

Reproductive trade-offs and phenotypic selection change with body condition, but not with predation regime, across island lizard populations

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Abstract

Trade-offs between reproduction and survival are central to life-history theory and are expected to shape patterns of phenotypic selection, but the ecological factors structuring these trade-offs and resultant patterns of selection are generally unknown. We manipulated reproductive investment and predation regime in island populations of brown anole lizards (*Anolis sagrei*) to test (1) whether previously documented increases in the survival of experimentally non-reproductive females (OVX = ovariectomy) reflect the greater susceptibility of reproductive females (SHAM = control) to predation and (2) whether phenotypic selection differs as a function of reproductive investment and predation regime. OVX females exceeded SHAM controls in growth, mass gain and body condition, indicating pronounced energetic costs of reproduction. Although mortality was greatest in the presence of bird and snake predators, differences in survival between OVX and SHAM were unrelated to predation regime, as were patterns of natural selection on body size. Instead, we found that body condition at the conclusion of the experiment differed significantly across populations, suggesting that local environments varied in their ability to support mass gain and positive energy balance. As mean body condition improved across populations, the magnitude of the survival cost of reproduction increased, linear selection on body size shifted from positive to negative, and quadratic selection shifted from stabilizing to weakly disruptive. Our results suggest that reproductive trade-offs and patterns of phenotypic selection in female brown anoles are more sensitive to inferred variation in environmental quality than to experimentally induced variation in predation.

KEYWORDS

agents of selection, costs of reproduction, life-history evolution, phenotypic selection, reproductive strategies

1 | INTRODUCTION

The tenet that increased reproductive investment leads to decreased survival is central to life-history theory (Roff, 2002; Stearns, 1989, 1992). Although this trade-off has been studied extensively in wild

populations (Cox et al., 2010; Flatt & Heyland, 2011; Reznick et al., 2004), much of what we know about its mechanistic basis comes from laboratory systems removed from their natural ecological context (Flatt, 2011; Harshman & Zera, 2007; Partridge et al., 2005; Zera & Harshman, 2001). Such laboratory studies are informative when

viewing reproductive trade-offs in terms of lifespan (Kirkwood, 2017; Speakman, 2020), but they may have limited relevance to actual survival in wild populations, which can be strongly influenced by predation and other ecological sources of mortality (Landwer, 1994; Losos et al., 2004, 2006; Reznick et al., 1990, 2004). Moreover, natural ecological variation in the availability of energy can strongly influence both reproduction and survival, as well as their relationship to one another (Maklakov et al., 2008, 2009; van Noordwijk & de Jong, 1986; Zajitschek et al., 2009). This concern is particularly relevant when testing for the predicted negative relationship between reproduction and survival because individuals in good energetic condition or favourable habitats may exhibit high levels of both survival and reproductive success, thereby obscuring any inherent trade-off between the two (Cox, 2006; van Noordwijk & de Jong, 1986; Partridge & Harvey, 1988; Reznick et al., 2000).

One way to address this concern is to manipulate reproduction in individuals that are randomized with respect to variation in condition and habitat (Cox & Calsbeek, 2010b; Landwer, 1994; Sinervo & DeNardo, 1996). We used this 'phenotypic engineering' approach to generate variation in reproductive investment by randomly assigning female brown anole lizards (*Anolis sagrei*) to either non-reproductive (ovariectomy, OVX) or reproductive (control surgery, SHAM) treatments and then releasing them to islands in the wild. Previous studies have shown that the elimination of reproduction via OVX significantly increases both breeding-season and post-breeding survival (Cox & Calsbeek, 2010b; Cox et al., 2010, 2014). Although the ecological factors structuring this trade-off are unknown, several lines of evidence suggest that reproduction may render anoles more susceptible to predation. First, the physical burden of a clutch reduces sprint speed and running endurance (Cox & Calsbeek, 2010b), as observed in other species (Cooper et al., 1990; Miles et al., 2000; Shine, 2003; Sinervo et al., 1991). Second, SHAM females have higher probabilities of recapture that may indicate higher activity levels and/or more conspicuous behaviour, relative to OVX (Cox et al., 2014). To test whether reproductive SHAM females are actually more susceptible to predation (i.e. to test whether predators structure the survival cost of reproduction), we combined individual-level manipulations of reproductive investment with population-level manipulations of predation by variably including or excluding bird and snake predators from entire island populations of OVX and SHAM anoles. If predator-mediated mortality shapes the trade-off between reproduction and survival, we predicted that the difference in survival between OVX and SHAM should decline (and overall survival should increase) as predators are excluded. Additionally, we used this experimental framework to test whether predators alter the strength and form of phenotypic selection (Calsbeek & Cox, 2010; Losos et al., 2004, 2006) and to test whether phenotypic selection differs as a function of experimental variation in reproductive status.

Elimination of reproduction in female brown anoles also increases their growth, body condition, fat storage, haematocrit and immune function, suggesting that reproductive investment may decrease the energy available for self-maintenance and immune defence, thereby

increasing mortality through a mechanism potentially independent of predation (Cox & Calsbeek, 2010b, 2011; Cox et al., 2010, 2014). In the present study, we observed pronounced inter-island variation in body condition (mass relative to length) at the conclusion of the experiment. Because islands were seeded randomly each year with animals from a single source population (see below), local environmental variation across islands is the most likely explanation for this population-level variation in body condition. Although it was not an *a priori* goal of our study, we opportunistically leveraged this population-level variation to ask whether the survival cost of reproduction changes as a function of average body condition, which we interpret as a holistic proxy for the ability of the local environment to support mass gain and positive energy balance. In support of this interpretation, body condition responds rapidly to food availability in captive *A. sagrei* (Kahrl & Cox, 2015). If energy allocation trade-offs between reproduction and self-maintenance become increasingly less pronounced as environmental quality improves, then the magnitude of the survival difference between OVX and SHAM should decrease as average body condition increases. Alternatively, if energy limitation reduces the extent to which OVX and SHAM females are able to differentially invest in reproduction versus self-maintenance, then the survival difference between OVX and SHAM should increase with average body condition. Spatial and temporal variation in resource availability and environmental quality have been linked to phenotypic selection in other systems (Caruso et al., 2017; Gibbs & Grant, 1987; Price et al., 1984; Wikelski & Trillmich, 1997), so we also tested whether inter-island variation in body condition predicted the strength, direction and form of phenotypic selection on body size.

2 | MATERIALS AND METHODS

2.1 | Study species and natural history

The brown anole (*Anolis sagrei*) is a small, semi-arboreal lizard native to Cuba, the Bahamas and other islands in the West Indies. Female anoles ovulate a single follicle per ovary and alternate ovulation between right and left ovaries, such that clutches typically consist of a single egg. Despite this low per-clutch reproductive investment, annual reproductive effort is substantial because females iteratively lay single eggs at 7–14 d intervals throughout a lengthy reproductive season (March–October). On average across years at our study sites, only 34% of the adult female population survives across the reproductive season (May–September) and only 8% survives from one season to the next (May–May). However, the elimination of reproduction via surgical ovariectomy increases breeding-season survival to 53% and triples inter-annual survival to 24% (Cox & Calsbeek, 2010).

Predators are an important source of mortality for Bahamian populations of brown anoles (Calsbeek & Cox, 2010; Losos et al., 2004; Schoener, 1979; Schoener & Schoener, 1980), but it is unknown whether they differentially impact the survival of OVX and SHAM females. Although other predatory lizard species have been

TABLE 1 Summary of experimental design and effects of surgical treatment on survival, growth in snout-vent length (SVL) and body condition across experimental islands (FC = Flamingo Bay Cay, HC = Heron Cay, NC = Nightmare Cay and MC = Mystery Cay) and the reference site on Great Exuma (FP = February Point)

Year	Site	Predation	N released			Survival			Growth in SVL (mm)			Body condition (residuals)				
			OVX	SHAM	78	OVX	SHAM	Cost	p	OVX	SHAM	Cost	p	OVX	SHAM	Avg.
2007	FP	Natural	80	78	0.525	0.359	0.166	0.035	2.390	1.393	0.997	<0.001	0.0186	-0.0089	0.0049	<0.001
2008	FC	None	78	81	0.359	0.543	-0.184	0.019	1.387	1.127	0.260	0.487	-0.0281	-0.0511	-0.0396	0.036
	HC	Birds	79	81	0.392	0.321	0.071	0.345	1.329	1.340	-0.011	0.971	-0.0194	-0.0329	-0.0262	0.126
	FP	Natural	114	110	0.561	0.327	0.234	<0.001	1.846	1.564	0.282	0.261	0.0165	0.0049	0.0107	0.076
2009	NC	None	75	75	0.347	0.293	0.054	0.484	2.549	1.236	1.313	<0.001	0.0155	-0.0133	0.0011	0.002
	FC	Birds	75	75	0.573	0.493	0.080	0.326	2.509	1.315	1.195	<0.001	0.0344	-0.0055	0.0145	<0.001
	HC	Birds, snakes	74	75	0.284	0.333	-0.049	0.513	2.429	1.518	0.911	<0.001	0.0115	-0.0157	-0.0021	<0.001
	MC	Birds, snakes	75	75	0.253	0.267	-0.014	0.852	1.536	1.505	0.031	0.915	-0.0045	-0.0265	-0.0155	0.011
	FP	Natural	106	105	0.340	0.229	0.111	0.073	2.433	1.650	0.783	0.001	0.0447	0.0155	0.0301	<0.001

Note: Survival is expressed as the proportion of individuals surviving in each treatment. Growth is expressed as the least-squares means from models run separately for each population and including initial SVL and the interaction between initial SVL and surgical treatment. Body condition is the mean of residuals from a single regression of \log_{10} mass on \log_{10} SVL across all years and populations. Costs of reproduction are expressed as the difference in survival or growth between OVX and SHAM. Average body condition is the average of the separate means for OVX and SHAM. *p*-Values are reported from tests for treatment differences conducted separately within each population.

Bold font indicates significant ($p < 0.05$) differences between OVX and SHAM.

shown to shape phenotypic selection on male anoles (Losos et al., 2004, 2006), experimental manipulation of bird and snake predators did not alter phenotypic selection on male anoles (Calsbeek & Cox, 2010), and no study to date has explored whether predation or reproductive investment shape phenotypic selection on female anoles. Confirmed predators of anoles at our study sites include birds (green heron, *Butorides virescens*; American kestrel, *Falco sparverius*) and snakes (Bahamian racer, *Cubophis vudii*), the latter of which are frequently observed hunting and consuming anoles and are suspected to be a major source of mortality (R. Cox and R. Calsbeek, pers. obs.). Other potential predators (i.e. species observed frequently and known to consume lizards, but never observed preying on anoles during our studies) include lizards (Cuban ameiva, *Ameiva ameiva*), snakes (Hispaniolan boa, *Epicrates striatus*) and birds (e.g. smooth-billed ani, *Crotophaga ani*; mangrove cuckoo, *Coccyzus minor*; mockingbirds, *Mimus gundlachi* and *M. polyglottos*).

2.2 | Reproductive manipulations

As a reference for our experimental manipulations of predation, we captured and released females from February Point, a peninsula on the mainland of Great Exuma (23°29'46"N, 75°46'01"W; $n = 158$, 224 and 211 females in 2007, 2008 and 2009, respectively). We refer to this site as a point of reference representing a natural predation regime, rather than as a control in the statistical sense, because it differs from our experimental islands in several ways (e.g. it is an open population with potential migration, it harbours different plant and animal species, and it includes man-made structures such as fences, roads and houses). For our predation experiments, we transplanted females from an area of February Point adjacent to our reference population (23°29'52"N, 75°45'37"W; $n = 599$ for 2009 experiments) or from nearby Stocking Island (23°31'59"N, 75°46'03"W; $n = 319$ for 2008 experiments), onto offshore islands on which we manipulated the predator regime (see below). In both reference and experimental populations, we manipulated reproduction by separating females into two size-matched treatment groups: (1) bilateral ovariectomy (OVX), in which we surgically removed both ovaries to eliminate reproduction, and (2) sham surgery (SHAM), in which we controlled for the effects of anaesthesia and surgery while leaving reproductive function fully intact. Descriptions of surgical procedures, which typically lasted 5 minutes and were accompanied by rapid recovery and high survival, are provided elsewhere (Cox & Calsbeek, 2010; Cox et al., 2010). As described in these previous publications, all individuals were permanently marked with a unique combination of subdermal elastomer tags (2007–2008) or toe clips (2009) to facilitate their identification upon recapture. We have previously show that the survival of SHAM females is nearly identical to that of unmanipulated females at a nearby site (Cox & Calsbeek, 2010), suggesting that our methods for anaesthesia and surgery do not detrimentally impact survival.

One day after surgery, we released females at their exact location of capture (reference site) or introduced them into a new

environment on one of four experimental islands (see below). We included similar numbers of each surgical treatment in each population (Table 1). We conducted surgeries in May, near the beginning of the breeding season, and then left females undisturbed until recapture in September, near the end of the breeding season. Upon recapture, we measured the snout-vent length (SVL, nearest mm) and body mass (nearest 0.01 g) of each individual to calculate its growth (change in mm or g) over the breeding season. We included initial size (SVL or mass) as a covariate in all analyses of growth due to the asymptotic growth trajectories exhibited by anoles and other reptiles, which typically results in a negative correlation between growth rate and initial size (Cox et al., 2009). We also estimated body condition using residuals from the regression of \log_{10} body mass on \log_{10} SVL. This residual index of body condition performs similarly to other indices derived from mass and length (Cox & Calsbeek, 2015), such as the scaled mass index (Peig & Green, 2009, 2010). When measuring selection on initial condition at release (see below), we calculated residuals from separate regressions for each population. When measuring final condition at recapture, we calculated residuals from a single regression to facilitate comparison across populations. Within each population, we inferred costs of reproduction from effects of surgical treatment on survival (logistic regression), SVL growth or mass change (ANCOVA with initial size or mass as a covariate) and body condition (using residuals and by testing for differences in body mass with SVL as a covariate). We conducted these analyses in JMP Pro (versions 15.2 and 16.0). Across populations, we tested for overall effects of surgical treatment on these variables using generalized linear mixed-effects models that also included predation treatment, its interaction with surgical treatment and a random effect of population, as described in the following section.

2.3 | Predator manipulations

In 2008, we used two small islands to experimentally manipulate predation by (1) enshrouding one island with No-Tangle bird netting (Gardener's Supply Company, Burlington, VT) to exclude avian predators and (2) encircling the perimeter of the second island with an identical quantity of netting as a control, while leaving the canopy and interior of the island accessible to birds. With the exception of a single, ephemeral instance of rat invasion on one island in 2007 (Gasc et al., 2010), before the current experiment began, we have never found evidence of snakes (i.e. shed skins), rats (i.e. gnawed branches) or other terrestrial predators on any of the four small islands used for these experiments. Our 2008 manipulations thus resulted in treatments in which lizards were presumably (1) protected from all known predators or (2) protected from terrestrial predators, but exposed to any resident or visiting avian predators, which included yellow-crowned night herons (*Nyctanassa violacea*), green herons (*Butorides virescens*), mockingbirds (*Mimus* spp.) and potentially other species. Experimental islands used in this study ranged from approximately 800 to 2700 m² in size and their vegetation consisted primarily of perennial shrubs and small trees such as buttonwood (*Conocarpus*

erectus) and seagrape (*Coccoloba uvifera*). We first removed all native brown anoles from each island, then established predation treatments and finally released OVX and SHAM females ($n = 78\text{--}81$ per treatment) onto each island by haphazardly distributing them in approximately constant densities throughout the available habitat. In September, we removed the netting and thoroughly searched each island until all visible survivors were recaptured.

In 2009, we repeated this experiment, but expanded its scope by including two additional islands and introducing a third treatment (replicated on two islands) in which we left the canopy open to birds while also introducing two adult male snakes (*Cubophis vudii*) per island. On the two remaining islands, we repeated the two treatments from 2008, rotated such that no island received the same predation treatment in both years. As in 2008, we first removed all native brown anoles from each island, then established predation treatments and finally released OVX and SHAM females ($n = 74\text{--}75$ per treatment) onto each island. Thus, across two years, we created two population-level manipulations of each of three predation treatments (1) no predators (2008 and 2009), (2) bird predators (2008 and 2009) and (3) bird and snake predators (2009 only), which we also compared to the mainland reference population with a natural predation regime (2007, 2008 and 2009). This resulted in a total of 6 island populations (2 replicates per predation treatment) and 3 temporal replicates from our mainland reference site (natural predation regime across 3 years). Below, we refer to these as 6 island or 3 mainland populations when the distinction is important and as 9 populations when pooled for analysis ('population' refers to a unique combination of site and year). We did not attempt to partition effects of birds from those of snakes by including the fourth treatment with only snake predators because preliminary trials indicated that snakes could become entangled in the netting used to exclude birds. Although each predation treatment was established twice and on two separate islands, not all treatments and islands were represented in each year. Consequently, we cannot assess statistical interactions with year, nor can we separate effects of year from those of predation in all cases. Although the sheer scope of our experiment precluded greater replication of predation treatments across a larger number of islands, it also facilitated robust tests for survival differences between OVX and SHAM by virtue of large sample sizes ($n = 74\text{--}81$ females per treatment) within each island.

We tested for effects of surgical treatment and predation treatment on survival using generalized linear mixed-effects models with binomial error distributions, logit link functions and a random effect of population. This random effect accounts for the fact that surgical treatments were administered at the individual level, whereas predation treatments were administered at the population level. We used a predation \times surgical treatment interaction to test the hypothesis that predators differentially impacted the survival of reproductive and non-reproductive females. If predators structure the survival cost of reproduction, we predicted that these interactions would correspond to higher survival of OVX relative to SHAM in the presence of bird and snake predators and that this effect would decrease in magnitude as these predators were sequentially removed,

such that survival would be equivalent in the absence of either predator. Although we did not have any *a priori* expectations that predators would influence SVL growth, mass gain or body condition, we analysed these responses in a similar linear mixed-effects framework to account for predation treatment, its interaction with surgical treatment and the random effect of population. We conducted these analyses using the `lmer` and `glmer` functions in the `lme4` package (Bates et al., 2015) for R (version 4.0.2; R_Core_Team, 2017). We assessed the significance of fixed effects using type 2 Wald chi-squared tests with the `ANOVA` function of the `car` package in R (Fox & Weisberg, 2019).

2.4 | Phenotypic selection analyses

We measured natural selection on body size (SVL) and body condition using standard methods for phenotypic selection analysis (Arnold & Wade, 1984a, 1984b; Lande & Arnold, 1983). Within each year, we calculated relative survival in each population by dividing individual survival from May to September (1 = lived, 0 = died) by the population mean (proportion of individuals that survived) and used this as our measure of relative fitness. We standardized phenotypes within each population to a mean of zero in units of standard deviation, pooling OVX and SHAM females to calculate relative fitness and standardize phenotypes. We estimated linear selection differentials ($\beta \pm \text{SE}$) using coefficients from regressions of relative survival on standardized phenotypes and non-linear selection ($\gamma \pm \text{SE}$) by doubling coefficients (and associated SE) from separate models that included a quadratic (phenotype²) term (Stinchcombe et al., 2008). The resultant estimates describe the extent to which viability selection favoured an increase or decrease in the mean phenotype (β , in units of phenotypic standard deviation) or an increase or decrease in phenotypic variance (γ) in each population. We estimated β and γ separately for OVX and SHAM, and also for both treatments combined. We used GzLM with logit link functions (i.e. logistic regressions) to account for the binomial distribution of survival when determining the significance of individual selection estimates (Janzen & Stern, 1998). Within each population, we used GzLM to test for differences between OVX and SHAM in the direction (positive or negative) and magnitude of linear selection differentials by including treatment-by-phenotype interactions, and for differences in the form (stabilizing or disruptive) and magnitude of non-linear selection by including treatment-by-phenotype² interactions in quadratic models. To test for effects of predation on linear and quadratic selection, we used population-level selection differentials ($\pm \text{SE}$) as units of observation and conducted mixed-effects meta-regressions in `metafor` (version 2.4; Viechtbauer, 2010) implemented in R (version 4.0.2; R_Core_Team, 2017) with predation as a fixed effect and population as a random effect. Among-population variance was estimated using restricted maximum likelihood (REML), and each selection differential was weighted by the inverse of the sum of the among-population variance and the square of the selection differential's standard error. We used the Knapp and Hartung (2003) adjustment for testing significance, which is more conservative and

preferable for smaller sample sizes. We also explored models that included average body condition on each island (see below) and models that separately analysed selection differentials in OVX and SHAM.

2.5 | Variation in body condition among populations

In addition to testing *a priori* predictions concerning experimental effects of predation on survival and phenotypic selection, we also conducted *post hoc* tests exploring effects of the pronounced variation in body condition that we observed among island populations at the conclusion of our study. This variation in body condition is largely due to population differences in the extent to which individuals gained or lost mass during our experiments and is therefore likely to reflect some aspects of environmental quality (e.g. food availability). To derive an index of body condition for each population independent of any differential survival between OVX and SHAM (which always differed significantly in body condition, see Results), we calculated the mean body condition of each group, then took the average of these two means as the measure for each population. We then tested whether variation in this measure of average body condition for each population could explain variation in (1) overall survival, (2) the survival cost of reproduction (difference in survival between OVX and SHAM), (3) the growth cost of reproduction (difference in growth between OVX and SHAM) and (4) the strength and direction of linear and non-linear selection. We tested for significant associations using mixed-effects meta-regressions in the metafor package for R, as described above for phenotypic selection analyses. In all cases, the results of these mixed-effects meta-regressions corroborated the results of simpler analyses using point estimates for each population.

3 | RESULTS

3.1 | Effects of reproductive manipulations

As we have previously shown (Cox & Calsbeek, 2010b; Cox et al., 2010, 2014), the survival of OVX exceeded that of SHAM across three years at the mainland reference site with a natural predation regime (Table 1; Figure 1). However, there was no overall effect of surgical treatment on survival across the 6 experimental island populations (Tables 1 and 2; Figure 1a). Similar to the mainland reference site, OVX females on experimental islands grew more than SHAM females in length (Tables 1 and 2; Figure 1b) and gained more mass (Table 2; Figure 1c). Treatment differences in growth and mass gain were more pronounced for individuals of smaller size at the start of the experiment (Table 2; interactions between surgical treatment and initial SVL or mass). Body condition was also consistently higher in OVX than in SHAM across the experimental islands (Tables 1 and 2; Figure 1d). Directional selection on SVL never differed significantly between OVX and SHAM, but in one population, quadratic selection on SVL was weakly disruptive in OVX versus stabilizing in

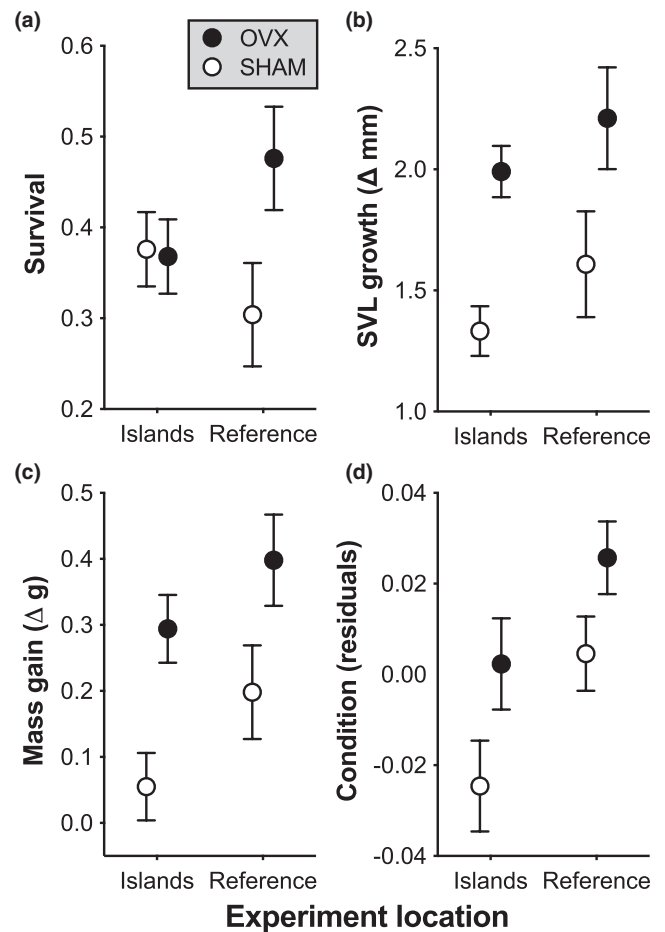


FIGURE 1 Costs of reproduction across experimental islands, compared with those previously demonstrated in the natural reference site, as illustrated by differences between OVX and SHAM females in (a) survival, (b) growth in snout-vent length (SVL), (c) mass gain and (d) body condition (residuals of \log_{10} mass on \log_{10} SVL). Data for experimental islands are least-squares means (\pm SE) from models with fixed effects of surgical treatment, predation treatment and their interaction, plus random effects of population (6 populations). Data for the reference site are least-squares means (\pm SE) from models with a fixed effect of surgical treatment and a random effect of population (3 annual replicates). Analyses of growth and mass gain also include initial SVL (panel B) or initial body mass (panel C), plus their interaction with surgical treatment

SHAM ($\chi^2 = 7.29$; $p = 0.007$; Table 3). Likewise, directional selection on body condition never differed between OVX and SHAM, but in two populations, quadratic selection on body condition was relatively more disruptive in OVX versus stabilizing in SHAM (treatment-by-condition²; both $\chi^2 > 4.1$; $p < 0.05$; Table 4).

3.2 | Effects of predator manipulations

Survival was low on islands exposed to both bird and snake predators, but higher on islands where one or both predators were excluded (predation: $\chi^2 = 6.32$; $p = 0.042$; Table 2; Figure 2a). However, predation regime did not differentially affect the survival of OVX

TABLE 2 Effects of surgical treatment (OVX, SHAM) and predation treatment (none, birds, and birds + snakes) on survival, growth in snout-vent length (SVL), change in body mass, \log_{10} body mass as a function of \log_{10} SVL and body condition (residuals from a single regression of \log_{10} SVL on \log_{10} body mass across all populations)

Fixed effects	df	Survival		Growth in SVL		Mass change		\log_{10} Body Mass		Body condition	
		χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>
Surgery	1	0.06	0.800	34.39	<0.001	78.69	<0.001	58.80	<0.001	68.01	<0.001
Predation	2	6.32	0.042	3.03	0.220	0.57	0.751	0.31	0.856	0.33	0.847
Surgery × Predation	2	3.72	0.155	3.36	0.186	3.10	0.212	0.49	0.783	0.47	0.790
Size covariate	1	—	—	169.54	<0.001	181.85	<0.001	407.46	<0.001	—	—
Surgery × Size covariate	1	—	—	15.23	<0.001	5.79	0.016	—	—	—	—

Note: Interactions between surgical treatment and predation treatment test the hypothesis that predators differentially affect OVX versus SHAM. Initial size (SVL or mass) was used as a covariate in analyses of growth and mass change because growth rate decreases with size. \log_{10} SVL was used as a covariate in analyses of \log_{10} body mass to demonstrate the equivalency of this method and the analysis of body condition residuals. All models include a random effect of population ($n = 6$ island populations) to account for the fact that predation was manipulated at the population level. Significant effects ($p < 0.05$) are indicated in bold.

TABLE 3 Summary of linear ($\beta \pm SE$) and quadratic ($\gamma \pm SE$) selection on standardized snout-vent length (SVL) across experimental islands (FC = Flamingo Bay Cay, HC = Heron Cay, NC = Nightmare Cay and MC = Mystery Cay) and the reference site on Great Exuma (FP = February Point)

Year	Site	Linear selection ($\beta \pm SE$) on SVL			Quadratic selection ($\gamma \pm SE$) on SVL		
		All	OVX	SHAM	All	OVX	SHAM
2007	FP	0.079 ± 0.089	0.023 ± 0.122	0.167 ± 0.129	0.148 ± 0.142	-0.108 ± 0.203	0.350 ± 0.197
2008	FC	0.221 ± 0.086	0.214 ± 0.118	0.209 ± 0.123	-0.328 ± 0.158	0.100 ± 0.220*	-0.824 ± 0.223
	HC	0.048 ± 0.107	0.129 ± 0.165	-0.005 ± 0.139	-0.116 ± 0.179	-0.501 ± 0.317	0.099 ± 0.221
	FP	0.058 ± 0.076	0.157 ± 0.110	-0.104 ± 0.100	0.079 ± 0.121	0.049 ± 0.179	0.099 ± 0.158
2009	NC	-0.138 ± 0.128	-0.121 ± 0.181	-0.141 ± 0.185	-0.134 ± 0.164	-0.214 ± 0.199	0.045 ± 0.300
	FC	-0.024 ± 0.077	-0.082 ± 0.105	0.037 ± 0.114	-0.009 ± 0.137	-0.091 ± 0.177	0.113 ± 0.222
	HC	0.103 ± 0.123	0.007 ± 0.187	0.167 ± 0.165	0.101 ± 0.240	0.044 ± 0.393	0.131 ± 0.319
	MC	0.273 ± 0.180	0.585 ± 0.248	-0.120 ± 0.181	-0.174 ± 0.300	0.100 ± 0.480	-0.292 ± 0.388
	FP	-0.163 ± 0.110	-0.139 ± 0.157	-0.176 ± 0.152	0.023 ± 0.179	0.129 ± 0.261	-0.136 ± 0.243

Note: Estimates of selection are presented separately for OVX and SHAM and for both treatments pooled. Bold font indicates significant ($p < 0.05$) selection. Asterisks indicate significant ($p < 0.05$) differences in selection between OVX and SHAM (i.e. SVL-by-treatment interactions). Sample sizes are indicated in Table 1.

versus SHAM (predation × surgical treatment: $\chi^2 = 3.72$; $p = 0.155$; Table 2; Figure 2b). The only island on which survival differed by surgical treatment was one from which all predators were excluded (SHAM > OVX, Table 1; Figure 2b). Predation treatment did not affect SVL growth, mass gain or body condition, either directly or via interactions with surgical treatment (Table 2). When using linear selection differentials ($\pm SE$) as units of observation in mixed-effects meta-regressions, we found no relationship with predation treatment when combining OVX and SHAM ($F_{2,3} = 0.45$; $p = 0.676$; including average condition on each island as a modifier: $p = 0.367$) or when analysing them separately (OVX: $F_{2,3} = 0.40$; $p = 0.702$; SHAM: $F_{2,3} = 0.11$; $p = 0.897$). When using quadratic selection differentials ($\pm SE$), we found no relationship with predation treatment when combining OVX and SHAM ($F_{2,3} = 1.86$; $p = 0.299$; including average condition on each island as a modifier: $p = 0.183$) or when analysing them separately (OVX: $F_{2,3} = 0.42$; $p = 0.688$; SHAM: $F_{2,3} = 1.15$; $p = 0.427$).

3.3 | Correlations with average body condition

Body condition at the conclusion of the study was always higher in OVX than in SHAM (Table 1), but it also differed substantially across populations (modelling population as a fixed effect across 6 experimental islands: $F_{5,306} = 27.31$; $p < 0.0001$; adding three population replicates from the reference site: $F_{8,495} = 29.69$; $p < 0.0001$). Given that individuals were randomly assigned to islands from a single source population at the start of each year and that we never detected directional selection on initial body condition (across 9 populations, all $p > 0.13$; Table 4), population differences in condition at the conclusion of the study most likely reflect differences in local environments (e.g. food availability). Consistent with this idea, average body condition on each island was strongly correlated with average mass gained on each island during the experiment ($r = 0.88$; $p = 0.002$; Table 5; Figure 4a), but unrelated to directional selection on initial body condition ($r = -0.14$; $p = 0.712$; Table 5). Body

TABLE 4 Summary of linear ($\beta \pm SE$) and quadratic ($\gamma \pm SE$) selection on standardized body condition. Notation as in Table 3

Year	Site	Linear selection ($\beta \pm SE$)			Quadratic selection ($\gamma \pm SE$)		
		All	OVX	SHAM	All	OVX	SHAM
2007	FP	-0.068 \pm 0.089	-0.037 \pm 0.125	-0.035 \pm 0.130	-0.087 \pm 0.124	-0.115 \pm 0.090	0.024 \pm 0.091
2008	FC	-0.022 \pm 0.089	-0.093 \pm 0.129	0.037 \pm 0.121	-0.171 \pm 0.098	0.189 \pm 0.073*	-0.007 \pm 0.067
	HC	0.104 \pm 0.107	0.082 \pm 0.164	0.125 \pm 0.147	0.151 \pm 0.153	0.194 \pm 0.103	-0.070 \pm 0.113
	FP	0.114 \pm 0.076	0.153 \pm 0.106	0.034 \pm 0.106	-0.029 \pm 0.124	-0.072 \pm 0.081	0.047 \pm 0.091
2009	NC	-0.154 \pm 0.129	0.082 \pm 0.208	-0.308 \pm 0.163	0.007 \pm 0.191	-0.017 \pm 0.213	0.061 \pm 0.108
	FC	0.034 \pm 0.078	0.107 \pm 0.102	-0.064 \pm 0.121	-0.068 \pm 0.109	0.070 \pm 0.071*	-0.204 \pm 0.083
	HC	0.085 \pm 0.124	0.186 \pm 0.164	-0.026 \pm 0.191	0.157 \pm 0.178	-0.023 \pm 0.114	0.229 \pm 0.143
	MC	0.048 \pm 0.179	0.104 \pm 0.252	0.001 \pm 0.262	-0.227 \pm 0.215	-0.069 \pm 0.186	-0.136 \pm 0.139
	FP	-0.030 \pm 0.111	-0.076 \pm 0.158	-0.010 \pm 0.155	0.095 \pm 0.169	0.031 \pm 0.122	0.048 \pm 0.120

Note: Sample sizes are indicated in Table 1.

Bold font indicates significant ($p < 0.05$) selection.

condition was also highly correlated with fat storage across individual OVX females ($r = 0.73$; $p < 0.0001$; $n = 27$ females). This pattern was not evident in SHAM females ($r = 0.01$; $p = 0.94$; $n = 19$ females), in which fat stores were minimal and body mass was strongly influenced by the presence of oviductal eggs (eggs: $F_{1,118} = 6.93$; $p = 0.01$; population: $F_{4,110} = 7.24$; $p < 0.001$).

Across populations, the magnitude of the survival difference between OVX and SHAM (i.e. the survival cost of reproduction) was strongly and positively correlated with average body condition at the end of the experiment ($r = 0.70$; $p = 0.037$; Figure 4c), and this association remained significant in a mixed-effects meta-regression accounting for error in the estimation of the survival cost (Table 5). This occurred because the survival of OVX tended to increase with average condition, whereas the survival of SHAM tended to decrease with average condition, although neither of these relationships were significant (Table 5). Consequently, there was no overall correlation between average survival (combining OVX and SHAM) and body condition ($r < 0.01$, $p > 0.99$; Table 5).

Across populations, average growth in SVL increased with average body condition ($r = 0.94$; $p < 0.001$; Table 5; Figure 4b). Although growth rate of OVX increased sharply as a function of average body condition ($r = 0.79$; $p = 0.011$; Table 5; Figure 4b), the slope of this relationship was relatively shallow and not significant in SHAM ($r = 0.64$; $p = 0.065$; Table 5; Figure 4b). Consequently, the magnitude of the growth difference between OVX and SHAM (i.e. the growth cost of reproduction) tended to increase with average body condition, although this relationship was not significant ($r = 0.60$; $p = 0.090$; Table 5; Figure 4d). These associations remained qualitatively similar when accounting for error in the estimation of growth and in the growth cost of reproduction using mixed-effects meta-regressions (Table 5).

Across populations, average body condition was also significantly correlated with point estimates of linear ($r = -0.71$; $p = 0.032$) and quadratic selection differentials for body size ($r = 0.74$; $p = 0.024$). These associations remained significant when accounting for error in the estimation of selection differentials (Table 5). As

condition improved, linear selection shifted from positive to negative (Figure 5a,c), whereas quadratic selection shifted from stabilizing to weakly disruptive (Figure 5b,d).

4 | DISCUSSION

Our results suggest that reproductive trade-offs and patterns of phenotypic selection in female brown anoles are more sensitive to inferred variation in environmental quality than to experimentally induced variation in predation. Although predators have been shown to preferentially consume gravid females in laboratory studies of some species (Koufopanou & Bell, 1984), it has proven difficult to definitively link reproductive status to predator-mediated mortality in natural systems, even when predators are implicated as important agents of mortality (Landwer, 1994; Sinervo & DeNardo, 1996). Likewise, we found no support for the hypothesis that predators differentially impact the survival of reproductive versus non-reproductive females. In part, this may be due to the absence of a consistent survival advantage of OVX relative to SHAM on our experimental islands, which differs from the pattern we have consistently documented in our reference population (Cox & Calsbeek, 2010b; Cox et al., 2010, 2014). One reason for this discrepancy may be that the magnitude of the difference in both growth and survival between OVX and SHAM was strongly correlated with variation in average body condition across populations. This is broadly consistent with the hypothesis that local variation in environmental quality influences the magnitude of life-history trade-offs by establishing the potential for differential allocation to reproduction versus survival.

Although the survival of OVX tended to exceed that of SHAM in the presence of bird predators, the overall survival was lower on the islands from which predators were excluded than on the islands exposed to birds, suggesting that patterns of mortality may not have been strongly influenced by bird predation. Additionally, although overall survival was low in the presence of birds and snakes,

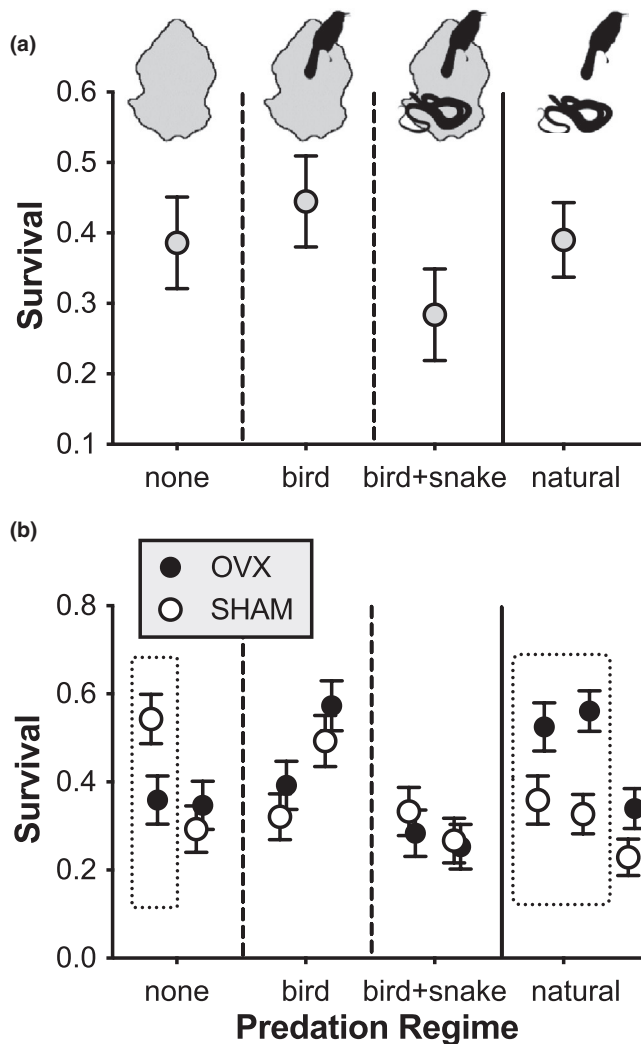


FIGURE 2 Mean (\pm SE) survival as a function of predation treatment (none, birds, birds + snakes) on experimental islands, alongside data from the reference site with natural predators (including birds and snakes). (a) Overall survival combining OVX and SHAM treatments and averaging across two replicates per treatment, illustrating overall low survival in the presence of bird and snake predators. Data are least-squares means from models including effects of surgical treatment, predation treatment, their interaction and a random effect of population. (b) Survival estimated separately for OVX and SHAM for each of the two replicates per predation treatment, illustrating variation between replicates within each predation treatment. Dashed boxes indicate the populations in which survival differed significantly ($p < 0.05$) between OVX and SHAM

evidence for a survival cost of reproduction was entirely absent in this treatment, which was predicted to induce the greatest survival difference between OVX and SHAM. Survival on islands exposed to birds and snakes was within the lower bounds observed across other replicates, so it is unlikely that we failed to detect a survival cost of reproduction simply due to homogenization of survival at unnaturally low levels. Although greater replication of predation treatments at the population level is necessary for stronger inference, our data do not currently support the hypothesis that predator-mediated

mortality is primarily responsible for the trade-off between reproduction and survival (Cox & Calsbeek, 2010b; Cox et al., 2010). Likewise, our results do not strongly support predation as a primary agent of selection on female body size, which agrees with the previously published data from males on these same experimental islands (Calsbeek & Cox, 2010).

This is not to say that extrinsic mortality due to predation has been unimportant in shaping life-history evolution and reproductive investment in *A. sagrei*. The relatively high levels of adult mortality (typically 90% between years) experienced by brown anoles in our populations are likely due, at least in part, to high levels of predation (Figure 1a; Calsbeek & Cox, 2010; Schoener, 1979; Schoener & Schoener, 1980). In other species, high adult mortality devalues the adult stage and favours the evolution of early maturation, small size at maturity and high reproductive effort (Gasser et al., 2000; Reznick et al., 1990, 2004; Stearns, 1992; Stibor, 1992). Likewise, female brown anoles mature within a year of birth at relatively small sizes (38 mm, 1.0 g) and invest heavily in reproduction, as inferred from experimental manipulation and by comparison with other *Anolis* species and lizards in general (Andrews & Rand, 1974; Cox et al., 2010; Reedy et al., 2019). Moreover, the single-egg clutch of anoles may itself be an adaptation to reduce the locomotor burden of reproduction and its associated predation costs (Kratochvil & Kubicka, 2007). Although elimination of this burden improves locomotor performance (Cox & Calsbeek, 2010b), female anoles may have evolved to minimize their locomotor costs to the extent possible while still reproducing. Thus, our results should be interpreted only as evidence against a direct role of predators in differentially impacting the survival of reproductive and non-reproductive females, not as evidence that mortality due to predation has been unimportant in shaping life-history evolution in anoles.

In this and previous studies of *A. sagrei*, elimination of reproduction via bilateral OVX dramatically increased skeletal growth, mass gain, body condition, fat storage, haematocrit and immune function (Figure 2; Cox & Calsbeek, 2010; Cox et al., 2010). Moreover, the removal of a single ovary preserves endocrine function while reducing reproductive investment by 45% and producing intermediate levels of growth, body condition, fat storage and survival (Cox et al., 2014). Therefore, reproduction is energetically expensive for anoles, raising the possibility that energy allocation trade-offs between reproduction and self-maintenance may lead to increased mortality as a cost of reproductive investment. Similar mechanisms have been proposed for a variety of species and represent one of the most prevalent explanations for phenotypic trade-offs between reproduction and survival (Stearns, 1992), and for the evolution of senescence under the disposable soma hypothesis (Kirkwood, 2017; Kirkwood & Holliday, 1979). In their simplest form, these energy allocation trade-offs have been conceptualized as 'Y-models' in which a pool of available energy is diverted into either reproduction or survival (van Noordwijk & de Jong, 1986). Although the utility of these simple Y-models as explanations for complex patterns of life-history evolution has been called into question (Barnes & Partridge, 2003;

Dependent variable	Point estimates		Accounting for error in dependent variable		
	<i>r</i>	<i>p</i>	Slope \pm 1 SE	<i>t</i>	<i>p</i>
Survival (both treatments)	0.001	0.999	-0.03 \pm 1.64	-0.02	0.985
Survival (OVX only)	0.359	0.343	1.94 \pm 1.97	0.99	0.356
Survival (SHAM only)	-0.417	0.265	-2.05 \pm 1.61	-1.28	0.242
Survival cost (OVX-SHAM)	0.697	0.037	3.91 \pm 1.55	2.52	0.040
SVL growth (both treatments)	0.936	<0.001	13.32 \pm 1.99	6.66	<0.001
SVL growth (OVX only)	0.793	0.011	18.69 \pm 5.88	3.18	0.016
SVL growth (SHAM only)	0.638	0.065	4.60 \pm 2.45	1.88	0.100
Growth cost (OVX-SHAM)	0.597	0.090	13.98 \pm 7.46	1.87	0.100
Mass change (both treatments)	0.875	0.002	7.42 \pm 1.59	4.66	0.002
Mass change (OVX only)	0.830	0.006	7.86 \pm 2.06	3.82	0.007
Mass change (SHAM only)	0.794	0.011	5.47 \pm 1.67	3.28	0.014
Mass difference (OVX-SHAM)	0.442	0.234	2.46 \pm 1.86	1.32	0.227
Linear selection on SVL	-0.709	0.032	-4.16 \pm 1.37	-3.03	0.019
Quadratic selection on SVL	0.736	0.024	5.51 \pm 1.81	3.05	0.019
Linear selection on condition	-0.144	0.712	-0.39 \pm 1.28	-0.30	0.770
Quadratic selection on condition	0.287	0.454	1.90 \pm 1.76	1.08	0.316

Note: Statistics are presented for regressions treating each point estimate as an observation ($n = 9$) and for mixed-effects analyses that account for error in the estimation of the dependent variables. Bold font indicates significant relationships.

TABLE 5 Summary of *post hoc* tests for associations between the average body condition in each of 9 populations at the conclusion of the experiment (mean condition of OVX + mean condition of SHAM)/2 and population-level dependent variables including survival, the survival cost of reproduction, SVL growth, the growth cost of reproduction, mass change, and linear and quadratic selection differentials

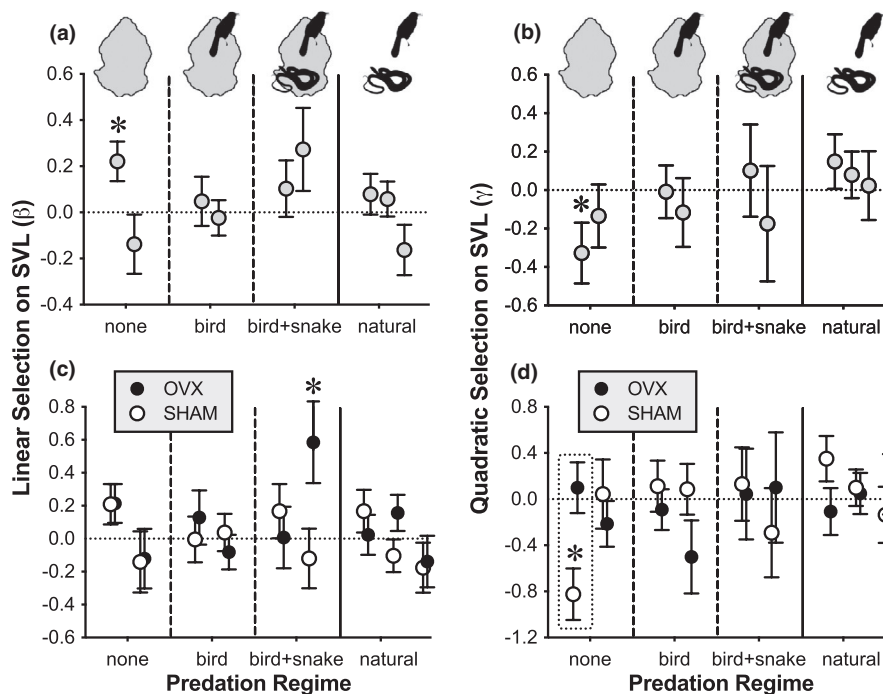


FIGURE 3 Linear (β , left panels) and quadratic (γ , right panels) selection differentials (\pm SE) for snout-vent length (SVL) as a function of predation treatment on experimental islands, alongside data from the reference population with natural predators. (a, b) Estimates pooling OVX and SHAM treatments for each of the replicates in a predation treatment, illustrating no overall effect of predation on the direction, magnitude or form of phenotypic selection on SVL. (c, d) Estimates separated by OVX and SHAM for each of the replicates in a predation treatment, illustrating the overall lack of an interaction between predation and reproductive investment with respect to the direction, magnitude or form of phenotypic selection on SVL. Asterisks indicate significant ($p < 0.05$) selection within a surgical treatment group. Dashed box indicates the only instance in which selection differed significantly between OVX and SHAM

FIGURE 4 Change in (a) body mass and (b) snout-vent length (SVL) for OVX and SHAM females as function of average body condition in each population (6 island populations plus 3 annual population replicates from the natural reference site) at the conclusion of the study. Data are least-squares means (\pm SE) from models with initial mass or SVL as a covariate. OVX and SHAM treatments are offset by 0.02 units along the x-axis for visual clarity. Costs of reproduction (differences in means between OVX and SHAM) with respect to (c) survival and (d) growth increased with average body condition across populations

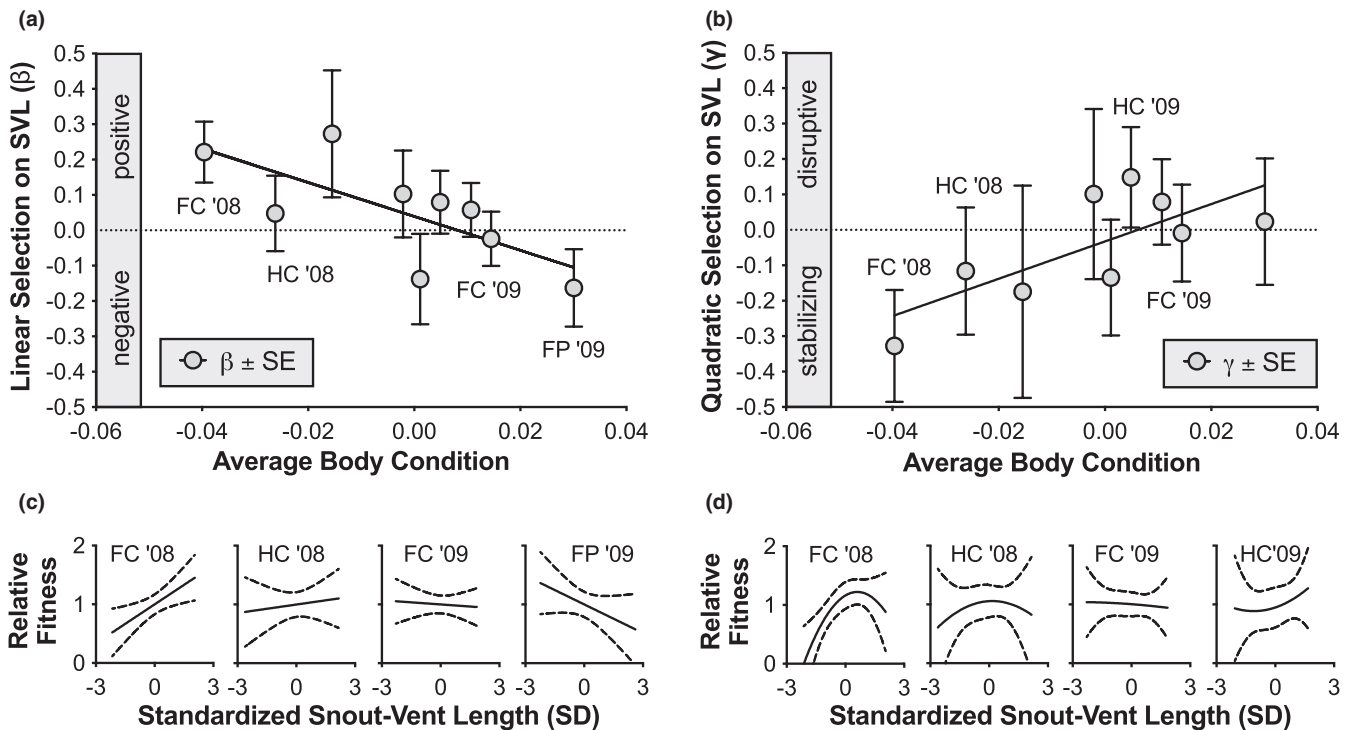
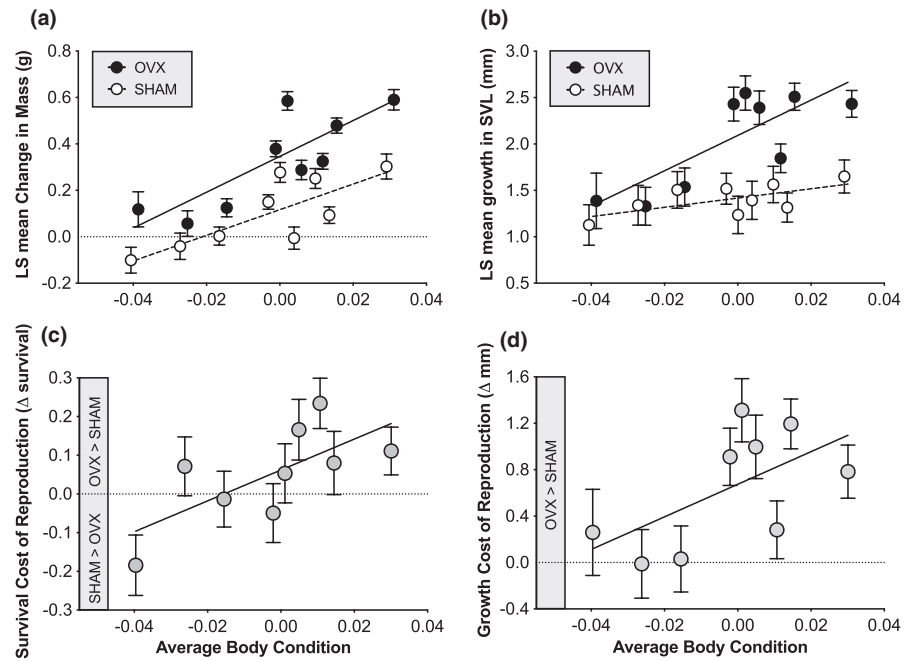


FIGURE 5 (a) Linear (β) and (b) non-linear (γ) selection differentials (\pm SE) for snout-vent length (SVL) as a function of average body condition in each population (6 island populations plus 3 annual population replicates from the natural reference site) at the conclusion of the study, illustrating a shift from positive to negative linear selection (a) and from stabilizing to weak disruptive selection (b), with increasing condition. Lower panels show a subset of corresponding fitness surfaces illustrated by (c) linear and (d) quadratic functions (\pm 95% CI). FC = Flamingo Bay Cay; HC = Heron Cay; FP = February Point; '08 = 2008; '09 = 2009

Edward & Chapman, 2011; Stearns, 2011), they provide a useful heuristic starting point.

Under this framework, it is often implicitly assumed and observed (Stearns, 1992) that reproductive costs become increasingly pronounced as energy availability decreases, forcing a reduction in allocation to self-maintenance. However, this need not be the case

(Reznick et al., 2000), and our results instead suggest that the survival cost of reproduction is only apparent as average body condition increases across populations (Figure 3b). This could occur whether energetically stressful environments preclude anoles from investing heavily in either reproduction (SHAM) or survival (OVX), whereas energetically favourable environments allow for the maximal expression

of Y-model allocation trade-offs by facilitating both high reproductive investment (prioritized by SHAM as the optimal life-history decision) and high investment in self-maintenance and growth (the only options available to OVX). Consistent with this interpretation, the magnitude of the survival cost increased with body condition specifically because the survival of OVX tended to increase with condition, whereas the survival of SHAM tended to decrease. Moreover, the improving 'condition' (mass relative to length) of SHAM females across this gradient may actually reflect an increase in reproductive investment in the form of larger and more frequent oviductal eggs, which strongly influence female body mass and, consequently, our measure of body condition. This scenario would still be consistent with the interpretation that our measure of body condition reflects some aspect of environmental quality or energy availability, but whereas OVX may translate this increased energy into larger fat reserves and improved condition, SHAM may instead increase their reproductive effort and the mass of reproductive tissues. This suggests a natural strategy of increasingly greater reproductive investment at the expense of survival as environmental quality or energy availability increases. Attenuation of the survival cost of reproduction as condition declines is also consistent with the observation that dietary restriction often increases lifespan in other species, potentially because energy is adaptively shunted from reproduction to self-maintenance, as predicted under some conditions by the disposable soma hypothesis and related ideas (Kirkwood, 2017; Shanley & Kirkwood, 2000; Speakman, 2020).

In addition to its association with reproductive costs, average body condition predicted the direction and magnitude of both linear and non-linear selection on body size. We did not have an *a priori* prediction for how selection on body size would shift with condition, and even in studies in which the ecological basis of selection is relatively well understood, shifts in food availability and related axes of environmental quality can generate different patterns of selection on body size. For example, when food resources crashed during El Niño events in the Galapagos Islands, marine iguanas (*Amblyrhynchus cristatus*) experienced strong selection for small body size, which has lower absolute energy requirements (Wikelski & Trillmich, 1997), whereas Darwin's finches (*Geospiza fortis* and *G. scandens*) experienced strong selection for large body size, which improved foraging success on the remaining seed resources (Boag & Grant, 1981; Grant & Grant, 2002). We found that selection tended to favour large size (positive directional selection) and reduce variance in size (negative quadratic selection) when average condition was low, similar to patterns of selection previously documented for females in two other populations of brown anoles (Cox & Calsbeek, 2010a). Selection on body size tended to weaken or reverse as average body condition increased (Figure 5), although the reasons for this shift are not known.

Our interpretations are based on *post hoc* comparisons across six experimental islands and three annual replicates at our reference site. Although our sample sizes within replicates are large ($n = 74\text{--}115$ females per treatment, per replicate) and resultant correlations between body condition and quantitative measures of the cost of reproduction (Figure 4) and phenotypic selection (Figure 5) are relatively strong ($r = 0.60\text{--}0.74$), these correlations may be influenced by

differences across years or by unmeasured dimensions of variation across sites. Greater replication across island populations is therefore desirable, and this is also relevant to our predator manipulations, particularly given that pronounced environmental variation across islands may have obscured any subtle effects of predation. Nonetheless, our experimental results provide no evidence for a role of predation in structuring the trade-off between reproduction and survival. Instead, they are consistent with the idea that energy availability and environmental quality structure the trade-off between reproduction and survival in brown anoles. We opportunistically used body condition as a holistic proxy for the ability of the environment to support mass gain and positive energy balance, and thus, future work would benefit from more direct measures of specific dimensions of environmental quality (e.g. prey abundance, habitat, thermal opportunity) or manipulations of resource abundance (Wright et al., 2013, 2020). Nonetheless, our findings raise the counterintuitive possibility that trade-offs between reproduction and survival may often be more pronounced in energetically favourable environments, while also calling attention to the importance of ecological context in structuring trade-offs among fitness components.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

RMC and RC designed the study and collected the data. RMC and TNW analysed the data. RMC wrote the initial manuscript draft. TNW and RC assisted with preparation of the final manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/jeb.13926>.

DATA AVAILABILITY STATEMENT

Supporting data are archived on Dryad: <https://doi.org/10.5061/dryad.cc2fqz668>.

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