a diameter
141 of 15 cm and a depth of 10 cm, were positioned in known anole habitat, and filled with an

142 aqueous formaldehyde (5%) solution with a small amount of soap added to reduce
143 surface tension. After 24h and 48h, all invertebrates were removed from the pitfalls and
144 stored in a 70% aqueous ethanol solution. At each site, potential prey residing among
145 the vegetation were sampled ten times for two minutes each using a reinforced sweep net
146 (40cm diameter, 75cm long); sweeps were conducted during periods of lizard activity.
147 Sweep samples were transferred to plastic bags and frozen upon return to the field
148 laboratory.

149

150 All potential prey were identified to the lowest possible taxonomic level (Order or below)
151 and grouped into morphotypes (for more information, see (Brecko *et al.* 2008)). Only
152 prey of type and size known to comprise the diet of anoles were included (Herrel *et al.*
153 2006). Prey were weighed (wet-mass) using a digital micro-balance (± 0.01 mg). For
154 each island, we estimated the total numbers of prey items and the total amount of prey
155 biomass captured per unit time. We also calculated the diversity of prey taxa per island
156 using Simpson's Diversity index, which is a measure of diversity that takes into account
157 both richness and evenness (i.e., relative abundance) of the different taxa.

158

159 LABORATORY EXPERIMENT

160 We conducted a feeding experiment to test the link between food availability and SSD in
161 *A. sagrei*, as well as whether SSD is mediated by developmental plasticity in males
162 and/or females. The experiment took place from August 2005 to July 2007 with
163 laboratory-reared F2 and F3 descendants of wild *A. sagrei* collected in June 2004 on the
164 island of Great Exuma, Bahamas. Offspring were kept on *ad libitum* food supplies for the

165 first two weeks of their lives to maximize survival, and were then randomly assigned to
166 either high food (*ad libitum*) or low food treatment. In the low food treatment, offspring
167 that weighed 0.5g or less received one cricket per feeding (14% of *ad lib*), those between
168 0.6 and 1.1g received two crickets per feeding (29% of *ad lib*), and those 1.2g or greater
169 received 3 crickets per feeding (43% of *ad lib*). These amounts were based on a
170 preliminary study of the minimum quantities of crickets required to sustain individuals of
171 each size category. A total of 106 offspring were included in this study, 53 in each
172 treatment (22 males and 31 females *ad lib*; 25 males and 28 females low-food). All
173 offspring were housed in 45 L terrariums and provided with a small houseplant and full
174 spectrum lighting on a 12:12 light : dark cycle. Siblings were randomly distributed across
175 food treatments to reduce shared-family effects on growth and morphology, and there
176 were no intra-sexual differences in SVL between those allocated to the two treatments
177 (for each sex, initial differences in body size were examined using mixed model with
178 family as a random factor and treatment as the explanatory variable (see methods below);
179 males: $F_{1,25}=1.02$, $p=0.322$; females: $F_{1,29}=0.19$, $p=0.667$). Body size ($\pm 0.1\text{mm}$) was
180 measured every 14 days following the onset of the experiment until they reached 196
181 days of age (range in mean age at sexual maturity of female anoles: 57 to 279 days;
182 (Andrews 1976)).

183

184 STATISTICAL ANALYSES

185 All statistical analyses were performed using SAS software version 9.3 (SAS Inc., Cary,
186 NC). For the field study, we first investigated sex differences in body size (SVL) among
187 the 6 populations of *A. sagrei* using a general linear model (PROC GENMOD) with a

188 normal error structure, and with sex, island and their interaction as fixed effects; in
189 addition, pairwise population comparisons were obtained within the same model using
190 the “estimate” statement. Effects of food availability on male and female body size in the
191 6 populations of *A. sagrei* were then analyzed using a general linear mixed model (PROC
192 MIXED) with a normal error structure, by specifying sex, total prey biomass (\log_{10}
193 transformed), Simpson’s diversity index of prey taxa richness and their interactions with
194 sex as fixed effects, and island as the random effect. The same model was re-run after
195 including total prey numbers and its interaction with sex as fixed effects. Using all three
196 estimates of prey availability (biomass, diversity and number) helps to clarify the precise
197 mediator of variation in SSD among populations, with diversity used to test the
198 opportunity for niche partitioning which could explain population-differences in SSD
199 (Schoener 1967; Camilleri & Shine 1990). These three estimates of prey availability were
200 not significantly correlated with each other (Pearson’s correlations; total prey numbers
201 and total prey biomass: $r=0.60$, $p=0.210$; total prey numbers and Simpson’s diversity
202 index of prey taxa richness: $r=0.63$, $p=0.180$; total prey biomass and Simpson’s diversity
203 index of prey taxa richness: $r=0.38$, $p=0.454$). Finally, we used Pearson’s correlations
204 (PROC CORR) to analyze correlations between SSD and total prey numbers, total prey
205 biomass (\log_{10} transformed) and Simpson’s diversity index of prey taxa richness.

206

207 For the laboratory study, we first verified that *A. sagrei* lizards had been randomly
208 allocated with respect to their body size to either of the two food treatments by running
209 two general linear mixed model with normal error structures, for males and females
210 separately; we specified treatment as the fixed effect and family as the random effect (see

211 results in method section above). We investigated differences in initial body size between
212 males and females using a general linear mixed model with sex as the fixed effect and
213 family as the random effect. We then examined the effects of food treatment on growth
214 and adult body size (i.e., at 196 days of age). The sex-specific effect of laboratory
215 treatments on adult body size was computed using a mixed model with a normal error
216 structure, and by specifying sex, food treatment and their interaction as fixed effects, and
217 family as a random factor. To assess the sex-specific effect of treatments on growth, we
218 ran a mixed model with normal error structures, including sex, treatment, age and their
219 interactions as fixed effects; we also included $(age)^2$ to account for non-linear effects of
220 time. In addition, since measurements were not independent with regards to both the
221 individual and the family, we included random effects by specifying the intercept, and
222 designating family and individual nested within family as subjects. Furthermore, some
223 hatchlings died during the experiment, so we also corrected for right censoring in the data
224 by fitting the age at last observation for each individual within the dataset (van de Pol &
225 Verhulst 2006). Within-sex effects of laboratory treatment on growth and adult body size
226 were investigated similarly, but after removing sex from the models; between-treatment
227 differences in adult body sizes for males and females separately were contrasted within
228 the models using the “estimate” statement. In these analyses of growth, SVL was log₁₀-
229 transformed to fulfill assumptions of normality and homoscedasticity. Finally, we
230 calculated the average growth rate during the primary phase of growth (between days 14
231 and 126) and tested for sex-specific differences in growth rate between treatments using a
232 mixed model with a normal error structure, and by specifying sex, food treatment and
233 their interaction as fixed effects, and family as a random factor. Among and within

234 treatment sex-differences in growth rates were obtained within this model by using the
235 “estimate” statement. Results were qualitatively similar if we considered growth rate over
236 the entire duration of the study (i.e., over 196 days).

237

238 **Results**

239 FIELD STUDY

240 The average snout-vent length (SVL) of *A. sagrei* varied significantly across populations
241 (Table S1, GLM, main island effect: $F_{5,226}=15.43$, $p<0.0001$), and males were
242 significantly larger than females (main sex effect: $F_{1,226}=268.99$, $p<0.0001$). Although
243 males were larger than females on all islands (all p values < 0.001), the degree to which
244 they were so varied, generating a marginally non-significant island by sex interaction
245 (sex \times island interaction: $F_{5,226}=2.18$, $p=0.054$). Overall, males were 19-39% larger than
246 females across the six islands (Fig. 1a). The SVL of both sexes increased as a function of
247 Simpson’s diversity index of prey taxa richness (GLMM, main prey taxa diversity effect:
248 $F_{1,229}=13.22$, $p=0.0003$; sex \times prey taxa diversity: $F_{1,229}=0.20$, $p=0.657$; Table S1). By
249 contrast, although there was no main effect of the total prey biomass on SVL, we found a
250 significant sex by prey biomass interaction (GLMM, main prey biomass effect:
251 $F_{1,229}=1.27$, $p=0.261$, sex \times prey biomass interaction: $F_{1,229}=5.71$, $p=0.018$; Table S2). This
252 significant interaction between sex and total prey biomass arose because there was a
253 positive association between total prey biomass and body size in males (GLMM:
254 $F_{1,126}=4.97$, $p=0.028$), but not in females (GLMM: $F_{1,100}=0.14$, $p=0.708$) (Fig. 1b and c).
255 This interaction remained significant when the total number of prey items was included

256 in the model (GLMM, main total number of prey items effect: $F_{1,227}=0.10$, $p=0.757$,
257 sex×total number of prey items: $F_{1,227}=0.77$, $p=0.381$; Table S1).

258

259 The effect of total prey biomass on SVL in the two sexes explained inter-population
260 variation in SSD in *A. sagrei*. The SSD of this species ranged from 2.19-2.40 among the
261 six populations (Fig. 2). Overall, islands with low total prey biomass showed low SSD,
262 while those with high total prey biomass showed the greatest SSD ($r=0.87$, $p=0.025$; Fig.
263 1d). By contrast, we found no evidence to suggest that total prey numbers ($r=0.67$,
264 $p=0.143$) or the diversity of prey taxa ($r=0.26$, $p=0.626$) were significantly associated
265 with SSD across the populations of *A. sagrei*.

266

267 LABORATORY EXPERIMENT

268 Our laboratory evidence supports the field-based evidence that prey biomass influences
269 SSD in *A. sagrei* lizards. At the start of the experiment (i.e., when individuals were 14
270 days old), males were <3% larger than females (GLMM, $F_{1,63}=4.49$, $p=0.038$; males:
271 $N=35$, mean= 23.31 ± 1.55 mm; females: $N=40$, mean= 22.68 ± 1.23 mm). Food treatment
272 affected male and female adult body sizes differently (GLMM, diet: $F_{1,38}=6.79$, $p=0.013$;
273 sex: $F_{1,38}=24.75$, $p<0.0001$; diet×sex: $F_{1,38}=5.08$, $p=0.030$). Because food treatment had
274 little effect on female body size at adulthood (GLMM, $F_{1,17}=0.47$, $p=0.502$), this
275 significant interaction was likely driven entirely by the differential effect of food
276 treatment on the body size of males (GLMM, $F_{1,14}=6.33$, $p=0.025$) (Fig. 3b and c). Under
277 high food treatments, males were 16% larger than they were under low food treatment,
278 and were 26% larger than females under high food treatment ($t_{38}=5.67$, $p<0.0001$) versus

279 only 10% under low food ($t_{38}=1.77$, $p=0.085$) (Fig. 2). Evidence suggests that larger SVL
280 in males under high food treatment could be generated both through faster growth (Table
281 1, Fig. 3b, c) and a delay in the reaching of growth asymptotes ($\text{Age}^2 \times \text{diet}$: $p < 0.0001$).
282 However, females on high food showed growth asymptotes more comparable to those of
283 males ($\text{Age}^2 \times \text{diet} \times \text{sex}$: $p=0.066$) and elevated growth rates only between 42 and 90 days
284 (Fig. 3c), suggesting that the primary effect of high food on SVL is to increase growth
285 rate rather than duration. These results are corroborated by specific analyses of mean
286 growth rates between days 14 to 126 (i.e., the primary linear phase of growth) (GLMM,
287 sex: $F_{1,56}=8.11$, $p=0.006$; diet: $F_{1,56}=18.80$, $p < 0.0001$). Males on high food diets grew
288 significantly faster between days 14 and 126 than females ($t_{55}=2.97$, $p=0.005$;
289 males= 0.17 ± 0.09 mm/day; females= 0.10 ± 0.02 mm/day), but this was not true of males
290 on low food treatments ($t_{55}=1.09$, $p=0.280$; males= 0.08 ± 0.09 mm/day;
291 females= 0.06 ± 0.05 mm/day).

292

293 **Discussion**

294 We combined comparative field and experimental laboratory approaches to show that
295 variation in prey biomass was significantly and positively correlated with the degree of
296 SSD among populations within an anole species. Comparisons of the body sizes of males
297 and females among populations of *A. sagrei* inhabiting six islands in the Bahamas
298 revealed that males were larger in areas of high food biomass availability, a difference
299 that could not be explained by diversity of prey taxa or total number of prey items. Our
300 laboratory data confirmed that males were developmentally more plastic than females,
301 and that high food biomass availability allowed males to attain greater larger body sizes

302 than females, which provided a mechanism for different populations achieving higher
303 values of SSD. Overall, our results suggest that the amount of food available might be an
304 important factor shaping SSD in *A. sagrei*, although other factors are also important, as
305 we note below.

306

307 Ecological explanations for the evolution of SSD in anoles have received less attention
308 than those involving sexual and/or natural selection (but see Shine 1989; Camilleri &
309 Shine 1990; Shine 1990; Shine 1991; Cox, Barrett & John-Alder 2008), despite the fact
310 that the latter sometimes fail to explain the full spectrum of variation in SSD observed in
311 the wild (Schoener & Schoener 1980; Stamps 1999; Cox & Calsbeek 2010). For
312 example, while a survival analysis of two wild populations of *A. sagrei* demonstrated
313 directional selection for large male SVL and stabilizing selection for intermediate female
314 SVL that was consistent with observed patterns of SSD (Cox & Calsbeek 2010), other
315 studies failed to find support for a role of natural selection in explaining differences in
316 male and female SVL in this species (Losos, Schoener & Spiller 2004; Calsbeek & Smith
317 2007; Calsbeek 2008; Calsbeek & Bonneaud 2008). Indeed, monitoring *A. sagrei*
318 populations in un-manipulated and experimentally-altered (predator introduced or density
319 altered) islands revealed either significant directional selection for increased female, but
320 not male, body size, or analogous selection for longer bodies in both sexes (Losos,
321 Schoener & Spiller 2004; Calsbeek & Smith 2007; Calsbeek 2008; Calsbeek & Bonneaud
322 2008). Our results are consistent with ecological factors acting as a constraint on
323 phenotypic responses to selection, with reduced levels of SSD occurring under restricted
324 food availability.

325

326 The importance of resource availability in shaping SSD is evidenced by the fact that 62%
327 of the variation in SSD that we measured in wild *A. sagrei* was accounted for in the
328 laboratory by rearing individuals under *ad libitum* versus restricted diets. Indeed, in the
329 laboratory, mean male body size varied between 42.5-49.4 mm depending on whether
330 individuals were reared in restricted or *ad lib* food availability, while mean male body
331 size varied between 44.5-55.7 mm in wild individuals. Thus, variation in male size in the
332 laboratory, under experimentally manipulated food conditions, accounted for 44% of that
333 observed in the wild. On the other hand, mean female body size only varied from 38.6-
334 39.1 mm in the laboratory under either food treatments, compared to 33.9-40.5 mm in the
335 wild. Although laboratory conditions only explained 7.5% of the variation in female body
336 size observed in the field, the body sizes of most laboratory females were in the upper
337 third quartile of wild females, a difference that was statistically significant (GLM,
338 $\chi^2=5.84$, $p=0.016$; wild= 37.3 ± 3.5 mm, laboratory= 38.9 ± 2.4 mm). Decreased sexual
339 differences in growth rate in captivity have been recorded previously in reptiles (John-
340 Alder, Cox & Taylor 2007) and suggest that, while our laboratory conditions were not
341 successful at recreating the full range of female body sizes, captive rearing did not inflate
342 our estimate of difference in SSD between high and low food diets. Overall, our results
343 show that laboratory variation resulted from an increase in adult male, but not female,
344 body size under high food treatment, indicating that the degree of SSD is mainly
345 determined by developmental plasticity in males rather than females.

346

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

363

364 The role of sex-specific plasticity in shaping intra-specific variation of SSD between
365 insular populations of *A. sagrei* begs the question of its contribution in driving
366 differences in SSD among different species of anoles. Given the vast radiation of anoles
367 in the Caribbean and the New World mainland (Roughgarden 1995; Irschick et al. 1997;
368 Butler, Schoener & Losos 2000; Losos 2009), testing this would require SSD data on
369 multiple anole species as well as measures of prey availability in each of their

370 microhabitats. We currently lack these data, but preliminary data for four Puerto Rican
371 *Anolis* species (*A. cristatellus*, *A. evermanni*, *A. pulchellus*, *A. cuvieri*), representing four
372 different ectomorphs (trunk-ground, trunk-crown, grass-bush, and crown-giant) shows a
373 strong positive association between SSD and the total amount of prey biomass measured
374 in each of their microhabitat (Herrel et al., unpub. data). These preliminary data suggest
375 that food abundance may also explain inter-specific differences in levels of SSD (Butler,
376 Schoener & Losos 2000; Butler & Losos 2002), although further work involving a wider
377 sampling of anole species and microhabitats is needed to verify this trend.

378

379 Sex-specific plasticity is thought to shape the evolution of SSD either through adaptive
380 canalization (Fairbairn 2005; Stillwell *et al.* 2010) or condition-dependent growth
381 (Bonduriansky 2007) of the larger sex. Canalization should occur under strong directional
382 selection for larger body size and has been shown in both water striders (*Aquarius*
383 *remigis*; (Fairbairn 2005)) and Mediterranean tarantulas (*L. tarantula*; (Fernandez-
384 Montraveta & Moya-Larano 2007)), with the smaller sex (males) exhibiting greater
385 plasticity in body size. Condition-dependent growth should, on the other hand, allow the
386 larger sex to take advantage of favorable environmental conditions, a pattern that has
387 been detected in the fly *T. angusticollis*, in which the larger sex (males) has been found to
388 exhibit the greatest sensitivity to diet (Bonduriansky 2007). Studies in invertebrate
389 species show mixed support for the relative roles of the canalization and condition-
390 dependence of the larger sex in mediating variation in SSD and a similar pattern is now
391 emerging from studies of vertebrate species (Taylor & Denardo 2005; Cox 2006;
392 Ceballos & Valenzuela 2011). For instance, in three vertebrate species displaying male-

393 biased SSD, variation in SSD in response to food treatment was found to be mediated
394 either by female plasticity (the Western Diamond-backed rattlesnake *Crotalus atrox*;
395 (Taylor & Denardo 2005)), male plasticity (the snapping turtle *Chelydra serpentine*,
396 (Ceballos & Valenzuela 2011)), or failed to be observed under laboratory conditions
397 (Yarrow's spiny lizard *Sceloporus jarrovi*; (Cox & Calsbeek)). Conversely, in two other
398 vertebrate species exhibiting female-biased SSD (the northern water snake *Nerodia*
399 *sipedon* and the garter snake *Thamnophis sirtalis*), diet-shaped variation in SSD was
400 mediated by greater plasticity in the larger sex (females) (Queral-Regil & King 1998;
401 Krause, Burghardt & Gillingham 2003). Our finding of variation in SSD driven by male
402 plastic growth responses to food availability in a reptile exhibiting male-biased SSD
403 lends further weight to the hypothesis that plasticity in the largest sex shapes SSD. While
404 so far a majority of studies therefore appear to be consistent with the condition-dependent
405 hypothesis, further work is required to understand why this is not always the case (e.g., in
406 water striders, tarantulas and rattlesnakes) and to identify the selective pressures that may
407 instead favor the canalization of body size in the larger sex.

408

409 **Acknowledgments**

410 We are very grateful to A. F. Russell, D. Pincheira-Donoso, the Associate Editor and two
411 anonymous reviewers for helpful comments on the manuscript, J. Clobert for discussion,
412 E. Ramsell and E. Toffelmier for their assistance with lizard husbandry, J. Meyers, M.
413 Ramos, D. Bickford and E. Toro for help in the field, and K. Hellemans for help with
414 prey type classification. C.B. was supported by a Marie Curie Reintegration Grant (FP7-
415 PEOPLE-IRG-2008 #239257); E.M. by a grant from the United States Environmental
416 Protection Agency and the UCLA Department of Ecology and Evolutionary Biology,

417 USA; B.V. by Fund for Scientific Research (FWO-VI), Belgium; D.I. by a grant from the
418 National Science Foundation (IBN9983003); T.B.S. by grants from the National Science
419 Foundation (IRCEB9977072). Protocols were approved by the UCLA Chancellor's
420 Animal Research Committee (IACUC ARC protocol 2004-047) and by the Institutional
421 Animal Care and Use Committee at Tulane University (IACUC approval 0189-2-16-
422 0301).

423

424 **Data accessibility:** The data will be made accessible on Dryad (doi:XXXX).

425

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589
590

591 **TABLE 1:** Sex-specific effects of diet on changes in snout-vent length with age in
592 laboratory-raised *A. sagrei*. We ran linear effects mixed models with family and
593 individual nested within family as subjects. All: df=724, males: df=368, females: df=425.
594 (A) Males and females, (B) males only, (C) females only. Estimates and standard errors
595 are provided for main effects only (see figures for interaction effects).
596

Model	Term	Estimate \pm se	Test statistics (F)	P value
A	intercept	1.310 \pm 0.012		
	sex	0.015 \pm 0.012	0.77	0.381
	diet	-0.029 \pm 0.012	14.74	0.0001
	sex \times diet		0.69	0.406
	age	0.025 \pm 0.001	1428.22	<0.0001
	sex \times age		114.04	<0.0001
	age \times diet		96.27	<0.0001
	age \times sex \times diet		51.86	<0.0001
	age of last observation	0.002 \pm 0.001	7.56	0.006
	age ²	-0.001 \pm 0.0001	284.46	<0.0001
	age ² \times diet		43.55	<0.0001
B	intercept	1.331 \pm 0.018		
	diet	-0.037 \pm 0.016	5.28	0.022
	age	0.026 \pm 0.004	1843.98	<0.0001
	age \times diet		16.00	<0.0001
	age ²	-0.001 \pm 0.0002	29.37	<0.0001
	age ² \times diet		6.52	0.011
	age of last observation	0.001 \pm 0.001	0.74	0.389
C	intercept	1.296 \pm 0.011		
	diet	-0.017 \pm 0.009	3.79	0.052
	age	0.029 \pm 0.002	492.97	<0.0001
	age \times diet		6.62	0.010
	age ²	-0.001 \pm 0.0001	113.55	<0.0001
	age ² \times diet		3.91	0.049
	age of last observation	0.002 \pm 0.001	15.04	0.0001

597

598

599 **Figure legends**

600 **Figure 1.** Male and female snout-vent length (SVL, in mm) and sexual size dimorphism
601 (SSD) in wild-caught *A. sagrei* sampled on six Bahamian islands. (a) Male and female
602 adult snout-vent length in the six populations; islands are given in order of increasing
603 mass of food available. Values show predicted means and standard errors. Asterisks
604 above histograms denote significant differences in snout-vent lengths between sexes
605 within islands, and those above the lines indicate significant differences in sexual size
606 dimorphism (SSD) between islands (* indicates $p < 0.05$, ** indicates $p < 0.001$ and ***
607 indicates $p < 0.0001$). (b) Male and (c) female SVL, and (d) SSD as a function of total
608 prey biomass (log-10 transformed, in mg). Dotted lines are presented to provide visual
609 aid of best fit lines.

610

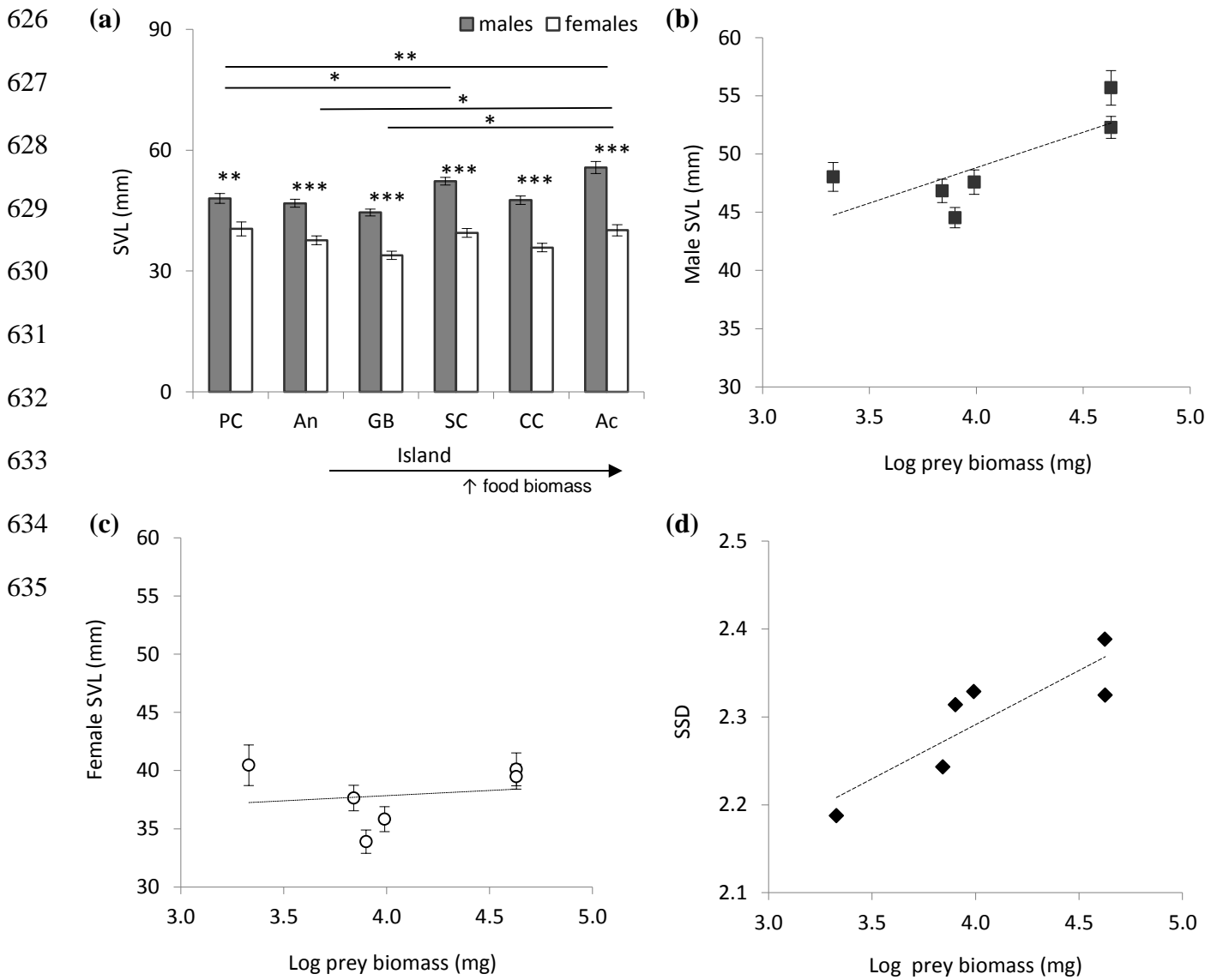
611 **Figure 2.** Sexual size dimorphism (SSD) in laboratory-raised and wild-caught *A. sagrei*.
612 SSD is given for laboratory individuals raised on low (restricted) and high (*ad libitum*)
613 food treatments and for wild individuals caught on each of the six islands sampled. PC:
614 Pidgeon Cay,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

616

617 **Figure 3.** Male and female snout-vent length (SVL, in mm) in laboratory-raised *A.*
618 *sagrei*. (a) Male and female adult SVL under high (*ad libitum*) and low (restricted) food
619 diets (***) indicates $p < 0.0001$); values shown are the predicted means and standard errors.
620 Changes in SVL with age of (b) male and (c) female *A. sagrei* raised under high (black)
621 and low (white) food diets; sexes are shown separately for illustrative reasons only, but

622 were entered in the same model. Values shown are the log-10 transformed predicted
623 means and standard errors.
624

625 **FIGURE 1**

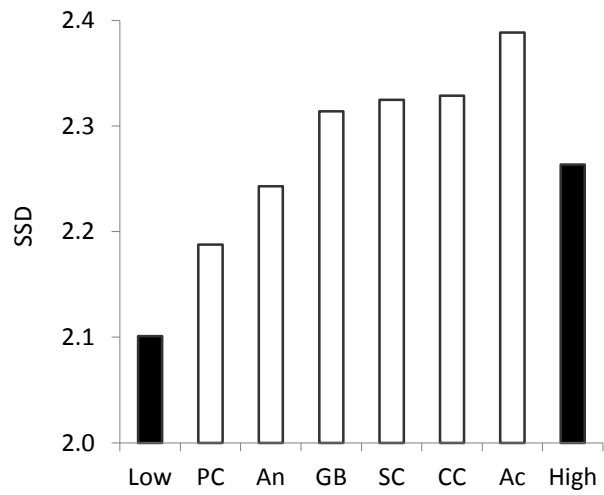


636 **FIGURE 2**

637

638

639



640 **FIGURE 3**

