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SEXUAL DIMORPHISM IN LIZARD BODY SHAPE: THE ROLES OF SEXUAL SELECTION AND FECUNDITY SELECTION

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Abstract.—Sexual dimorphism is widespread in lizards, with the most consistently dimorphic traits being head size (males have larger heads) and trunk length (the distance between the front and hind legs is greater in females). These dimorphisms have generally been interpreted as follows: (1) large heads in males evolve through male-male rivalry (sexual selection); and (2) larger interlimb lengths in females provide space for more eggs (fecundity selection). In an Australian lizard (the snow skink, *Niveoscincus microlepidotus*), we found no evidence for ongoing selection on head size. Trunk length, however, was under positive fecundity selection in females and under negative sexual selection in males. Thus, fecundity selection and sexual selection work in concert to drive the evolution of sexual dimorphism in trunk length in snow skinks.

Key words.—Fecundity selection, lizards, sexual dimorphism, sexual selection.

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In lizards, as in many other kinds of organisms, the sexes often differ in body shape as well as overall body size (Andersson 1994). Two of the body components that display sexual dimorphism most consistently are the relative size of the head and the relative length of the trunk. Compared to conspecific females of the same overall body length (or snout-vent length, SVL), male lizards tend to have larger heads and shorter trunks (i.e., interlimb length, the distance between the points of insertion of the fore- and hindlimbs; Vitt 1983; Cooper and Vitt 1989; Hews 1996; Olsson and Madsen 1998; but see Vitt and Cooper 1985).

These sex divergences are generally attributed to sex differences in the ways in which morphology affects organismal fitness (Darwin 1871; Andersson 1994). The relatively larger heads of males are believed to enhance male success in male-male rivalry and, hence, to have arisen through sexual selection. The longer trunks of females have been attributed to fecundity selection for increased space to hold the developing eggs or embryos (reviewed in Andersson 1994). Nonetheless, there have been no direct tests of these hypotheses. To evaluate them, we need to measure the ways in which morphological variation translates into fitness. In other words, are sexually dimorphic traits under selection in extant populations? If so, do these selective pressures conform to the conventional wisdom, that is, sexual selection for larger heads in males and fecundity selection for longer trunks in females?

MATERIALS AND METHODS

The snow skink (*Niveoscincus microlepidotus*) is a small (<5 g) ground-dwelling lizard endemic to the island of Tasmania off the southern coast of the Australian mainland, living above 800 m in rocky habitat with hardy vegetation (for more details, see Olsson and Shine 1999; Olsson et al. 1999). Females are viviparous. They reproduce biennially or triennially and produce one to five young upon emergence from hibernation in early spring (around September). Males fight severely for females and guard their mated, but not yet ovulated partner until ovulation takes place (around October).

Our study site was situated at 1270-m elevation on Mount Wellington about 10 km south of the city of Hobart, Tasmania, and consists of bare dolerite rock interspersed with hardy vegetation. Over the five-year study period (1992–1997) more than 3000 lizards (including juveniles) were marked within a quarter hectare (50 m × 50 m). During this period, we monitored male mating success on most days of the field season when weather permitted lizard activity. An area that small and still sufficient for monitoring a large number of lizards strongly facilitated our gathering of a high-resolution dataset, aided by three field assistants. For the descriptions of sexual dimorphism we used all lizards measured throughout the study period. Comparisons of male and female reproductive success in relation to sexually dimorphic traits are based on data from the two seasons for which we have the most comprehensive information (1993–1994 and 1994–1995).

The lizards were caught by hand or by noose, whereafter they were measured by ruler (SVL to the nearest mm) and digital calipers (interlimb length, head length [from the snout to the anterior suture of the occipital scales], to the nearest 0.01 mm) and weighed to the nearest 0.01 g. Each lizard was marked permanently by toe clipping and temporarily with oval cloth tape with an identification number on the lizard's back. In addition, we estimated litter sizes in gravid females by abdominal palpation. The accuracy of the palpation technique was tested in a pilot study using laparoscopy. The correlation between palpated and laparoscoped clutch size was very high ($r_s = 0.78$, $P = 0.006$, $n = 14$); 13 of 14

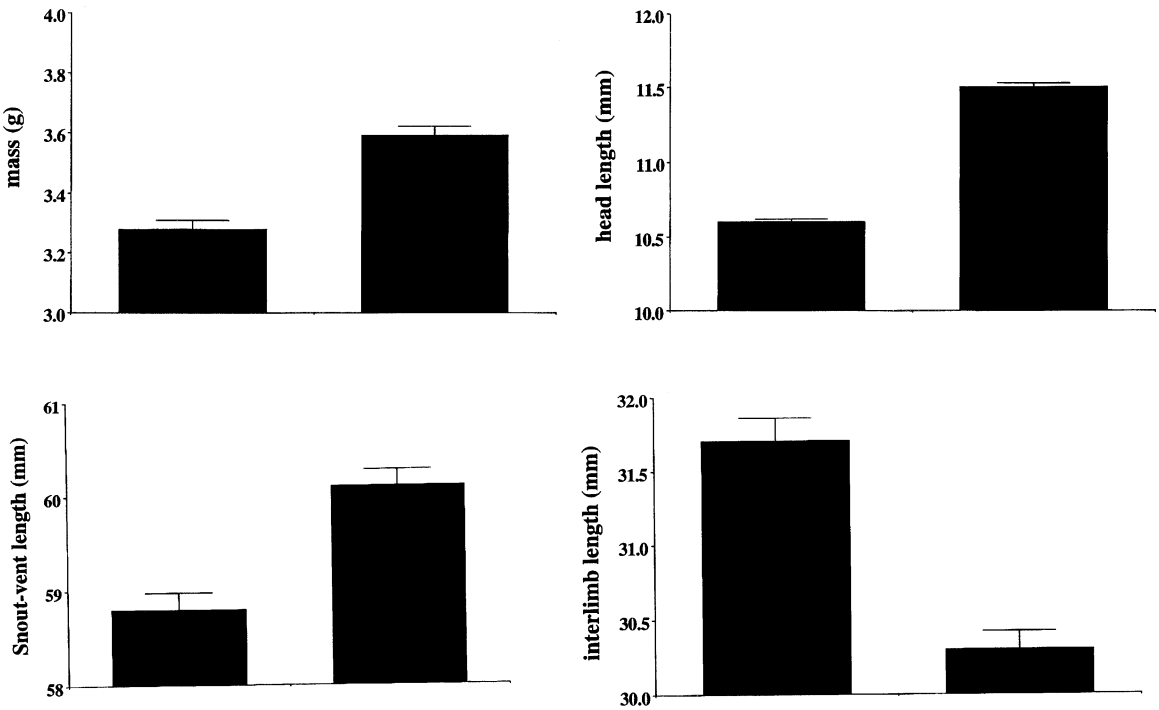

FIG. 1. Sexual dimorphism in aspects of mean adult body size in snow skinks, *Niveoscincus microlepidotus*. The graphs show mean values and associated standard errors. In all panels: left columns, females; right columns, males. The difference between the sexes is statistically significant for body mass (g, $n_{females} = 476$, $n_{males} = 527$; $t = 6.76$, $P \ll 0.0001$), snout-vent length (mm, $n_{females} = 481$, $n_{males} = 533$; $t = 5.09$, $P \ll 0.0001$), head length (mm, $n_{females} = 478$, $n_{males} = 533$, $t = 25.80$, $P \ll 0.0001$), and interlimb length (mm, $n_{females} = 368$, $n_{males} = 439$; $t = 7.28$, $P \ll 0.0001$).

females were scored correctly. In the remaining one the deviation between scores was one enlarged follicle (Olsson et al. 2001).

Statistical Analysis

Females sometimes mate with more than one male, and our unpublished data for a subset of males show that this results in high frequency of within-clutch multiple paternity (AFLP analysis: six of eight, 75%, examined clutches showed multiple paternity, mean clutch size = 2.75 ± 0.70 young; M. Olsson, B. Ujvari, E. Wapstra, T. Madsen, R. Shine, and S. Bensch, unpubl. ms.). For logistic reasons, we did not assign paternity by using molecular genetics techniques for our large dataset (>350 males). Instead, we

TABLE 1. Analysis of selection on sexually dimorphic traits in male and female snow skinks. Response variable in all models is an individual's estimated number of produced eggs (i.e., clutch size in females and cumulated number of eggs for all partners in males, devalued by her number of sexual partners assuming sperm competition).

Trait	Type III SS	*F*	*P*	β	SE_β
Extended models					
Females: Model SS = 65.9, MS = 22.0, $F = 33.7$, $P = 0.0001$, $df_{model} = 3$, $df_{error} = 220$, $R^2 = 0.32$					
Snout-vent length	2.71	4.16	0.042	0.28	0.14
Interlimb length	2.30	3.53	0.062	0.20	0.11
Head length	1.03	1.59	0.21	0.12	0.09
Males: Model SS = 19.1, MS = 6.4, $F = 10.8$, $P = 0.0001$, $df_{model} = 3$, $df_{error} = 351$, $R^2 = 0.08$					
Snout-vent length	6.60	11.21	0.0009	0.38	0.11
Interlimb length	3.36	5.70	0.018	−0.19	0.08
Head length	0.008	0.01	0.91	−0.01	0.09
Reduced models					
Females: Model SS = 67.7, MS = 33.8, $F = 51.1$, $P = 0.0001$, $df_{model} = 2$, $df_{error} = 224$, $R^2 = 0.31$					
Snout-vent length	7.08	10.7	0.001	0.37	0.11
Interlimb length	2.6	3.92	0.049	0.21	0.11
Males: Model SS = 19.2, MS = 9.6, $F = 16.4$, $P = 0.0001$, $df_{model} = 2$, $df_{error} = 354$, $R^2 = 0.08$					
Snout-vent length	13.0	22.4	0.0001	0.37	0.08
Interlimb length	3.4	5.8	0.016	−0.19	0.08

TABLE 2. Between-sex differences in selection on interlimb length as analyzed by a heterogeneity of slopes test while controlling for snout-vent length (included as covariate in the model).

Parameter	Type III SS	F/t	P	β	SE_β
Model SS = 87.3, MS = 29.1, F = 47.5, P = 0.0001, df_{model} = 3, df_{error} = 580, R^2 = 0.20					
Interlimb length × sex	22.1	18.0/—	0.0001		
Females		—/−2.81	0.005	0.21	0.08
Males		—/−2.72	0.007	−0.19	0.07
Snout-vent length	20.2	32.9/5.7	0.0001	0.38	0.06

calculated a reproductive success score for each male in the following way. If a female was accompanied by only one male, we allocated the paternity of her entire litter to him. The four studies that have analyzed paternity using molecular markers in lizard populations in a very similar nonterritorial mating system, as in snow skinks, concluded that male proximity to a female was highly indicative of paternity in that female's clutch (Abell 1997; Gullberg et al. 1997; Bull et al. 1998; Lewis et al. 2000). Furthermore, in all four studies there was high extrapair paternity, even in the scincid lizard *Tiliqua rugosa*, which shows unusually long pair bonds that may last several years (Bull et al. 1998). Therefore, when a female was observed with more than one male, we divided her litter size by the number of males with whom she was seen pairing during the mating season and allocated an equal proportion of the litter to each male, on the assumption that each was likely to share equally in paternity of the litter. We then added together all of these partial litters to estimate the total number of offspring likely to have been fathered by that male in that season. The reproductive success score for a female was simply the number of young in her litter.

We then performed analyses of standardized selection coefficients (standardized by year with mean set to zero and standard deviation set to unity) as outlined by Lande and Arnold (1983) and Arnold and Wade (1984a,b). SVL, interlimb length, and head length were included in the first set of analyses. When head length generated P-values of 0.21 (females) and 0.91 (males) in the first set of models, we followed the advice for backward elimination procedures given by Sokal and Rohlf (1981, pp. 662–666; eliminate predictors with $P > 0.10$) and repeated the analyses without entering head length. With respect to the hypotheses we set out to test, the elimination procedure is primarily relevant to the sexual selection hypothesis in males (on relative head size), because the fecundity hypothesis for larger trunk length in females is silent with respect to head size. When a lizard was observed in more than one year (or was measured more than once in the descriptive study), we used mean values for all traits to avoid pseudoreplication.

Finally, we analyzed sexual dimorphism in two traits that both contribute to SVL but have been overlooked in all previous work on sexual dimorphism in lizards (Olsson and Madsen 1998), namely neck length (from where the occipital scale starts to the shoulder) and the diameter of the legs at the insertion to the shoulder and pelvic girdles. Sexual dimorphism in these traits was established on 15 preserved lizards of each sex, sampled from the study site (M. Olsson's collection).

RESULTS

Sexual Dimorphism in the Snow Skink

Male snow skinks are slightly larger than females both in body mass and SVL. Males averaged 3.6 g and 60.1 mm and females 3.3 g and 58.8 mm, respectively (Fig. 1, see caption to figures for all test statistics). Males also have significantly longer heads than conspecific females (Fig. 1). This effect is not only due to the larger overall body size of males. Using residual scores from a pooled linear regression of head length on SVL, males have significantly larger heads than females at the same body length (Fig. 2).

Despite being smaller than males in overall size, females have a larger absolute interlimb length (Fig. 1). Again, the difference in body shape between the sexes becomes even more pronounced when the effect of body size is removed by using residual scores from the interlimb length–SVL regression (Fig. 2).

In the study of the preserved lizards, male SVL was significantly longer than female SVL (59. 0 ± 0.82 mm [SE] and 55.9 ± 0.62 mm, respectively; t = 2.95, df = 28.0, P = 0.006). Furthermore, males had longer necks (9.5 ± 0.20 mm vs. 8.3 ± 0.30; t = 3.1, df = 28.0, P = 0.004) and wider leg diameters of both front legs (2.6 ± 0.06 mm vs. 1.9 ± 0.05; t = 9.4, df = 28.0, $P < 0.0001$) and hind legs (3.8 ± 0.1 mm vs. 2.8 ± 0.06; t = 8.6, df = 28.0, $P < 0.0001$). Homogeneity of slopes tests showed that both neck length and leg diameters increased more steeply with SVL in males than in females (the interaction term between sex and SVL as predictor variable, neck and leg traits as response variables; $P < 0.01$ in all cases; neck length, regression coefficient, β = 0.101 vs. 0.087; front leg diameter, β = 0.036 vs. 0.025; hind leg diameter, β = 0.074 vs. 0.060). Thus, the diameter of the neck and the legs contribute significantly to sexual dimorphism in SVL and body shape, with shorter relative interlimb length and larger heads, necks, and more robust leg structure in males for a given SVL.

Selection on Body Shape

In both sexes, SVL was positively correlated with reproductive success ($r_{females}$ = 0.55, $P < 0.0001$, n = 236; r_{males} = 0.26, $P < 0.0001$, n = 381). However, selection pressures on body shape did not support the predictions from theory. Head length was not identified as a direct target of selection in either sex (Table 1, extended model). When head length was eliminated from the models, the coefficients of determination for the GLMs were reduced by only 1% in females and by less than 1% in males (Table 1). As evident from

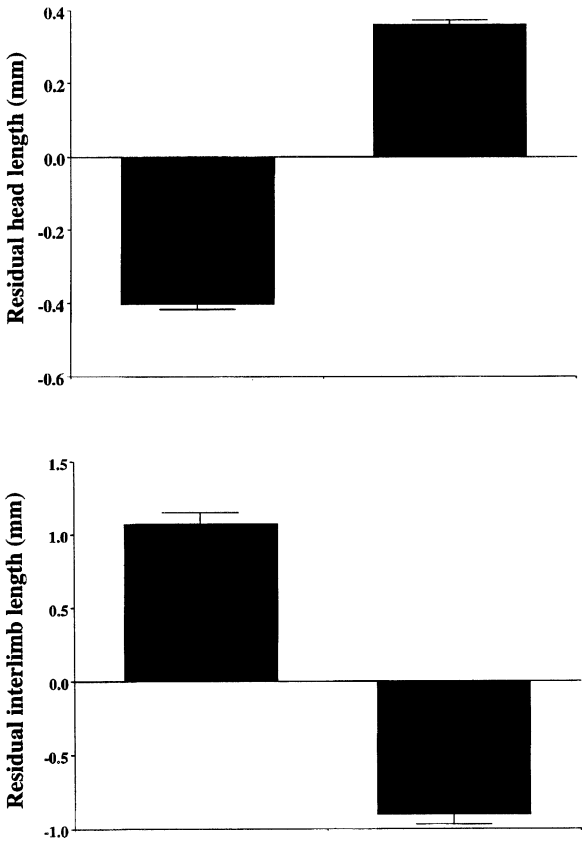

FIG. 2. Sexual dimorphism in relative sizes of different components of adult snow skinks, after removing the effects of sex differences in absolute size. The graphs show residual scores from general linear regressions of (top panel) head length versus snout-vent length, and (bottom panel) interlimb length versus snout-vent length. In both panels: left columns, females; right columns, males. The differences between the sexes were statistically significant, as indicated by heterogeneity of slopes tests, using head length or interlimb length as response variables and the interaction between sex and snout-vent length as predictor (for head length, $F = 2291.50$, df model = 2, df error = 1008, $P < 0.0001$; for interlimb length, $F = 1062.99$, df model = 2, df error = 804, $P < 0.0001$).

Table 1 (reduced models), body size was still the trait with the strongest influence on the reproductive success score in both sexes, but now interlimb length was marginally significant also in females ($P = 0.049$).

More importantly, the effect of selection on interlimb length differed strongly between the sexes. Females showed a significant positive regression coefficient (i.e., selection gradient) for interlimb length, but for males there was a significant negative selection coefficient for the same trait (Table 1, Fig. 3). This difference between the sexes in how selection operates on body shape was further analyzed in a homogeneity of slopes test with reproductive success as response variable and the interaction between gender and interlimb length as predictor (Table 2). This analysis strongly supported the hypothesis that selection on interlimb length acts in opposite directions in the two sexes. Females are under positive fecundity selection to increase relative interlimb length, whereas sexual selection in males favors a reduction in this trait (Fig. 3, Table 2).

DISCUSSION

Sexual differences in relative interlimb length are among the most widespread expressions of sexual dimorphism within lizards, including skinks (Greer 1989; Forsman and Shine 1995; Hudson 1997). Our data confirm that sexual dimorphism in trunk length in snow skinks is a direct target of significant selection. The microevolutionary forces currently active in shaping sexual dimorphism in trunk length in this species involve not only fecundity selection in females but reflect the cumulative effects of significant selection acting in opposite direction in the two sexes.

Our analysis of ongoing selection on body size and relative trunk length also agrees well with the observed patterns of sexual dimorphism in the natural population. Males are larger than females and are under stronger selection for body size, as depicted by the higher selection gradient in males (Table 1, extended model; 0.38 vs. 0.28). Theory predicts a relationship between the summed difference in the strength of direct and indirect forces of selection acting on body size in the two sexes and their realized sexual dimorphism, and interspecific comparisons have supported this prediction (Arak 1988).

Nonetheless, other aspects of our selection analysis are more difficult to reconcile with patterns of sexual dimorphism in snow skinks, such as relative head size. Interestingly, there is sexual dimorphism in this trait from birth, with neonatal males having a longer head than females (means = 6.85 vs. 6.76 mm, respectively; $t = 2.79$, df = 202.0, $P = 0.006$; M. Olsson and R. Shine, unpubl. data). There is, however, no such sexual dimorphism in interlimb length (13.1 vs. 13.2 mm, $t = 0.88$, df = 152.0, $P = 0.38$; M. Olsson and R. Shine unpublished). These results hold true when the effects of body size are removed from the analysis. Thus, we know that the sex divergence in relative head sizes is hard-wired genetically, and we cannot rule out the possibility that sexual dimorphism in adult (or neonatal) head length is a result of positive intercorrelations among life-history stages (Cheverud et al. 1981).

The functional basis for the effects of relative interlimb length on reproductive success presumably differs between the sexes. In the case of females, the most obvious linkage involves an increased abdominal volume to carry the developing offspring (Vitt and Congdon 1978; Shine 1992). The functional basis for interlimb length versus mating success in male skinks is less obvious, but may involve effects of size allometries on a male's fighting ability: A male with a more robust leg structure and longer neck should have a competitive advantage in contests. Regardless of the nature of these advantages, it is clear that the degree of sexual dimorphism in a trait reflects the balance of selective forces acting on both males and females (e.g., Ralls 1976; Clutton-Brock et al. 1982).

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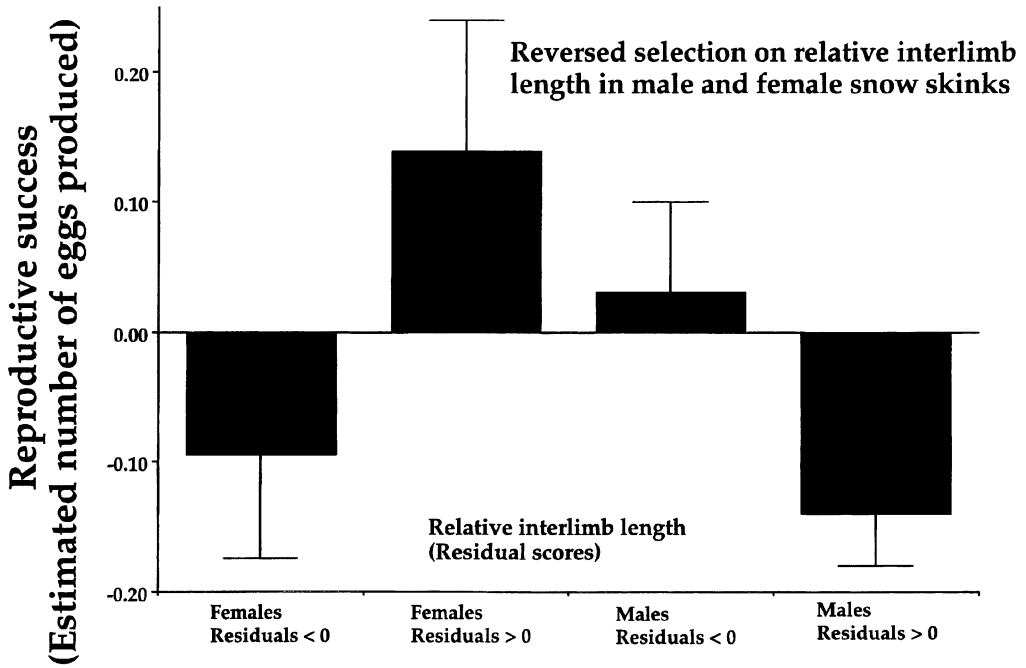

FIG. 3. The relationship between relative interlimb length and reproductive success in male and female snow skinks. Females with relatively shorter torsos (residual scores below zero) had significantly lower reproductive success than females with relatively longer torsos (residual scores > 0). For males, however, the opposite relationship applies; males with shorter torsos had relatively higher reproductive success (see Table 2 for test statistics).

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