Survival of the fattest? Indices of body condition do not predict viability in the brown anole (*Anolis sagrei*)

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Summary

1. Measures of body mass and length are commonly used to derive indices of condition, which are often assumed to reflect the energetic state of an animal and, by extension, to predict its fitness. However, the relationship between condition and fitness is rarely quantified, and the appropriate method(s) for deriving indices of condition are frequently debated.

2. Data from a decade of mark–recapture studies involving over 4,600 individual lizards (*Anolis sagrei*) and 41 replicates of selection across seven populations were used to test the common assumption that condition, as estimated from body mass and length, is a strong predictor of adult survival, an important component of fitness. Inferences about natural selection were compared between two alternative indices of condition: the popular residual index (R_i), and the scaled mass index (M_i), which was recently proposed as a more appropriate method.

3. Linear, quadratic and correlational selection gradients obtained using R_i and M_i were highly correlated with one another. Relative to variance in selection among replicates and to error associated with the estimation of selection gradients, variance due to the use of alternative condition indices was minor and effectively negligible.

4. Contrary to the intuitive prediction that individuals in better condition should exhibit higher survival, there was no evidence for strong or consistent linear (directional) selection for higher condition indices in either males or females. Significant quadratic (stabilizing or disruptive) selection on condition was similarly rare in both sexes. Correlational selection favoured combinations of large size and high condition in males, but not females.

5. Collectively, these results indicate that inferences about natural selection may be robust to the choice between indices of condition but that indices of condition can be unreliable as proxies for fitness, particularly when relationships between fitness components and condition are contingent upon interactions with other traits.

Key-words: correlational selection, directional selection, quadratic selection, residual index, scaled mass index, selection gradient, viability selection

Introduction

The concept of body condition has a long tradition in animal ecology, serving as both verbal shorthand and empirical proxy for the physiological state or energetic well-being of an individual. Due to the relative ease with which body mass and length (or some other measure of structural size) can be quantified, these measures are frequently used to derive indices of body condition that express the mass of an individual relative to its length (Jakob, Marshall & Uetz 1996; Schulte-Hostedde *et al.* 2005; Peig & Green 2010). Relatively 'fat' individuals with high indices of condition are then assumed to be in a superior energetic or physiological state, and this assumption has been validated by measures of lipid stores, lean muscle mass and other energetic parameters (Ardia 2005; Schulte-Hostedde *et al.* 2005; Peig & Green 2009). Given the intuitive reasoning that individuals in a better energetic state should generally exhibit higher survival and reproductive success, indices of condition have also been proposed as convenient proxies for fitness itself (Jakob, Marshall & Uetz 1996). However, the validity of the assumption that 'fatter is better' is questionable because different studies yield conflicting results about the extent to which indices of condition are correlated with fitness, and because the appropriate methods for calculating indices of condition are subject to debate.

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Generalizations about the extent to which indices of condition predict individual variation in some component of fitness (e.g. survival, mating success, fecundity) are complicated by the fact that relatively few studies have addressed this issue from the standardized framework of selection analyses (Lande & Arnold 1983; Arnold & Wade 1984). For example, the combined data sets from three extensive meta-analyses of phenotypic selection (Kingsolver *et al.* 2001; Cox & Calsbeek 2009; Siepielski, DiBattista & Carlson 2009) included only five studies in which an index of body condition was treated as a phenotypic trait in a standardized selection analysis. Though several of these studies documented fairly strong and consistent selection for high body condition (Lindén, Gustafsson & Pärt 1992; Merilä, Kruuk & Sheldon 2001; Le Galliard, Clobert & Ferriere 2004), others have found no consistent evidence for directional selection on indices of condition (Civantos & Forsman 2000; Hendry, Letcher & Gries 2003; Dibattista *et al.* 2007; Chaine & Lyon 2008). Even in studies that did not quantify selection gradients *per se*, there is no general consensus about the extent to which indices of condition predict variation in survival and reproductive success (Robb, Martin & Hannon 1992; Schmutz & Ely 1999; Husak 2006; Morrison, Davidson & Wilson 2007). This suggests that, despite the intuitive appeal of the maxim that 'fatter is better', indices of condition themselves may often be poor proxies for fitness (Dibattista *et al.* 2007).

Selection analyses quantify the relationship between a measure of relative fitness (or a component of fitness) and standardized variance in one or more phenotypes of interest. Accurate measures of phenotypic variance in body condition are thus required, but the appropriate methods for deriving indices of condition are subject to debate (García-Berthou 2001; Green 2001; Schulte-Hostedde *et al.* 2005; Moya-Laraño *et al.* 2008; Peig & Green 2009, 2010). Most selection analyses have used residuals from the regression of body mass on some aspect of structural size or length as indices of condition (Lindén, Gustafsson & Pärt 1992; Civantos & Forsman 2000; Merilä, Kruuk & Sheldon 2001; Le Galliard, Clobert & Ferriere 2004; Cox *et al.* 2011). However, these residual indices (R_i) have been criticized because they fail to properly account for scaling between mass and length, among other statistical concerns (García-Berthou 2001; Green 2001; Peig & Green 2009, 2010). The scaled mass index (M_i) was recently proposed as a superior alternative to R_i and other indices of condition on statistical grounds, and it also performs better as an empirical predictor of the relative size of energy reserves and related body components (Peig & Green 2009, 2010). Whether these two alternative indices generate appreciably different results in selection analyses has not been tested.

The goal of this study was to assess the relationship between body condition and survival in the brown anole (*Anolis sagrei*, Fig. 1), a small lizard for which natural selection has been measured via mark–recapture studies on

Fig. 1. A female brown anole, *Anolis sagrei*. Illustration by Amy Y. Zhang.

over 4600 individuals spanning 10 years and multiple populations in the Bahamas. This large, multi-year data set was used to test whether body condition, as commonly estimated from body mass and snout-vent length (SVL), is actually correlated with adult survival, an important component of fitness. The second objective of this study was to directly compare two alternative indices of condition to determine whether and how the choice between indices might influence estimates of natural selection. For simplicity, this comparison was restricted to R_i, currently the most widespread method for assessing condition, and M_i, which has recently been proposed as a superior alternative (Peig & Green 2009, 2010). If the choice between indices were to significantly alter inferences about the relationship between condition and fitness, this would strengthen the argument for adopting an index (such as M_i) that more accurately accounts for scaling and reflects underlying differences in energetics.

Materials Methods

STUDY SPECIES AND SAMPLING DESIGN

The brown anole (*Anolis sagrei*) is a small, sexually dimorphic lizard with many attributes that facilitate large-scale studies of natural selection. Adults occur at extremely high densities (typically 0·1–0·4 per m²), exhibit high site fidelity, are visually conspicuous and have low rates of survival (typically 25–50%) over the breeding season (May–September). Survival from one year to the next is also low (typically 5–15%), such that most individuals die before their second breeding season. Since 2004, mark–recapture studies have been conducted on seven *A. sagrei* populations in the Commonwealth of the Bahamas. Two of these populations are located on the main islands of Great Exuma (23°29′N, 75°45′W) and Eleuthera (24°50′N, 76°19′W). Five others are located on small (500–1600 m²) cays offshore from Georgetown, Great Exuma. Details on these populations and analyses of natural selection on various phenotypic traits are reported in a series of previous papers (Calsbeek & Irschick 2007; Calsbeek & Smith 2007, 2008; Calsbeek 2008, 2009; Calsbeek & Bonneaud 2008; Calsbeek, Bonneaud & Smith 2008; Calsbeek, Bonvini & Cox 2010; Calsbeek & Cox 2010, 2012; Cox & Calsbeek 2010a,b, 2011). The present study synthesizes a decade of mark–recapture data from these populations to compile 22 replicates of selection on males and 19 replicates of selection on females. Each replicate represents an

episode of viability selection measured over a single breeding season for a single population. Several previous mark–recapture studies included phenotypic manipulations of reproductive investment (Cox & Calsbeek 2010a, 2011; Cox *et al.* 2010), but data reported herein are restricted to unmanipulated individuals and, in several replicates, comprise the control groups from experimental studies. A complete accounting of total lifetime fitness would require additional data on juvenile survival, mating success, fertilization success and fecundity, but these components of fitness were not quantified during the decade of mark–recapture studies synthesized here, so this analysis focuses exclusively on the relationship between condition and adult survival as a component of fitness.

INDICES OF BODY CONDITION

To restrict selection analyses to adults, mark–recapture data sets were filtered to exclude any females below 38 mm SVL (the minimum size at which oviductal eggs are observed, Cox & Calsbeek 2011) and any males below 40 mm SVL (a minimum estimate of sexual maturity, at which point many adult secondary sexual characters first develop and testes begin to enlarge; Cox & Calsbeek 2010a,b). This resulted in a data set of 4608 adults (2344 females, 2264 males).

To calculate the residual index of condition (R_i), residuals were obtained from ordinary least squares (OLS) regressions of $\log_{10}$ body mass on $\log_{10}$ SVL, using separate regressions for each sex and each selection replicate. Correlations between mass and SVL from these regressions were high for males (mean $r^2 = 0.89$; range = 0·81–0·95 across 22 replicates) and somewhat lower for females (mean $r^2 = 0.66$; range 0·52–0·80 across 19 replicates). This difference presumably reflects the greater range in body size of adult males (40–73 mm, 0·7–8·2 g) relative to adult females (38–52 mm, 0·6–3·2 g), along with potential confounding variation the body mass of females due to the presence or absence of oviductal eggs at the time of capture (anoles lay single-egg clutches at *c*. 10-day intervals throughout the breeding season, such that females variably contain zero, one or two eggs at the time of capture). Nonetheless, these strong correlations between mass and length satisfy an important assumption underlying the interpretation of residuals as indices of condition (Schulte-Hostedde *et al.* 2005). The scaled mass index of condition (M_i) was calculated as follows:

$$M_i = M * [SVL_0/SVL]^{b_{SMA}}$$

where M and SVL are the mass and SVL of the individual, SVL_0 is the arithmetic mean SVL of the population, and b_{SMA} is the standardized major axis slope from the regression of ln mass on ln SVL for the population (Peig & Green 2009, 2010). The b_{SMA} exponent was calculated indirectly as the slope of the OLS regression divided by Pearson's correlation coefficient (LaBarbera 1989; Peig & Green 2009, 2010).

As an alternative method for assessing body condition, some authors advocate the direct analysis of body mass (in lieu of a condition index derived from a separate regression) using ANCOVA with length as a covariate (García-Berthou 2001). However, treating mass and SVL as traits in a multivariate selection analysis is problematic because the two are highly correlated (see above), such that resultant estimates of selection gradients can be highly unstable due to multicollinearity (Fairbairn & Preziosi 1996; Fairbairn & Reeve 2001). Moreover, this approach does not permit a condition phenotype to be estimated for each individual, thus complicating the visualization of selection on condition. In the Supporting Information, we report the results of multivariate selection analyses with standardized body mass used in lieu of condition indices. In nearly every case, replicates characterized by significant linear or quadratic selection on condition indices were also characterized by significant linear or quadratic selection on body mass itself (compare Tables S1 and S2 with Table S4 in Supporting Information).

ANALYSES OF NATURAL SELECTION

Natural selection was quantified following standard procedures for calculating selection gradients (Lande & Arnold 1983; Arnold & Wade 1984). All phenotypes (R_i, M_i, SVL, mass) were standardized to a mean of zero and unit variance (SD) within each replicate and each sex. Relative survival was calculated by dividing individual survival (0 or 1) by mean survival within each replicate and each sex. Linear selection gradients (β ± SE) were calculated as the partial regression coefficients from multivariate regressions of relative survival on standardized SVL and body condition (R_i or M_i). Statistical significance ($P < 0.05$) of each selection gradient was assessed by repeating these multivariate regressions using generalized linear models (GzLM) with survival (0 or 1) as the dependent variable and logit links to account for binomial survival distributions (Janzen & Stern 1998). Six females and six males with extreme condition values were omitted from selection analyses due to potential measurement error in either mass or SVL.

Nonlinear (quadratic and correlational) selection was estimated using analogous models that included standardized SVL and condition (R_i or M_i), quadratic (squared) terms for SVL and condition, and the interaction between SVL and condition (correlational selection) (Lande & Arnold 1983; Brodie, Moore & Janzen 1995). Quadratic selection gradients (γ ± SE) were obtained by doubling the partial regression coefficients (and their associated SE) for squared terms (Stinchcombe *et al.* 2008). Correlational selection gradients ($\gamma_{1,2}$ ± SE) were obtained from the partial regression coefficients of cross-product terms. Significance ($P < 0.05$) was tested using GzLM with survival (0 or 1) as the dependent variable and logit links to account for binomial survival distributions (Janzen & Stern 1998). Overall patterns in selection across replicates were examined by treating each point estimate of linear, quadratic or correlational selection from an individual replicate as an observation and testing whether each type of gradient differed significantly ($P < 0.05$) from zero using *t*-tests or Wilcoxon tests (when selection gradients were not normally distributed).

To maximize statistical power and to test for overall selection on SVL and condition within each sex, data were pooled across all replicates and analysed by GzLM with survival (0 or 1) as the dependent variable and SVL, condition (R_i or M_i), and replicate as independent variables. These models also included squared terms for SVL and condition (to assess quadratic selection), the interaction between SVL and condition (to assess correlational selection), and all interactions between replicate and linear, quadratic, and cross-product terms (to assess variation in linear, quadratic and correlational selection among replicates). Logit links were used to account for binomial survival distributions. Not all populations were studied in all years, so effects of year could not be distinguished from effects of population, which were jointly modelled as effects of replicate. The results of these global analyses were visualized with projection surfaces derived from analogous models excluding replicate effects (for visual clarity). All tests of significance were derived from models that included effects of replicate and its interactions with linear, quadratic and cross-product terms.

Results

COMPARISON OF R_i AND M_i AS INDICES OF CONDITION

The two measures of condition (R_i and M_i) were highly correlated across individual females (overall: $r^2 = 0.89$;

$n = 2338$; within replicates: $0.81 < r^2 < 0.95$) and males (overall: $r^2 = 0.93$; $n = 2258$; within replicates: $0.90 < r^2 < 0.95$) (Fig. S1, Supporting information). Measures of linear selection (β) on condition using either index were highly correlated in females ($r^2 = 0.97$, $n = 19$; Fig. 2a) and males ($r^2 = 0.97$, $n = 22$; Fig. 2b). Correlations between selection gradients for R_i and M_i were slightly weaker for measures of quadratic selection (γ) on condition in females ($r^2 = 0.83$ overall, $r^2 = 0.93$ when excluding one outlier with low sample size and high SE; Fig. 2c) and males ($r^2 = 0.93$; Fig. 2d), as well as for correlational selection ($\gamma_{1,2}$) on combinations of condition and SVL (females: $r^2 = 0.83$; Fig. 2e; males: $r^2 = 0.91$; Fig. 2f). The extent to which estimates of selection tended to converge when estimated from R_i vs. M_i increased with sample size, particularly for quadratic and correlational selection gradients (Fig. 3). Irrespective of sample size, the standard errors associated with selection gradients for R_i and M_i were broadly overlapping for every estimate of linear, quadratic and correlational selection. When combining data across replicates and assessing global patterns of selection on SVL and condition, inferences about the factors influencing survival in males and females were highly congruent using either R_i or M_i (Table 1).

LINEAR SELECTION ON CONDITION AND SIZE

Statistically significant ($P < 0.05$) linear selection for higher condition was detected in only one of 19 (using R_i) or zero of 19 (using M_i) replicates for females, and in only one of 22 (using R_i) or zero of 22 (using M_i) replicates for males (Table S1, Supporting information). Similar patterns are expected purely from chance at $\alpha = 0.05$, and none of these estimates of selection are significant after correction for multiple comparisons. When treating the point estimate of selection (β) for each replicate as an observation, mean values of linear selection gradients for M_i did not differ from zero for females ($t = 0.24$; d.f. = 18; $P = 0.182$; Fig. 4a) or males ($t = 1.26$; d.f. = 21; $P = 0.22$; Fig. 4a). Results were qualitatively similar using R_i (each $P > 0.14$).

Linear selection on SVL tended to be positive, but this trend was only significant in females ($t = 2.22$; d.f. = 18; $P = 0.035$; Fig. 4a), not males ($t = 1.35$; d.f. = 21; $P = 0.19$; Fig. 4a). However, significant linear selection on SVL occurred in over a quarter of individual selection replicates for males (6 of 22 replicates, Table S1). Moreover, global analyses of individual survival across all replicates revealed positive associations between SVL and survival in both females and males, but no relationship between condition and survival in either sex using either R_i or M_i
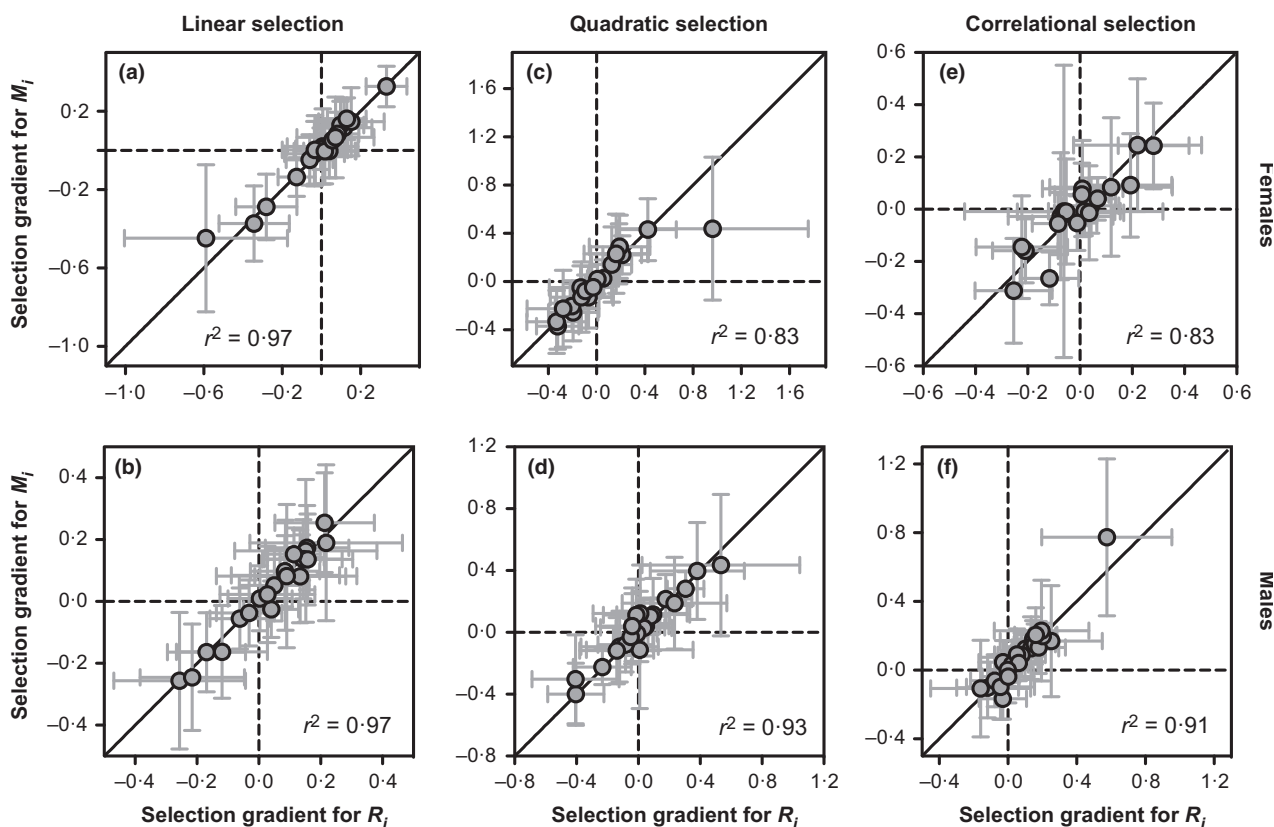

Fig. 2. Scatterplots illustrating correlations between selection gradients ($\pm$ SE) estimated using either R_i or M_i as indices of condition. Gradients are shown separately for (a–b) linear selection on condition, (c–d) quadratic selection on condition and (e–f) correlational selection on SVL and condition. Top panels correspond to females ($n = 19$ replicates), and bottom panels correspond to males ($n = 22$ replicates). Diagonal lines indicate equivalence of selection gradients estimated using R_i and M_i.
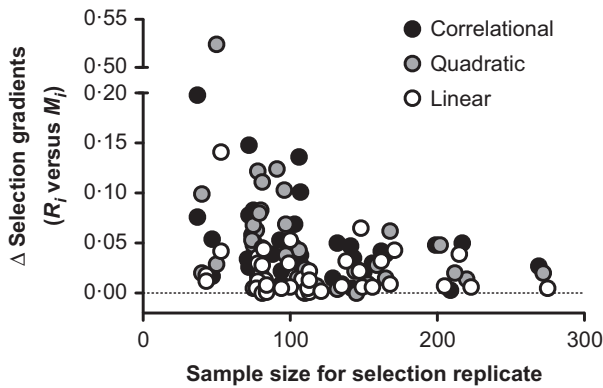
Fig. 3. Funnel plot illustrating the discrepancy between selection gradients estimated using R_i vs. M_i (calculated as the absolute value of the difference between gradients) as a function of sample size for each selection replicate. Symbols for linear and correlational selection are slightly offset (+3 or −3 units, respectively) along the *x*-axis to facilitate visualization.

(Table 1). The relationship between survival and SVL also varied among replicates in both sexes (Replicate*SVL effects, Table 1), but interactions with replicate were not observed for condition (Table 1).

QUADRATIC SELECTION ON CONDITION AND SIZE

Statistically significant ($P < 0.05$) quadratic selection on condition was observed in zero of 19 (using R_i) or one of 19 (using M_i) replicates for females, and in two of 22 (using either R_i or M_i) replicates for males (Table S2, Supporting information).

Similar patterns are expected purely from chance at $\alpha = 0.05$, and none of these estimates of selection are significant after correction for multiple comparisons. When treating the point estimate of selection (γ) for each replicate as an observation, the mean of quadratic selection gradients for M_i did not differ from zero for females ($t = 0.20$; d.f. = 18; $P = 0.84$; Fig. 4b) or males ($t = 0.78$; d.f. = 21; $P = 0.44$; Fig. 4b). Thus, quadratic selection on M_i exhibited no clear trend towards stabilizing or disruptive selection in either sex, and results were qualitatively similar using R_i (each $P > 0.67$).

Quadratic selection gradients for SVL tended to be positive (disruptive selection) for males ($t = 2.44$; d.f. = 21; $P = 0.024$; Fig. 4b). Although quadratic selection gradients for SVL in females were not significantly different from zero across replicates ($t = 0.99$; d.f. = 18; $P = 0.33$; Fig. 4b), they tended towards negative values (stabilizing selection) and were significantly negative within three individual replicates (Table S2). Global analyses of individual survival across all replicates generally corroborated these patterns, showing no evidence for quadratic selection on condition (R_i or M_i) in either sex (Table 1). Females exhibited an overall pattern of negative quadratic (stabilizing) selection on size (SVL^2) that also varied among replicates (Replicate*SVL^2 effects, Table 1), but no evidence for quadratic selection on size was evident in males (Table 1).

CORRELATIONAL SELECTION ON CONDITION AND SIZE

Correlational selection on condition and SVL was rarely significant within individual selection replicates (Table S3,

Table 1. Global patterns of selection on SVL and condition (R_i or M_i) based on generalized linear models with survival (live/die) as the dependent variable and logit links for binomial distributions

Sex	Effect	d.f.	R_i condition		M_i condition	
			χ^2	P	χ^2	P
Females	SVL	1	**17·08**	**<0·001**	**13·66**	**<0·001**
	Condition	1	0·04	0·839	0·03	0·863
	SVL^2	1	**4·27**	**0·039**	**4·21**	**0·040**
	$Condition^2$	1	0·29	0·593	0·47	0·495
	SVL*Condition	1	0·47	0·495	0·00	0·995
	Replicate	18	**88·08**	**<0·001**	**86·58**	**<0·001**
	Replicate*SVL	18	**32·14**	**0·021**	26·75	0·084
	Replicate*Condition	18	26·47	0·089	25·16	0·121
	Replicate*SVL^2	18	**35·37**	**0·009**	**31·93**	**0·022**
	Replicate*$Condition^2$	18	21·33	0·263	21·93	0·235
	Replicate*SVL*Condition	18	21·78	0·242	21·78	0·242
Males	SVL	1	**7·13**	**0·008**	**11·26**	**<0·001**
	Condition	1	1·99	0·158	1·58	0·209
	SVL^2	1	0·38	0·539	0·04	0·852
	$Condition^2$	1	0·00	0·973	0·07	0·797
	SVL*Condition	1	**6·10**	**0·013**	**6·24**	**0·013**
	Replicate	21	**58·75**	**<0·001**	**57·82**	**<0·001**
	Replicate*SVL	21	**34·87**	**0·029**	**34·98**	**0·028**
	Replicate*Condition	21	21·08	0·454	22·36	0·379
	Replicate*SVL^2	21	26·09	0·203	22·62	0·365
	Replicate*$Condition^2$	21	27·01	0·170	29·29	0·107
	Replicate*SVL*Condition	21	17·94	0·653	22·59	0·366

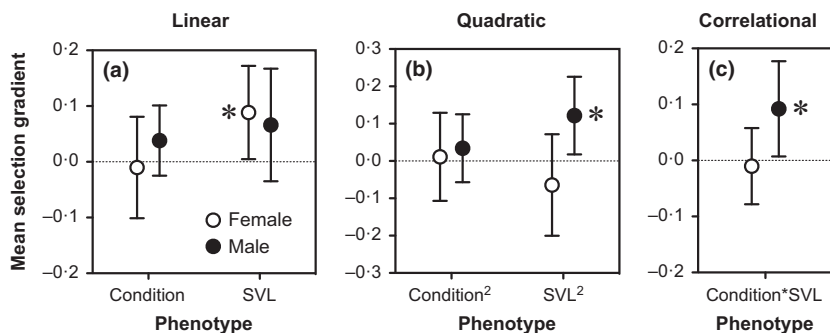Bold values indicate statistical significance at $P < 0.05$.

Fig. 4. Overall mean (± 95% CI) strength and direction of (a) linear, (b) quadratic and (c) correlational selection gradients for condition (M_i) and SVL, shown separately for females (means of $n = 19$ replicates) and males (means of $n = 22$ replicates). Asterisks indicate that the mean is significantly ($P < 0.05$) different from zero based on a one-sample *t*-test.

Supporting information). However, treating the point estimate of correlational selection ($\gamma_{1,2}$) from each replicate as an observation revealed a significant overall tendency towards positive correlational selection favouring combinations of large SVL and high M_i in males ($t = 2.26$; d.f. $= 0.21$; $P = 0.034$; Wilcoxon $P = 0.021$; Fig. 4c). R_i yielded similar results ($P < 0.02$ for parametric and Wilcoxon tests). This pattern was also evident in global analyses combining individual data from all replicates (SVL*Condition effects, Table 1). No trend towards positive or negative correlational selection on condition and SVL was evident in females when using point estimates of correlational selection as observations ($t = 0.32$; d.f. $= 0.18$; $P = 0.76$; Fig. 4c) or when assessing global patterns across all individuals (Table 1). These patterns are illustrated by projection surfaces from generalized linear models pooling data across replicates (similar to the above analyses, but without effects of replicate). Whereas selection acted only on SVL in females (Fig. 5a), it favoured combinations of large SVL and high condition in males (Fig. 5b).

Discussion

Indices of body condition derived from mass and length are often used as convenient proxies for energetic state and as presumed correlates of fitness (Jakob, Marshall & Uetz 1996). However, the actual relationship between such indices of body condition and fitness is rarely assessed, and the appropriate method(s) for deriving indices of condition are frequently debated (Green 2001; Ardia 2005; Schulte-Hostedde *et al.* 2005; Peig & Green 2009, 2010). These two concerns are related because selection analyses that quantify the relationship between body condition and fitness require accurate measurements of phenotypic variation in condition among individuals. Although recent work (Peig & Green 2009, 2010) suggests that the scaled mass index (M_i) is a better descriptor of individual variation in condition than the popular residual index (R_i), inferences about natural selection on condition in this study were robust to the choice between these indices. In the brown anole, either index of condition is a surprisingly weak predictor of survival, influencing this component of fitness only through interactions with body size, and then only in males. This conclusion is based on a decade of selection analyses

involving over 4600 individuals from seven different locations; thus, it is unlikely to reflect the idiosyncrasies of spatial or temporal variation in selection (e.g. Moller *et al.* 2006; Siepielski, DiBattista & Carlson 2009). Below, we discuss the equivalence of alternative condition indices and the apparent lack of selection on condition as these findings relate to anoles and other animals.

The scaled mass index (M_i) has been advocated as an alternative to the residual index (R_i) and other measures of condition on both theoretical and empirical grounds (reviewed in Peig & Green 2010). Theoretically, M_i accounts for scaling relationships between mass and length more appropriately than R_i and other indices (Peig & Green 2009). Empirically, M_i is a better indicator of the relative size of energy reserves and related body components, compared to R_i and other indices (Peig & Green 2009, 2010). Although R_i and M_i were highly correlated in the data sets for this study ($0.91 < r < 0.98$; Fig. S1), they were not perfectly correlated; thus, they generated slightly different results in the context of selection analysis (Figs. 2–3; Tables S1–S3, Supporting information). However, relative to variance in the strength and form of selection among replicates, and relative to the error typically associated with estimating selection gradients within replicates, variance due to the use of R_i vs. M_i was minor and effectively negligible (Fig. 2). In particular, estimates of linear selection were highly correlated ($r^2 = 0.97$ across replicates) using either index of condition (Fig. 2a–b). Measures of quadratic and correlational selection were slightly more variable between condition indices (Fig. 2c–e), but this is not surprising, given that robust estimates of nonlinear selection typically require sample sizes in the hundreds (Brodie, Moore & Janzen 1995). Indeed, the largest discrepancies between quadratic and correlational selection gradients for R_i and M_i occurred for replicates with low sample sizes (Fig. 3).

Because most *a priori* hypotheses are likely to be concerned with directional relationships between fitness and condition (i.e. 'fatter is better'), the results of this study suggest that R_i and M_i are unlikely to yield substantially different inferences about natural selection on condition. This is particularly true when sample sizes are sufficiently large for robust estimates of selection (Fig. 3). Of course, indices of condition should still be selected on the basis of
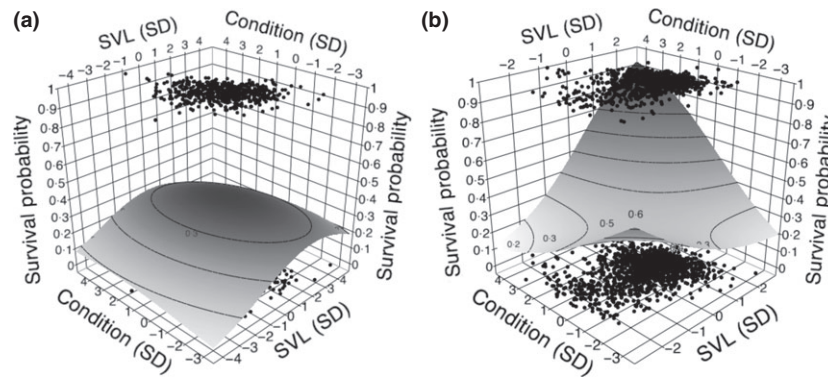
Fig. 5. Projection surfaces illustrating predicted survival probability as a function of condition (M_i) and size (SVL) for (a) females and (b) males. Surfaces are from generalized linear models using survival (0,1) and standardized (mean = 0, unit SD) values for condition, SVL, condition*SVL and quadratic terms for each trait. Each point represents an individual that lived or died (n = 2338 females, 2258 males). For clarity, replicates are pooled and replicate effects are not modelled, although the corresponding statistical tests for correlational selection included replicate effects and interactions (Table 1). Selection acted purely on SVL in females, but favoured combinations of large SVL and high condition in males.

first principles and, whenever possible, their empirical ability to predict relevant aspects of organismal energetics and physiology (Green 2001; Peig & Green 2009, 2010). An alternative to the 'fatter is better' hypothesis is that indices of condition should be subject to stabilizing selection in which the 'fattest' individuals also suffer reduced fitness. The present study provided no empirical support for this hypothesis, and though measures of quadratic selection occasionally differed when estimated from R_i vs. M_i (Figs 2–3), this was generally only the case for replicates in which sample sizes were too small for precise estimates of quadratic selection.

Contrary to the intuitive prediction that individuals in better condition should exhibit higher survival, significant linear (directional) selection for higher condition was rarely observed in *A. sagrei* females or males (Table S1). This is not simply an issue of weak statistical power due to insufficient sample sizes within replicates, as the overall means (and medians) of linear selection gradients across all replicates did not differ from zero in either sex (Fig. 4a), nor did individual variation in condition predict survival when combining data from over two thousand individuals of each sex (Table 1). By contrast, selection on body size (SVL) was frequently significant within replicates (in males, Table S1), differed from zero when treating each selection gradient as an observation (in females, Fig. 4a), and was highly significant in both sexes when combining individual data from all replicates (Table 1). Thus, the analyses in this study were generally capable of detecting significant phenotypic selection on traits under somewhat stronger and/or more consistent selection, such as SVL (though selection on SVL was also variable in both strength and direction, see Tables S1–S3, Supporting information). Indeed, the only evidence for natural selection on body condition in *A. sagrei* occured in the form of correlational selection favouring males who were both large and in high body condition (Figs 4c and 5b, Table 1). Similar

patterns of correlational selection on size and condition have been observed in hatchlings of the lizard *Psammodromus algirus* (Civantos & Forsman 2000). This illustrates the importance of testing for correlational selection even when traits are mathematically uncorrelated, as is often the case for indices of body condition and the measures of length or size from which they are derived.

The lack of any strong and consistent relationship between body condition and survival challenges the use of condition as a proxy for this component of fitness (Jakob, Marshall & Uetz 1996), at least in adult brown anoles. Given that brown anoles are short-lived (only 5–15% of adults typically survive to a second breeding season) and experience substantial mortality due to predation (Schoener 1979; Losos, Schoener & Spiller 2004; Losos *et al.* 2006; Calsbeek & Cox 2010), one possibility is that extrinsic sources of mortality (which may often be random with respect to body condition) are the primary determinants of survival in this species. However, a previous study of *A. sagrei* hatchlings and juveniles revealed positive directional selection for high body condition (R_i) in both males and females (Cox *et al.* 2011). In this previous study, fitness components were measured as survival in captivity over the first 1–3 months following hatching, and as survival in the wild over the subsequent 8 months of life, at which point most individuals were approaching reproductive maturity. In each successive episode of selection, hatchlings and juveniles in high condition exhibited higher survival rates (Cox *et al.* 2011). Indices of condition (typically using some variant of R_i) also predict survival in juveniles of other lizard species (Le Galliard, Clobert & Ferriere 2004), but are unrelated to survival in juveniles and/or adults of several others (Civantos & Forsman 2000; Husak 2006).

Across other taxa, indices of condition predict survival in fledgling songbirds (Lindén, Gustafsson & Pärt 1992; Kruuk, Merila & Sheldon 2001; Merilä, Kruuk & Sheldon

2001), but are unrelated to survival in salmon and sharks (Hendry, Letcher & Gries 2003; Dibattista *et al.* 2007). Moreover, indices of condition are often correlated with adult survival in one sex, age class or season, but unrelated to survival in another (Robb, Martin & Hannon 1992; Schmutz & Ely 1999; Civantos & Forsman 2000). Indices of condition also predict variation in other components of fitness, such as fecundity and mating success, in some species, but not others (Chastel, Weimerskirch & Jouventin 1995; Dobson & Michener 1995; Wauters & Dhondt 1995; Chaine & Lyon 2008). Even when identical methods are applied to related species in the same environments, the relationship between indices of condition and fitness often differs between species (Lindén, Gustafsson & Pärt 1992; Chastel, Weimerskirch & Jouventin 1995). These results corroborate the main conclusion of this study: indices of body condition may often be unreliable as proxies for fitness or its components.

The lack of a correlation between indices of condition and adult survival in brown anoles raises the question of whether this primarily reflects a weak correspondence between R_i or M_i and actual energetic condition, or the absence of a relationship between energetic condition and adult survival. For example, more direct measures of energetic condition, such as lipid stores, are often subject to positive directional selection (Blanckenhorn, Kraushaar & Reim 2003; Blanckenhorn *et al.* 2004). In either sex, body mass could vary due to factors that are unrelated to energetic condition *per se*, such as reproductive status, hydration status, the presence or absence of food in the gut, or variation in mass related to disease or parasitism. In female anoles, the correlation between mass and SVL within each population was generally weaker than in males, and the presence or absence of an oviductal egg at the time of measurement likely introduced a substantial amount of variance in body mass of females that was unrelated to energetic condition. Although R_i has been shown to be a strong predictor of individual variation in fat reserves (wet mass of abdominal fat bodies) for non-reproductive, ovariectomized females ($r^2 = 0.54$; $n = 27$; $P < 0.0001$), this index of condition did not predict the size of fat reserves for intact, reproductive females ($r^2 < 0.01$; $n = 19$; $P = 0.94$; Cox & Calsbeek, in review). In captive females, variation in body condition was unrelated to fecundity, sex ratio of progeny or the size and condition of progeny at hatching, although captive mothers in high condition did produce daughters (but not sons) with higher survival when released to the wild (Cox *et al.* 2011). On the whole, indices of body condition derived from mass and length appear to be unreliable predictors of actual energetic condition in reproductive female anoles, and are probably also unsuitable as proxies for most components of female fitness. Moreover, although manipulations of reproductive investment that increase body condition and fat storage also increase survival (Cox & Calsbeek 2010a; Cox *et al.* 2010), direct manipulations of fat stores have no appreciable effect on survival (Cox, Lovern & Calsbeek 2014). Thus, even direct measures of energetic condition (and manipulations thereof) may be unrelated to female survival.

In male brown anoles, indices of condition are less likely to be confounded by reproductive state, although the extent to which they predict energy stores or body composition is not known. However, body size (SVL) is an important determinant of survival and male–male competition (Tokarz 1985; Cox & Calsbeek 2010b), and although condition influences survival, it does so only via interactions with size (Fig. 5b). In competitive mating trails, captive males in high condition produced more sons and more total offspring than males in low condition, even when competing males had equal access to reproductive females and direct male–male interactions were prevented (Cox *et al.* 2011). Dietary manipulations of male condition are consistent with the interpretation that this reproductive advantage could be mediated through condition dependence of sperm number and quality (A.F. Kahrl and R.M. Cox, unpublished data), but whether this effect is characteristic of natural variation in male condition is unknown. Whether individual variation in condition is correlated with mating success in the wild is also unknown in *A. sagrei*. Nonetheless, in terms of survival, the results of this study indicate that 'fatter is better' only applies to the largest adult males in the population.

In summary, the results of this study show that alternative indices of body condition yield highly congruent inferences about the strength and direction of natural selection on condition. This may be a general feature of studies in which the components of fitness (e.g. survival) are measured with greater error than that which is introduced by the use of alternative indices. Although indices of body condition should be selected on the basis of first principles and their ability to predict relevant variation in energetic or physiological state, indices such as R_i and M_i are probably likely to perform similarly in most analyses of selection with sufficient sample sizes. In brown anoles, indices of condition are poor predictors of survival in adult females, and they only predict the survival of adult males through interactions with body size. As in other species, the simplistic view that 'fatter is better' is misleading in brown anoles (Civantos & Forsman 2000; Hendry, Letcher & Gries 2003; Dibattista *et al.* 2007). Collectively, these studies argue that indices of condition should be empirically confirmed as predictors of survival and reproductive success before being interpreted as proxies for fitness.

Acknowledgements

Data accessibility

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Supporting Information

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

Fig. S1. Correlation between standardized (mean = 0, unit SD) values of the Scaled Mass Index (M_i) and the Residual Index (R_i) of body condition across (A) 2258 males, and (B) 2338 females.

Table S1. Summary of multivariate linear selection gradients ($\pm$SE) for two indices of condition and SVL across 22 selection replicates in males and 19 selection replicates in females.

Table S2. Summary of multivariate quadratic selection gradients ($\pm$SE) for two indices of condition and SVL across 22 selection replicates in males and 19 selection replicates in females.

Table S3. Summary of correlational selection gradients ($\pm$SE) for two indices of condition and SVL across 22 selection replicates in males and 19 selection replicates in females.

Table S4. Summary of linear, quadratic and correlational selection gradients ($\pm$SE) for body mass and SVL across 22 selection replicates in males and 19 selection replicates in females.