Oecologia (2007) 153:489–499
DOI 10.1007/s00442-007-0726-y

BEHAVIORAL ECOLOGY

An analysis of the relative roles of plasticity and natural selection in the morphology and performance of a lizard (*Urosaurus ornatus*)

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Received: 14 February 2006 / Accepted: 14 March 2007 / Published online: 24 April 2007

Abstract Evolutionary ecologists have devoted substantial attention to understanding which factors dictate processes of mortality within populations. Our goal was to understand the dynamics of natural selection on two performance traits (bite force and sprint speed) and associated morphological variables. We first quantified performance and morphology for a sample of marked tree lizards (*Urosaurus ornatus*) at the middle of the breeding season. We then sampled the same population in the nonbreeding season to determine which of the original lizards survived, and we also remeasured morphological and performance variables for surviving lizards. We found evidence for directional selection favoring fast sprinters in male lizards, but also a nonsignificant stabilizing trend that disfavored the very fastest lizards. However, we also detected substantial seasonal plasticity in bite force and head width, suggesting that an analysis of selection on only preselection (breeding season) values may be overly simplistic. *Urosaurus* males and females with low bite forces (and narrow heads) in the breeding season generally increased their bite forces and head widths during the nonbreeding season. In contrast, lizards that were initially strong biters in the breeding season diminished in head width and declined dramatically in bite force (up to about 35%). We suggest that seasonal plasticity could act as a retarding force for selection on performance, and could dampen seasonal and year-to-year fluctuations in selective pressures. We argue that this phenomenon may be particularly likely for performance traits important for social interactions related to breeding, such as bite force.

Keywords Lizards · Performance · Selection

Introduction

Studies of natural selection form a natural link between ecology and evolution because they describe ecological processes of mortality in the context of microevolutionary theory (Lande and Arnold 1983; Brodie et al. 1995; Kingsolver et al. 2001; Fuller et al. 2005). However, despite numerous studies of natural selection, both in the field and in the laboratory, we understand remarkably little about how natural selection operates on functional capacities. Prior reviews (Endler 1986; Hoekstra et al. 2001; Kingsolver et al. 2001) have documented strong selection on various morphological and behavioral traits in nature, but relatively few studies have examined selection on performance capacities (Bennett and Huey 1990), such as sprinting speed, bite force, or endurance (Jayne and Bennett 1990; Le Gaillard et al. 2004; Miles 2004). Indeed, natural selection is expected to operate first on functional capacities, and only secondarily on morphology (Arnold 1983; Hertz et al. 1988; Jayne and Bennett 1990; Bonine and Garland 1999). This is because organisms interact most directly with their environment through their functional capacities (Irschick and Garland 2001; Wainwright et al. 2005). For example, animals with unusually high levels of speed or endurance may be better able to capture prey, escape predators, and oust intruders. Because functional capacities are often tightly linked with underlying morphological features (Biewener 2003), directional selection on high values of speed should also result in selection on limb morphology, for example.

Communicated by William Resetarits.

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Another unresolved issue for researchers interested in natural selection concerns the potentially confounding role of seasonal plasticity in traits (Trexler and Travis 1990a, 1990b; Scheiner and Callahan 1999; Kingsolver and Gomulkiewicz 2003). Although researchers have appreciated that morphological and functional traits can be plastic over an individual's lifetime (e.g., Schlichting 1986; Trexler and Travis 1990a, 1990b; Scheiner and Callahan 1999; Van Buskirk and Saxer 2001; Schmitt et al. 2003), few studies have simultaneously examined the roles of natural selection and plasticity on functional traits (but see Garland and Else 1987). This is despite the fact that seasonal plasticity is well documented for many morphological traits that are presumably linked to functional traits. Examples include brain morphology in birds (Deviche and Gulledge 2000; see also Tramontin and Brenowitz 2000), cartilage morphology in rodents (Heldmaier and Steinlechner 1981; Ruf et al. 1993), and bone metabolism in marine iguanas (Wikelski and Thom 2000). Finally, one must also consider the possibility that seasonal changes in behavior and/or motivation can alter performance across seasons (Garland and Else 1987; Garland and Losos 1994) .

Our goal was to understand the dynamics of natural selection on two ecologically relevant performance traits (bite force and sprint speed) and associated morphological variables. We investigated whether either these traits were under selection, and also whether they display seasonal plasticity. We focused on lizards because of the rich literature surrounding the ecology, field behavior, and performance capacities of numerous lizard species (e.g., Garland and Losos 1994; Jenssen et al. 2000, 2001; Robson and Miles 2000; Irschick and Losos 1998). Recent studies have provided compelling evidence that both biting and bite force are important for consuming prey and resolving male–male territorial disputes in lizards (Stamps and Krishnan 1997; Herrel et al. 1999; Perry et al. 2004; Lailvaux et al. 2004; Lappin and Husak 2005; Vanhooydonck et al. 2005). Other studies on lizards have shown that head shape (linked to bite force) is correlated with both the ability to acquire territories (Hews 1990; Lappin and Husak 2005), and the ability to win male contests (Lailvaux et al. 2004; Perry et al. 2004). Additionally, there is increasing evidence that directional selection favors high levels of locomotor performance in squamate reptiles (Jayne and Bennett 1990; Le Gaillard et al. 2004; Miles 2004). However, these studies were typically conducted at a single point of time, and did not account for the potential influence of seasonal plasticity.

We studied a common lizard (the tree lizard, *Urosaurus ornatus*) across breeding and nonbreeding seasons. We examined this lizard species because it is polygynous, well studied, and at higher elevations, highly seasonal, and thus a potential candidate for exhibiting plastic traits. We quantified bite force and sprint speed and associated morphological variables for a large sample of marked tree lizards during the middle of the breeding season (May and June of 2005). We then sampled the same population in the nonbreeding season (late September of 2005) to determine which of the original lizards survived. We remeasured morphological and performance variables for the surviving lizards and examined both selection and plasticity in these traits. For the sake of this paper, we examined survivorship (i.e., whether the lizard was alive or dead, Janzen and Stern 1998), which we argue is an important component of overall fitness (see Freeman and Herron 2001 for a discussion).

Materials and methods

Field site and sampling

We examined a 500-m-long by 30-m-wide transect consisting of a strip of riparian habitat (about 1,100 m elevation) near Sedona, AZ (coordinates available from the authors upon request). At this elevation, *Urosaurus* lizards are markedly seasonal; males actively fight for and defend territories during the summer months (approximately May–July), followed by a more quiescent nonbreeding season (September and October) during which lizards are active but do not actively defend territories (Tinkle and Dunham 1983). This site consists of a boulder field intermixed with trees and bushes. Lizards in the transect were isolated, as a continually flowing creek formed a boundary on one side, and an elevated dense thicket of mesquite trees and grass (in which *Urosaurus* were rarely encountered) ran parallel to the creek on the other side.

Lizards were captured during daytime hours using a noose attached to the end of a pole, and were released within 24 h of capture at their original location. During the breeding period sample, we marked lizards permanently by toe clipping, which is a common method of marking lizards (Dunham et al. 1994), and is not known to affect maximum speed in lizards (Huey et al. 1990; Dodd 1993). We clipped combinations of toes (excluding the longest toes on each foot), and avoided clipping more than two toes per foot. We sampled lizards during two periods: first, we attempted to sample during the middle of the breeding season (May 15–June 24, 2005) during which we processed 100 adult male ($N = 57$) and female ($N = 43$) lizards. These sampling periods span a crucial period for polygynous lizards such as *Urosaurus*, as during the breeding season, most males are actively acquiring and defending territories, and females are actively engaged in laying eggs (especially near the end of the breeding season). This breeding period is also a time of high activity for potential predators of *Urosaurus* (e.g., snakes, birds, Tinkle and Dunham 1983). Therefore, both bite force and sprint speed could be important to these lizards in a variety of ecological contexts (e.g., escaping predators, territorial interactions). *Urosaurus* lizards consist of different male morphs (Moore et al. 1998), but a recent paper (Meyers et al. 2006) showed that these morphs do not differ significantly in morphology, bite force, or sprint speed, and hence do not confound our analyses.

We were confident that we had marked the majority of lizards in our transect based on two grounds: first, at the end of the breeding sampling period, we achieved a rate of 90% lizards marked (e.g., nine lizards marked for every ten captured). Second, during the nonbreeding season sampling period (23 September–2 October, 2005), we recaptured a total of only 26 adults, of which 21 were marked (81%). We assumed that animals that were not captured were dead (following other mark-recapture studies of selection, e.g., Jayne and Bennett 1990; Miles 2004). On consecutive days across this single time period, we repeatedly walked up and down the transect and captured every adult lizard, resulting in 21 recaptures (twelve males, nine females). The estimated mortality (about 79% pooling across males and females) is consistent with demographic studies showing high breeding season mortality (about 60–70%) in *U. ornatus* (Tinkle and Dunham 1983). We note that the home ranges of *Urosaurus* lizards are relatively small, and hence immigration and emigration into the population is limited (Moore et al. 1998).

Measurement of morphology and performance

Linear dimensions were measured using digital calipers (CD-15 DC, Mitutoyo, Aurora, IL, USA; precision 0.01 mm). For each lizard, we measured the following traits: mass (measured to 0.01 g using a Pesola scale), snout vent length (SVL; measured from the tip of the snout to the cloaca), head length (measured on the dorsal side), head height (measured at the highest point of the head), head width (measured at the widest point of the head), and hindlimb length (measured from the insertion of the limb to the tip of the longest toe). We measured the same group of adult *Urosaurus* ($N = 10$) twice (all measurements taken by J. Meyers), and found that all repeatibilities (intraclass correlation coefficients) were greater than 0.98. Other work shows that the repeatability of bite force in various lizard species is very high (>0.95, Herrel et al., unpublished data). Bite force was measured using an isometric Kistler force transducer (type 9023, Kistler Inc., Wintherthur, Switzerland) connected to a Kistler charge amplifier (type 5058a, Kistler Inc.). We induced lizards to bite forcefully on the free ends of the bite force device (Herrel et al. 1999, 2001a, 2001b). We measured bite forces five times for each lizard, with a short rest (30–40 s) between successive bites. If the lizard did not bite effectively (i.e., we did not observe substantial flexion of jaw muscles during biting, resulting in low bite values), it was allowed to rest for 30 min before retesting. The largest bite force obtained from each session was taken as the maximal bite force for that individual. This method has been shown to be effective for eliciting repeatable and maximum bites from lizards (Herrel et al. 2001a, 2001b; Irschick et al. 2006), and from other animals (e.g., finches, Herrel et al. 2005).

We measured sprint speed for each lizard (three trials per individual per season) using a field-portable racetrack consisting of a 3-m-long × 0.20-m-wide board covered with cork that provided good traction. Cardboard sides prevented lizards from running laterally. Infrared sensors and emitters (connected to a processor and laptop computer) were positioned every 0.25 m along the track, and hence, we used the fastest speed over these 0.25 m segments as the maximum speed for a given individual. Lizards rested for 30 min between trials. Lizards were tested at ambient field temperatures for sprint speed and bite force, which ranged from 28 to 32 °C, and is similar to active body temperatures of lizards at this site. Further, both sprint speed (Huey 1983) and bite force (A. Herrel, unpublished data) show broad plateaus with temperature, and therefore we felt confident that we elicited maximum performance.

Data analyses

We conducted three analyses:

(1) Morphology–performance analyses: we tested for significant relationships among morphology and performance by conducting multiple regressions within both males and females for bite force and sprint speed. For bite force, the independent variables were log-transformed values of snout-vent length, head length, head width, and head height, whereas for sprint speed, the independent variables were log-transformed values of snout-vent length and hindlimb length.

(2) Selection analyses: following recent syntheses, we first tested for directional selection on performance using logistic regression (Brodie et al. 1995; Janzen and Stern 1998). As suggested by Brodie et al. (1995), we conducted separate analyses for both linear (directional selection) and quadratic (stabilizing selection) effects. We focused our selection analyses on performance both because morphology and performance were generally strongly related (see below), and we did not want to unnecessarily inflate the number of statistical comparisons. We compared the initial (breeding season) measurements of the 21 survivors to the initial measurements of the 79 individuals who were not recaptured and hence were assumed to be dead (see Janzen and Stern 1998). We conducted separate logistic

regression tests using log-transformed snout-vent length as a covariate, as body size tends to be generally correlated with performance and morphology, and we were most interested in selection on relative performance values (Van Damme and Van Dooren 1999). We conducted separate analyses for males and females, as selection may operate differently on these two groups.

(3) Plasticity analyses: we adopted the same methodology here as in previously published work (Irschick et al. 2006). We tested for seasonal plasticity in morphology and performance by comparing values of both traits between seasons for the 21 survivors. We tested whether both the mean (using paired *t* tests) and the variance (using *F* tests) differed significantly between seasons for males and females (analyses conducted separately per sex). Snout-vent length did not change significantly between seasons for either males (*t* value $= -0.96$, $df = 11$, $P > 0.15$), or females (*t* value = 1.53, $df = 8$, $P > 0.05$), indicating that growth was minimal, which is consistent with our observation that the 21 survivors were all large adults when captured in the breeding season. Indeed, the average percent change in SVL for males and females, respectively, between the two seasons was 1.2 and 2.5%, which is far smaller than the documented seasonal changes in bite force. Hence, we did not adjust for the effects of body size when comparing variables across seasons.

Results

Morphology–performance analyses

The overall multiple regression model was statistically significant for bite force (independent variables; SVL, head length, head height, and head width, dependent variable; bite force) in males ($r^2 = 0.58$, $df = 4{,}50$, $P < 0.001$) and females ($r^2 = 0.56$, $df = 4{,}38$, $P < 0.001$), with head height ($P < 0.05$) and SVL ($P < 0.05$) being the significant terms for females, and head width ($P < 0.005$) and head height ($P < 0.05$) both being significant predictors for males (nonsignificant terms; females; head length $P > 0.90$, head width $P > 0.80$; males; SVL $P > 0.20$, head length $P > 0.90$). Neither multiple regression for sprint speed (independent variables; SVL, hindlimb length, dependent variable; sprint speed) was significant for males ($r^2 = 0.03$, $df = 4{,}50$, $P > 0.15$) or females ($r^2 = 0.06$, $df = 4{,}38$, $P > 0.30$). Thus, no relationship between hindlimb length and sprint speed was apparent.

Selection analyses

There was no evidence of significant selection on body size (SVL) for males [logistic regression, dependent variable; survivorship (1,0), independent variables; SVL, $\chi^2 = 1.98$, $P > 0.15$], or females ($\chi^2 = 1.61$, $P > 0.20$). We found evidence that directional selection favored fast male sprinters [logistic regression, dependent variable: survivorship (1,0), independent variables; SVL, sprint speed, Tables 1, 2; Fig. 1, $P = 0.054$]. Indeed, many of the worst male sprinters were eliminated from the population (Fig. 1), resulting in the surviving 12 males being on the far right hand side of the original breeding season sprint speed distribution. However, we also detected a weak and nonsignificant trend for a stabilizing component for male sprint speed ($P = 0.07$; Table 2), which was manifested by an approximate halving of the variance from the initial sample (1,571) compared to the survivors (647). Because of the complex nature of this fitness relationship, we used the cubic spline approach to visualize fitness with the univariate GLMS1 Windows-based program (Schluter 1988; Schluter and Nychka 1994). Maximum speed was standardized to a mean of 0 by subtracting each individual value from the mean, and then dividing resulting values by the standard deviation. Figure 2 presents the fitness surface for male *Urosaurus* lizards in relation to maximum speed, and reveals generally higher fitness for individuals with higher sprint speeds, with

Table 1 Summary statistics (mean ± 1SE, range in parentheses) for performance and associated morphological variables (data from the breeding season only) of surviving and nonsurviving adult male and female *U. ornatus* lizards

Variable	Survivors, males ($N = 12$)	Non-survivors, males ($N = 45$)	Survivors, females ($N = 9$)	Non-survivors, females ($N = 34$)
SVL (mm)	49.42 ± 0.62 (45.1–52.7)	50.51 ± 0.36 (45.68–55.29)	50.64 ± 1.18 (44.82–55.84)	49.19 ± 0.49 (41.66–55.06)
Bite force (*N*)	4.98 ± 0.31 (3.30–6.90)	5.02 ± 0.13 (3.30–7.00)	4.16 ± 0.30 (2.80–6.00)	4.18 ± 0.15 (2.60–6.00)
Sprint speed (cm/s)	215.16 ± 7.35 (192.30–277.78)	196.04 ± 6.33 (78.13–277.78)	181.17 ± 10.70 (131.60–227.27)	185.66 ± 5.83 (119.05–277.78)
Head length (mm)	11.36 ± 0.18 (10.09–12.04)	11.69 ± 0.09 (10.53–13.35)	10.86 ± 0.18 (9.81–11.43)	11.09 ± 0.11 (9.50–12.49)
Head width (mm)	9.47 ± 0.12 (8.63–10.21)	9.68 ± 0.07 (8.57–10.82)	8.82 ± 0.14 (7.98–9.49)	8.83 ± 0.09 (7.83–9.95)
Head height (mm)	6.18 ± 0.14 (5.41–6.86)	6.32 ± 0.05 (5.49–7.09)	6.02 ± 0.09 (5.60–6.50)	5.93 ± 0.08 (5.18–7.19)
Hindlimb (mm)	36.14 ± 0.43 (33.9–37.9)	36.14 ± 0.28 (32.65–41.16)	33.75 ± 0.60 (30.2–36.1)	33.09 ± 0.29 (29.70–36.61)

Table 2 Statistics from logistic regression analyses (whole model test results, log-transformed SVL also included in model, but results not shown) comparing performance variables between survivors and non-survivors from the summer breeding period

Variable	Linear test	Quadratic test
	Wald's χ^2	Wald's χ^2
Male sprint speed	3.71*	3.34**
Female sprint speed	0.28 NS	0.05 NS
Male bite force	0.65 NS	0.55 NS
Female bite force	1.63 NS	0.03 NS

NS nonsignificant

* $P = 0.054$, ** $P = 0.07$

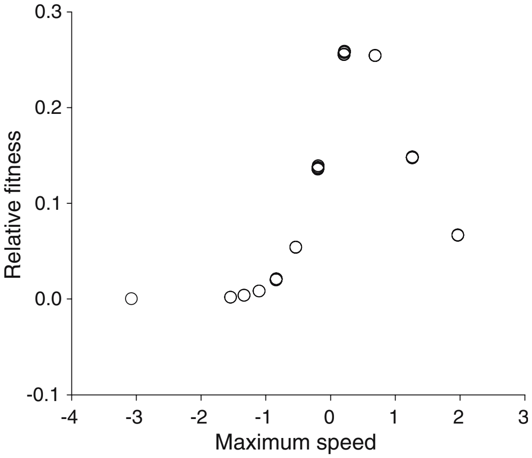

Fig. 2 A plot of relative fitness versus maximum sprint speed (standardized to a mean of 0) for male *Urosaurus* lizards. Note that many male lizards had similar sprint speeds, and hence their points overlap on this plot but they were segregated slightly by adding in random jitter

a stabilizing component at the higher end of sprint speeds, implying that selection generally favors high speeds, but that the very best (and worst sprinters) may be disfavored. The other results, from the logistic regression analyses (Table 2) and the comparisons of variances (all other *P* values > 0.15), were clearly nonsignificant.

Plasticity analyses

Seasonal changes in mean values

The average values of several variables changed significantly when comparing survivors between the breeding and nonbreeding season (*t* tests, Tables 3, 4). Average head length increased significantly in both males and females in the nonbreeding season. Head width showed the opposite trend in that both sexes had significantly smaller head widths during the nonbreeding season compared to the breeding season. Male but not female sprint speed declined significantly between the breeding and nonbreeding season. Hindlimb lengths were significantly smaller in the non-breeding season compared to the breeding season, although the magnitude of change was relatively small (1.5 and 0.02% changes for males and females, respectively).

Fig. 1a–d Frequency histograms of bite forces (**a**, **c**) and sprint speeds (**b**, **d**) for female and male *Urosaurus* lizards. Bite forces and sprint speeds for non-survivors from the breeding season (*white bars*) were compared to survivors with their initial breeding season bite force values (*black bars*)

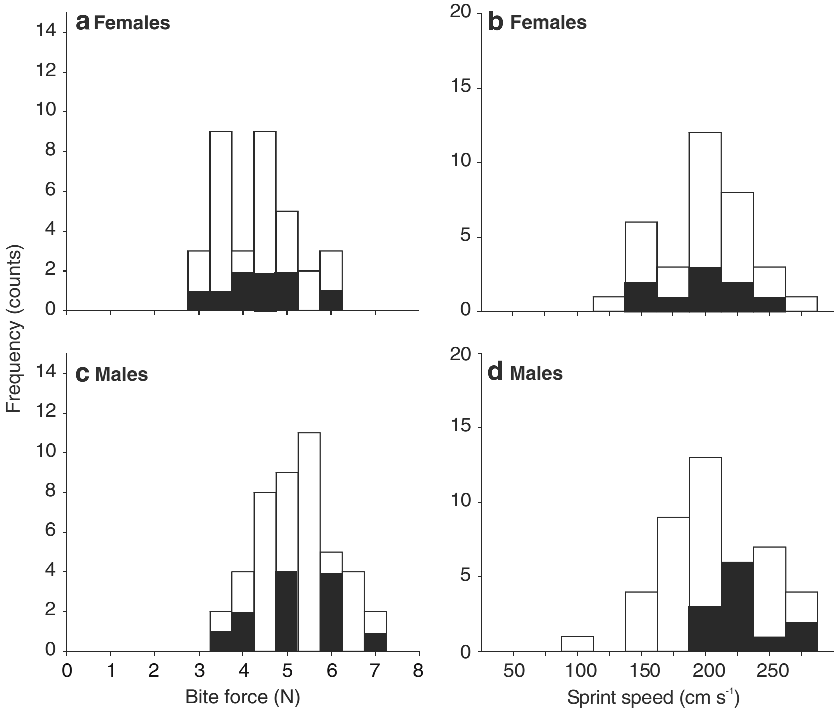

Table 3 Results from both means *t* tests and variance *F* tests comparing the same males and females between seasons (breeding vs. nonbreeding) for performance and morphological variables

Variable	*df*	Means *t* test	Variance *F* test
Male bite force	11	0.79 NS	5.74**
Female bite force	8	0.29 NS	3.15***
Male sprint speed	10	2.24*	0.18**
Female sprint speed	8	0.56 NS	0.86 NS
Male head length	10	−2.37*	2.38 NS
Female head length	8	−3.64**	1.90 NS
Male head width	10	1.79*	2.32***
Female head width	8	2.10*	3.17***
Male head height	10	0.98 NS	2.41 NS
Female head height	8	1.38 NS	0.67 NS
Male hindlimb	10	2.10*	1.01 NS
Female hindlimb	8	2.20*	0.68 NS

NS nonsignificant, * $P < 0.05$, ** $P < 0.01$, *** $P = 0.06$

Seasonal changes in variances

The variance for male bite force was significantly greater (about fivefold) in the breeding season compared to the nonbreeding season (variance *F* tests, Tables 3, 4). Females exhibited a similar decline in variance for bite force between seasons (about threefold higher in the breeding season, a difference that was marginally nonsignificant). Sprint speed in males showed the opposite pattern by being about fivefold higher during the nonbreeding season compared to the breeding season. Head width exhibited a threefold higher variance in the breeding season compared to the nonbreeding seasons for both males and females, although these differences were marginally nonsignificant for both sexes.

Plasticity as a function of initial values

To understand plasticity in morphology and performance, we followed the same analyses used in Irschick et al. (2006), which consisted of plotting percent seasonal change in various traits on the *y*-axis, and the initial (summer) value on the *x*-axis. This seasonal decrease in variance for bite force, and to a lesser extent, head width, occurred because individuals with high values for either variable during the breeding season tended to decrease disproportionately in the nonbreeding season (Fig. 3). By contrast, individuals with low values for bite force or head width in the breeding season tended to increase in the nonbreeding season. For example, individuals with high initial breeding values of bite force declined dramatically in bite force between seasons, in some cases by as much as 35% (Fig. 3). Because body size did not change significantly between seasons, this result cannot be due to differential growth between seasons. Some individuals increased in bite force dramatically between seasons (from 20 to 40%). Accordingly, the relationship between initial breeding season values for either bite force or head width and the percent change in these variables between the breeding and nonbreeding season were statistically significant (bite force; Pearson $r = -0.82$, $df = 19$, $P < 0.001$, head width; $r = -0.66$, $df = 18$, $P < 0.001$). Seasonal changes in head width were significantly correlated with seasonal changes in bite force (Fig. 3c) such that individuals with unusually high bite forces (and accordingly wide heads) in the breeding season diminished both in head width and in bite force in the nonbreeding season ($r = 0.64$, $df = 18$, $P < 0.001$, Fig. 3c). Percent change between seasons in sprint speed did not correlate significantly with either initial breeding season values of sprint speed ($r = 0.34$, $df = 18$, $P > 0.10$), or percent change in hindlimb length ($r = 0.25$, $df = 18$, $P > 0.25$).

Discussion

An important aim of evolutionary ecology is to understand which factors dictate processes of mortality within populations. A long-standing assumption is that individual animals that exhibit high values of ecologically relevant

Table 4 Summary statistics (mean ± 1SE, variance in parentheses) for the morphology and performance of 21 recaptured male ($N = 12$) and female ($N = 9$) *U. ornatus*, showing breeding and nonbreeding values

Variable	Males breeding	Males nonbreeding	Females breeding	Females nonbreeding
SVL (mm)	49.42 ± 0.62 (4.54)	49.96 ± 0.30 (1.09)	50.64 ± 1.18 (12.60)	49.24 ± 0.66 (3.92)
Bite force (*N*)	4.98 ± 0.30 (1.11)	4.74 ± 0.13 (0.19)	4.16 ± 0.30 (0.82)	4.10 ± 0.17 (0.26)
Sprint speed (cm/s)	215.16 ± 7.35 (647.98)	170.88 ± 18.94 (3227.83)	181.17 ± 10.70 (1024.50)	173.88 ± 11.50 (1191.27)
Head length (mm)	11.36 ± 0.18 (0.37)	12.13 ± 0.11 (0.16)	10.86 ± 0.18 (0.28)	11.61 ± 0.13 (0.15)
Head width (mm)	9.47 ± 0.12 (0.16)	9.22 ± 0.07 (0.06)	8.82 ± 0.14 (0.17)	8.64 ± 0.08 (0.05)
Head height (mm)	6.18 ± 0.14 (0.20)	6.14 ± 0.08 (0.08)	6.02 ± 0.09 (0.07)	5.90 ± 0.10 (0.10)
Hindlimb (mm)	36.14 ± 0.43 (2.38)	35.58 ± 0.43 (2.26)	33.75 ± 0.60 (3.28)	32.97 ± 0.50 (2.24)

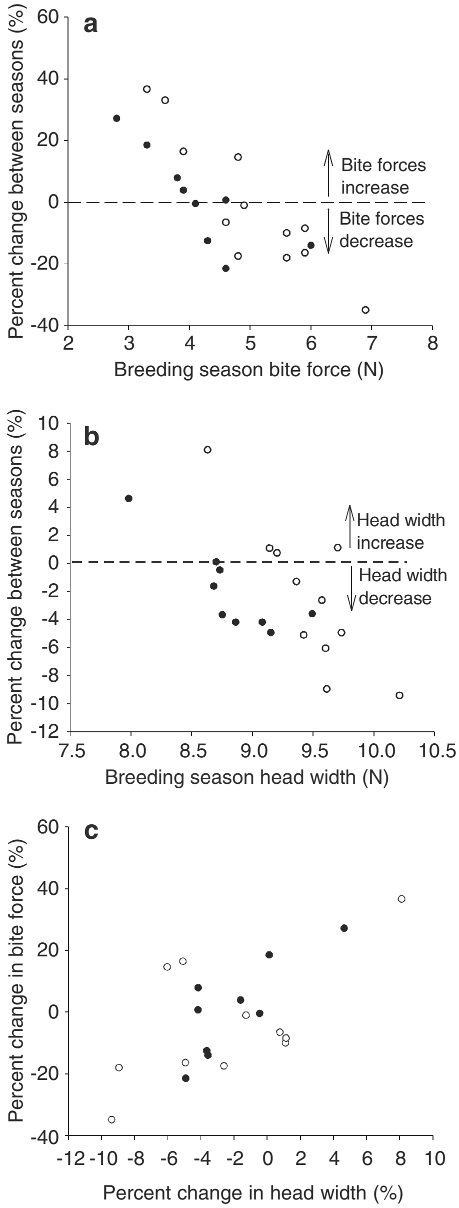

Fig. 3a–c **a** Initial values of bite force during the breeding season versus percent change in bite force between the breeding and nonbreeding seasons in female and male lizards. **b** Initial values of head width during the breeding season versus percent change in head width between the breeding and nonbreeding seasons. **c** Percent change in head width (*x*-axis) versus percent change in bite force. For all three plots, positive values of percent change represent increases between the breeding and nonbreeding season

performance traits should also enjoy high fitness values relative to low-performance individuals (Arnold 1983; Jayne and Bennett 1990; Irschick and Garland 2001; Le Galliard et al. 2004; Miles 2004). We found evidence ($P = 0.054$) for directional selection favoring high sprint speeds in male *Urosaurus* lizards, and a weaker nonsignificant component of stabilizing selection on the same trait ($P = 0.07$). This finding suggests that selection generally favors good sprinters, with the caveat that there was a nonsignificant trend for extreme individuals (either very poor or very good sprinters) to be eliminated from the population (Fig. 2). By comparison, we did not detect significant selection on maximum bite force in either male or female lizards.

The power of selection within populations is modulated by several factors, including the overall strength of selection as well as the heritability of traits. Because the directional component of selection on sprint speed was not strong from a statistical point of view ($P = 0.054$), we wanted to evaluate how our difference in sprint speed between survivors and nonsurvivors (~10% greater in survivors) compared to other selection studies. To provide a more standardized point of comparison, we calculated this difference in Darwins (see Hendry and Kinnison 1999). We calculated a value of 219,287 Darwins, which is near the top of the reviewed cases of "rapid evolution" outlined in Table 1 of Hendry and Kinnison (1999). Of course, this value should be interpreted cautiously because we calculated selection over a relatively short time period (four months), but this analysis suggests that the selection on sprint speed is biologically relevant. We note that we have not documented heritability for either performance or morphology here, although other studies have provided data on heritability (sprint speed, Van Berkum and Tsuji 1987; Garland et al. 1990) and repeatability (Huey and Dunham 1987) of sprint speed in various squamate reptiles.

We also detected substantial seasonal plasticity in bite force and head width, suggesting that an analysis of selection on only preselection (breeding season) values may be overly simplistic. *Urosaurus* males and females with relatively low bite forces (and relatively narrow heads) in the breeding season generally increased their bite forces and head widths during the nonbreeding season. By contrast, individual lizards that were initially strong biters in the breeding season diminished in head width and declined in bite force (up to about 35%). A key issue is the repeatibilities of morphology and bite force, which we note are extremely high, and hence the plasticity is unlikely to be explained by measurement error (see Kelly and Price 2005).

These plastic seasonal shifts resulted in lower variances for bite force and head width in the same individuals during the nonbreeding season. Sprint speed declined significantly between seasons for male *Urosaurus*, but the decline in this variable was not linked to seasonal declines in hindlimb length, and rather than decreasing in variance between seasons, variance increased dramatically during the nonbreeding period. This seasonal increase in the variance of sprint speed occurred because surviving males were uniformly good sprinters in the breeding season, but some declined dramatically in the nonbreeding season.

Few researchers have addressed the potential for functional variables to change seasonally. Potential factors include alterations in motivation, condition, and underlying morphology and physiology (Garland and Else 1987). We suggest that at least two of these three factors may be important here. First, we argue that bite force in *Urosaurus* fits the criterion of a seasonally plastic trait that is linked to seasonal changes in head width, although the manner by which it changes is unusual (see below). By comparison, we suggest that the seasonal decline in sprint speed may occur because of a decline in overall condition, as opposed to underlying changes in related biomechanical traits (e.g., limb length). We note that male condition declined dramatically between seasons, with males losing on average 16% of their body mass in the nonbreeding season. Females also lost an average of 25% in mass in the nonbreeding season, but this decline was primarily due to loss of eggs (all females were gravid when captured in breeding season), and females did not decline significantly in sprint speed between seasons. Finally, although hindlimb length declined significantly between seasons, the magnitude was small (average decreases of 1.5 and 0.02%, respectively, for males and females, Table 3), and was not linked to declines in sprint speed. The significant difference in hindlimb length between seasons merits further study, but seems minor from a functional perspective when compared to the plasticity in bite force and head width. While we cannot exclude the possibility that seasonal variation in motivation (Losos et al. 2002) was a factor for both sprint speed and bite force, we observed that lizards appeared to sprint and bite with equal intensity in both seasons, although the end outputs between seasons clearly differed.

Prior reviews have emphasized a general lack of information on how natural and sexual selection operate on performance capacities (Hoekstra et al. 2001; Irschick and Garland 2001; Kingsolver et al. 2001). Fortunately, there has been a resurgence of interest in expanding selection studies beyond morphology and behavior (Jayne and Bennett 1990; O'Steen et al. 2002; Le Galliard et al. 2004; Miles 2004; Lappin and Husak 2005; Husak 2006). Prior to these more recent studies, there was little comparative evidence that could be used to determine whether selection on performance would follow a model in which only a single adaptive "peak" was present (e.g., high performance), or alternatively, whether selection might favor several "peaks," such as in cases of disruptive selection (Smith 1993). Our own data are more consistent with the single peak perspective, but also suggest a mix of directional and stabilizing selection. Therefore, an emerging theme from these prior studies, as well as the current work, is that directional selection that favors high performance seems most prevalent, although some exceptions exist (e.g., Jayne and Bennett 1990). In a review of selection studies of morphology and behavior spanning 13 years, Kingsolver et al. (2001) found few cases of strong directional selection, and it would be interesting to compare the above studies of performance (most published after that review) to these reviewed studies. Regardless, these performance–selection studies generally do not support the model of several adaptive "peaks" for performance within natural populations. However, they beg the question of how long directional selection on performance can persist before depleting available additive genetic variance. We suggest that studies employing a longer term approach, as has been used successfully on other taxa (e.g., finches, Grant 1999), would be particularly useful for performance studies, because selection might for example favor high performance one year but not the next.

Our work suggests that future selection work on performance needs to address the potential for plasticity between the pre- and post-selection periods, particularly when the analysis is examined across different seasons (Kingsolver and Gomulkiewicz 2003). We suggest that the kind of plasticity observed in the head dimensions and bite force of *Urosaurus* lizards could act as a retarding force on the evolution of performance by enabling individuals to alter their performance over relatively short time periods. Similarly, Huey et al. (2003) highlighted the role of behavior as a retarding force in the evolution of physiology and morphology, and performance plasticity could likewise slow the pace of evolution for morphological traits linked to performance. In the case of traits important for social interactions (e.g., bite force), seasonal plasticity may also enable polygynous animals to exhibit peak performance at different points in time, thus providing a mechanism for reducing intense territorial rivalries (especially males, see Moore et al. 1998). Consider the possibility that some *Urosaurus* individuals may peak in bite force early in the breeding season, and then rapidly diminish, whereas others may acquire higher bite forces near the end of the breeding season. Accordingly, some males may fight for and establish territories early in the breeding season (early high bite forces), whereas other males may fight for and establish territories later in the breeding season (later high bite forces). This form of plasticity may be especially important for animals that typically live only a single breeding season (e.g., *Urosaurus*, Tinkle and Dunham 1983), and thus need to adopt strategies to ensure successful mating. Because we did not sample multiple times within the breeding season, the plastic changes in bite force observed in Fig. 2 could have occurred anytime during this period, and hence more data are needed to test the above possibility.

Regardless, we argue that our finding of seasonal plasticity in performance could be more widespread than previously recognized. For example, seasonal hormonal fluctuations are well documented in vertebrates (e.g., Moore et al. 1984; Moore 1988; Greenberg and Crews 1990; Tokarz et. al. 1998), and hormones are known to affect muscle and functional properties (Garland and Else 1987; Sinervo et al. 2000). Indeed, bite force in lizards is a function of overall head shape and various head muscles (Herrel et al. 1999, 2001a, 2001b), and head muscles are likely candidates for being influenced by hormones, such as testosterone, which fluctuate seasonally in *Urosaurus* (Moore et al. 1998; see also Cooper and Vitt 1985). The seasonal decreases in head width and bite force in initially hard-biting *Urosaurus* could be due to declines in hormones and concomitant atrophy of heads muscles that influence bite force. The seasonal increases in head width and bite force for some *Urosaurus* individuals are more puzzling, but imply that hormones may decline in some individuals, and increase in others across the same time period.

A recent study with green anole lizards (*Anolis carolinensis*, Irschick et al. 2006) showed a similar trend to that for the *Urosaurus* lizards; adult green anole males underwent seasonal plasticity in bite force that was dependent on their initial state (i.e., individuals with high bite forces diminished to the fall, individuals with low bite forces increased to the fall). Based on field data, green anoles appeared to "return" to their original state a year later, implying that these seasonal changes are temporary, and not driven by permanent structural changes in morphology. We can offer no strong evidence for why lizards should undergo such striking seasonal changes in morphology and performance, particularly in regards to the nonlinear pattern of seasonal change. We suggest that behavioral studies that follow individual animals across different seasons, and relate seasonal fluctuations in morphology and performance with social behavior (e.g., degree of territoriality) and potential underlying factors (e.g., hormones) might be particularly useful. In summary, our findings reveal differing roles of selection on different performance traits, and we suggest that selection and plasticity may interact in at least one trait (bite force), underscoring the importance of measuring the same traits both before and after evaluating selection. We further suggest that seasonal plasticity could act as a retarding factor on how selection operates on performance.

Acknowledgments This work was supported by an NSF grant to D. Irschick (IOB 0421917). We thank E. McElroy, J. Pilarski, and C. Pace for assistance with capturing specimens, and R. Van Damme, A. Herrel, K. Nishikawa, K. Lappin, two anonymous reviewers, and the Nishikawa lab group for helpful comments on a previous version of the manuscript.

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