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Sexual dimorphism and sexual selection in a montane scincid lizard (*Eulamprus leuraensis*)

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Abstract Sex-based divergences in body sizes and/or shapes within a species imply that selective forces act differently on morphological features in males *versus* females. That prediction can be tested with data on the relationship between morphology and reproductive output in females, and between morphology and realized paternity (based on genetic assignment tests) in males. In a sample of 81 field-collected adult Blue Mountains water skinks (*Eulamprus leuraensis*), males and females averaged similar overall body sizes (snout–vent lengths (SVLs)). Reproductive success (based on 105 progeny produced by the females) increased with SVL at similar rates in both sexes (as expected from the lack of sexual size dimorphism). Multiple paternity was common. Males had larger heads than females of the same body size, and (as predicted) reproductive success increased with relative head size in males but not in females. Males also had relatively longer limbs and shorter trunks than females, but we did not detect significant sex differences in selection on those traits. Reproductive success in both sexes was increased by relatively longer hind limbs. Our data clarify mating systems in this endangered species, and suggest that mating systems are diverse within the genus *Eulamprus*.

Key words: fecundity selection, mating system, multiple paternity, reptile, Scincidae.

INTRODUCTION

Darwinian theory predicts that patterns of phenotypic variation within a population are strongly influenced by the ways in which those variations translate into underlying fitness differentials among individuals. Thus, for example, geographic variation in the frequency of alternative morphotypes (such as colouration or body shape) is thought to reflect corresponding geographic variation in the selective advantages or disadvantages of those alternative trait values (e.g. Endler 1995; Endler & Houde 1995). Unfortunately, spatial variation of this kind also can be generated by factors such as variable local conditions (inducing phenotypically plastic trait expression, e.g. Downes 1999; Shine & Elphick 2001), and by phylogenetic history (different lineages in different areas, e.g. Dubey *et al.* 2007). Even greater confounding factors plague attempts to interpret the selective basis of interspecific variation in phenotypic traits (e.g. Harvey & Pagel 1991). Charles Darwin (1871) suggested that comparisons of selective forces and responses between males and females within a single species might provide a way to overcome some of these logistical problems.

Conspecific males and females experience similar environmental conditions, and have the same genetic heritage. Thus, if the sexes differ in some genetically-determined trait, only a limited set of selective forces can be invoked to explain that divergence. For example, larger body size might enhance female reproductive success because it allows greater fecundity, or might enhance male reproductive success if it increased a male's ability to win battles with rival males (e.g. Vitt & Cooper 1985; Lebas 2001; Olsson *et al.* 2002; Du *et al.* 2005; Stuart-smith *et al.* 2008; Dubey *et al.* 2009). Hence, studies on sexual dimorphism provide an excellent opportunity to examine the putative selective basis for divergence in morphological traits (Vitt & Cooper 1985; Andersson 1994; Madsen & Shine 1995; Shine *et al.* 1998). Some of the data needed for such analyses are relatively straightforward to obtain. It is easy to measure morphological traits in the two sexes, and to monitor reproductive output of females (at least on a per-litter basis). Quantifying male reproductive success poses greater logistical challenges, but the development of genetic methods for paternity assignment now enables us to make direct comparisons between the sexes in terms of reproductive output (e.g. Stapley & Keogh 2005; Dubey *et al.* 2009). Ideally, such comparisons should measure lifetime reproductive success, but few studies have achieved that ambitious aim (e.g. Clutton-Brock 1988; Madsen & Shine 1994; Krüger 2002). If selective forces diverge strongly between the sexes, comparisons based on data from a single reproductive season can be used to look for the predicted correlations between sexually dimorphic traits and

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sex-specific selective forces. We have conducted such an analysis for a montane lizard species from south-eastern Australia.

METHODS

Study species, area and sampling protocol

The Blue Mountains water skink, *Eulamprus leuraensis*, is a medium-sized (to 85-mm snout–vent length (SVL), 15 g) viviparous lizard restricted to a scarce and highly fragmented habitat type ('hanging swamps') along the Great Dividing Range west of Sydney. Known from less than 40 populations, the species is classified as endangered under both state and federal legislation (Threatened Species Conservation Act – NSW 1995; Environmental Protection and Biodiversity Conservation Act – Commonwealth 1999; Dubey & Shine 2010). We collected tissue samples (tail clips) from 81 adult *E. leuraensis* during fieldwork from November 2008 to April 2009, from six small populations (Table 1). Our sample comprised 40 males and 45 adult (and thus, potentially gravid) females, and the latter were retained in captivity until parturition. We housed lizards individually in plastic boxes (320 × 220 × 100 mm) in a room maintained at 18°C (daylight period: 07.00–19.00 hours). Underfloor heating cables allowed each female to control her body temperature over the range 20–33°C for part of the day. Each female was fed five crickets twice weekly. The 41 females produced a total of 105 neonates, all of which were weighed and measured <24 h after birth.

DNA extraction and microsatellite analysis

Tissues were placed in 200 μL of 5% Chelex containing 0.2 mg mL^{-1} of proteinase K, incubated overnight at 56°C, boiled at 100°C for 10 min and centrifuged at 12 000 rpm for 10 min. Then the supernatant (containing purified DNA) was removed and stored at −20°C.

Table 1. Sample sizes of free-ranging Blue Mountains water skinks for which genetic data were gathered

Site	Adult females sampled	Litters	Neonates	Potential fathers sampled
BH3	8	7	20	5
BH4	13	13	32	5
KT1	5	5	12	7
MH4	3	3	7	3
MRP1	10	8	19	9
WF7	6	5	15	11
Total	45	41	105	40

The table shows the number of adult (and thus, potentially gravid) females sampled, litters, neonates and potential fathers (number of adult males tested) sampled for each site. Specific locations for these sites are given by Dubey and Shine (2010).

Six microsatellite loci isolated and characterized from *Eulamprus kosciuskoi* (Scott *et al.* 2001: EK8, EK23, EK37, EK100, EK107) and *Gnypetoscincus queenslandiae* (Sumner *et al.* 2001: GQ20/21) were amplified and scored. Amplified products were genotyped with a 3130 xl genetic analyser (Applied Biosystems) using Genemapper software V3.7 (Applied Biosystems). Polymerase chain reaction amplifications were performed in a 9800 Fast thermal cycler (Applied Biosystems) as 5 μL reactions containing 0.075 U *Taq Ti* DNA polymerase (Biotech), 0.1 mmol dNTPs, 0.4 mmol of each primer, 20 mmol Tris-HCl, pH 8.5, and 50 mmol KCl, 1.25 mmol $MgCl_2$. Cycling conditions included a hot start denaturation of 95°C for 3 min, followed by 35 cycles of 95°C for 30 s, 60°C (55°C for EK23, GQ20/21 and EK37) annealing temperature for 30 s, 72°C for 30 s (1 min for EK23, GQ20/21 and EK37), and a final extension of 72°C for 30 min.

Statistical analyses of morphology and reproductive success

We compared mean SVLs between the sexes with ANOVA. To compare body proportions between the sexes, we first conducted a Principal Components (PC) analysis on all morphological variables (SVL, head length, limb lengths, interlimb distance, body mass) and took the first PC axis (which explained 78.3% of the total variance: loading factors for SVL, head, front limbs, back limbs, interlimb and mass were 0.433, 0.425, 0.420, 0.392, 0.346 and 0.427, respectively) as our index of overall body size. We used this PC axis as a covariate in ANCOVAs with sex as the factor and morphological traits as dependent variables.

To explore links between morphology and reproductive success, we conducted two types of analyses. In each case, the morphological variables were SVL, and residual scores from the general linear regression of each trait (e.g. head length) against our overall measure of body size (i.e. PC axis 1). The first analysis was based on whether or not an individual was known to have reproduced in the year of collection (based on maternity and paternity of the captive-born offspring); this category plus sex were included as factors in a two-factor ANOVA with morphological variables as dependent variables. We cannot exclude the possibility that some males classified as 'non-reproductive' did indeed sire offspring with females other than the ones we sampled. However, this potential error in classification should be randomly distributed among individuals of different body sizes, and consequently should not create any directional bias in patterns of correlation between morphology and mating success.

The second set of analyses treated reproductive success as a continuous variable (based on the number of offspring produced by each adult lizard), using the morphological measures as covariates, sex as a factor, and reproductive success as the dependent variable. To generate a measure of reproductive success that can be compared between the sexes, we calculated the number of offspring per parent divided by the mean number of offspring for adults of that sex. The standardization was necessary because our raw data consistently underestimated male reproductive success relative to female reproductive success. Males averaged 1.18 offspring in our dataset and females averaged 2.37, because

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we counted every offspring born to each female that we captured, but missed many of the offspring sired by male lizards (i.e. offspring in litters born to females other than the ones we collected).

Statistical analyses of genetic data

Gene diversities comprising observed (H_O) and expected heterozygosities (H_S) were estimated following the methods of Nei and Chesser (1983). Genotypic disequilibrium between loci in each sample was tested based on 10 000 randomizations in order to check for potentially linked loci (e.g. situated on the same chromosome). Deviations from Hardy–Weinberg equilibrium (HWE) within samples were tested based on 10 000 randomizations, to check for the presence of allelic dropouts, founder effects, substructure within populations (Wahlund effect), inbreeding or null alleles. Wright's fixation indices for within-population deviation from random mating (F_{IS}) were estimated following Weir and Cockerham (1984). Deviations from random mating within populations (F_{IS}) per locus and sample were computed with a bootstrap procedure (10 000 randomizations). All summary statistics and tests were computed using FSTAT Version 2.9.3.2 (Goudet 1995). Significance values were corrected for multiple tests using the sequential Bonferroni method (Rice 1989). Detection of null alleles was tested according to Chakraborty and Jin (1992).

Paternity analyses

We determined paternity on the basis of a maximum likelihood method via the programme CERVUS 3.0 (Marshall *et al.* 1998; Kalinowski *et al.* 2007). It conducts a comparison between an infant–mother pair and all the potential fathers in the dataset, and calculates a LOD score (i.e. the logarithm of the likelihood ratio) for every potential father. The difference between the LOD scores of the male with the highest value and the male with second highest value is the Δ-criterion (Δ LOD) (Marshall *et al.* 1998). Δ LOD is compared with the critical Δ values calculated after a simulation and provided with a statistical confidence level. The simulations were based on allele frequency data from the adult samples in each of the populations, because the juvenile sampling was skewed (7–20 juveniles per site for 5–13 litters). Parameters used for the simulation differed from site to site and we based our choices on the following criteria: (i) total number of candidate males; (ii) mean proportion of candidate males sampled; (iii) mean proportion of data typed ≥0.95 (i.e. ≤5% of data missing); and (iv) rate of typing errors = 0.00. We chose the confidence level proposed by Marshall *et al.* (1998) (strict confidence ≥95%). Candidate males were determined using a size criterion (SVL > 50 mm) in order to minimize incorrect assignments.

RESULTS

Sexual dimorphism

Male *E. leuraensis* attain sexual maturity at about 53 mm SVL, and females at 67 mm (based on the smallest reproductive animals in our sample). Despite the smaller minimum size at maturation in males, mean adult SVLs were similar in the two sexes ($F_{1,74} = 1.91$, $P = 0.17$). Using an index of overall body size (first PC axis – see above) as a covariate, we detected significant sex differences in relative head length, limb length, trunk (interlimb) length and mass. Head size relative to body length increased more rapidly in males than females (ANCOVA, interaction PC1 size measure * sex $F_{1,72} = 4.69$, $P < 0.035$). Interaction terms were non-significant ($P > 0.05$) in all other ANCOVAs, but significant main effects of sex showed that compared with females of the same overall size, adult male skinks had longer legs (main effect front leg length $F_{1,72} = 7.79$, $P < 0.007$; rear leg length $F_{1,72} = 19.23$, $P < 0.0001$), shorter trunks ($F_{1,72} = 76.14$, $P < 0.007$) and weighed more ($F_{1,72} = 22.91$, $P < 0.007$).

Tests for linkage disequilibrium, heterozygosity and random mating

Within samples from the adult skinks, we did not detect any significant linkage disequilibrium or null alleles. Consequently, all loci were included in the following analyses. For the six microsatellite loci, the number of alleles per locus ranged from 3 to 16, with a total of 77 alleles across six loci. Observed heterozygosity within the adult population (H_O) was 0.63, and expected heterozygosity (H_E) was 0.67 (Table 2).

Within the sample of 105 neonates, no linkage disequilibrium was detected if we analysed each litter separately. If we combined data for all litters into a single analysis, significant linkage disequilibrium was observed between the pairs of loci EK107/EK23. This result clearly reflects the skewed sampling (i.e. high relatedness of juveniles within each of the 41 litters). For the six microsatellite loci, the number of alleles per locus ranged from 2 to 16 (Table 2), with a total of 73 alleles across six loci. Observed heterozygosity within the juvenile population (H_O) was 0.72, compared with expected heterozygosity (H_E) values of 0.64 and 0.56 (based on calculations treating each litter separately *vs.* combined: Table 2). There were significant deviations from random mating (dissociative; $P < 0.001$), regardless of whether we treated the data for each litter separately (global $F_{IS} = -0.256$), or combined the data for all litters (global $F_{IS} = -0.087$).

Incidence of multiple paternity

Of the 105 offspring with known mothers, 40 were assigned at ≥95% certainty to fathers sampled in the same population (38.1%). The proportion of offspring to which a father was assigned at ≥95% varied from 0% to 100% among litters. The number of different

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Table 2. Characteristics of microsatellite loci used for the paternity analyses

Loci	$N_{A\,Ad}$	$N_{A\,Ju}$	$H_{O\,Ad}$	$H_{O\,Ju}$	$H_{E\,Ad}$	$H_{E\,Ju}$	$^{\dagger}H_{E\,Ju}$	$Fis_{\,Ad}$	$Fis_{\,Ju}$	$^{\dagger}Fis_{\,Ju}$
GQ20/21	15	15	0.692	0.767	0.724	0.690	0.663	0.052	–0.116	–0.248*
EK107	16	15	0.729	0.853	0.817	0.778	0.666	0.081	–0.048	–0.256*
EK37	16	16	0.711	0.876	0.746	0.741	0.674	0.005	–0.138*	–0.267*
EK8	3	2	0.203	0.241	0.216	0.204	0.173	0.040	–0.185*	–0.166*
EK100	14	13	0.775	0.794	0.751	0.735	0.600	–0.046	–0.044	–0.271*
EK23	13	12	0.674	0.793	0.754	0.698	0.591	0.088	–0.066	–0.263*
Total mean	77	73	0.631	0.721	0.668	0.641	0.561	0.037	–0.087*	–0.256*

The Table shows data for the number of alleles (N_A), observed (H_O) and expected (H_E) heterozygosities for the adults and juveniles considering each litter separately or all litters combined within sites (†), respectively. EK, *Eulamprus kosciuskoi;* GQ, *Gnypetoscincus queenslandiae.* *FIS values significantly different from zero ($P < 0.05$).

fathers assigned with ≥95% certainty per litter (for litters with at least one father assigned) varied from 1 to 2, with a mean of 1.24 (*n* litters = 21). Fathers were assigned in all the populations except BH4, with this anomalous case reflecting the small number of potential fathers sampled in this large swamp compared with the number of mothers (5 males *vs.* 13 females).

Based on alleles found within a litter for a given locus and the genotype of the mother, 11 litters (26.8%) revealed clear evidence of multiple paternity (i.e. more than two paternal alleles present within a litter). At least 54% of litters containing more than two offspring showed multiple paternity.

Morphological correlates of reproductive success in males and females

MANOVA with population and sex as factors, and morphological measures as dependent variables, showed highly significant sexual dimorphism ($F_{6,64} = 24.50$; $P < 0.0001$) but no significant divergence among populations ($F_{30,258} = 1.27$; $P = 0.16$), nor interaction between sex and population of origin ($F_{24,210.53} = 1.53$; $P = 0.06$). Thus, we combined data from the six populations to examine relationships between lizard morphology and reproductive success.

Lizards known to have reproduced during the year of sampling averaged larger (in terms of SVL; 74.9 mm) than non-reproductive animals (70.5 mm), in both sexes (two-factor ANOVA – effect of sex $F_{1,72} = 0.12$, $P = 0.73$; reproductive status $F_{1,72} = 5.19$, $P < 0.03$; interaction $F_{1,72} = 0.13$, $P = 0.72$). Males not only had larger heads relative to body size than did females (see above), but reproductively successful males (mean relative head size score: 0.086) had relatively larger heads than unsuccessful males (mean relative head size score: 0.047; interaction between sex and reproductive status $F_{1,72} = 5.86$, $P < 0.02$). Males also had longer legs and shorter trunks than females (relative to overall body size: see above), but these body-shape variables were not significantly linked to reproductive status (main effects and interaction terms both have $P > 0.10$).

Analyses that treated reproductive success as a continuous variable (standardized number of offspring) generated similar results to those above. Increased SVL enhanced reproductive success overall ($F_{1,72} = 10.29$, $P < 0.002$) with no significant differences between males and females ($F_{1,72} = 0.21$, $P = 0.65$) or interaction between sex and SVL ($F_{1,72} = 0.17$, $P = 0.68$; see Fig. 1a). Reproductive success increased with increasing head length (relative to body size) in males but not in females (interaction sex * relative head size $F_{1,72} = 4.29$, $P < 0.05$; Fig. 1b). The only other significant effect that we detected was that lizards with relatively longer hindlimbs tended to produce more offspring ($F_{1,72} = 5.30$, $P < 0.025$) regardless of sex (sex effect $F_{1,72} = 1.92$, $P = 0.17$; interaction sex * leg length $F_{1,72} = 2.60$, $P = 0.10$).

DISCUSSION

Lizards are highly speciose (more than 3000 recognized taxa, of which 30% are skinks) and encompass a great diversity in terms of body sizes, shapes, colours, physiological attributes and ecological traits (Greer 1989; Vitt & Pianka 1994). That diversity is likely to be reflected in mating systems also, but our understanding of social structure within lizard populations lags well behind our growing knowledge of other facets of squamate biology (Uller & Olsson 2008). Most lizard species remain unstudied, and the taxa that have attracted detailed research on social systems comprise a small and highly random subset (taxonomically, geographically and morphologically) of the world's lizard species (Uller & Olsson 2008; While *et al.* 2009). Nonetheless, it is clear from behavioural data (the primary type of information available from previous work) that lizard mating systems are diverse (Stamps

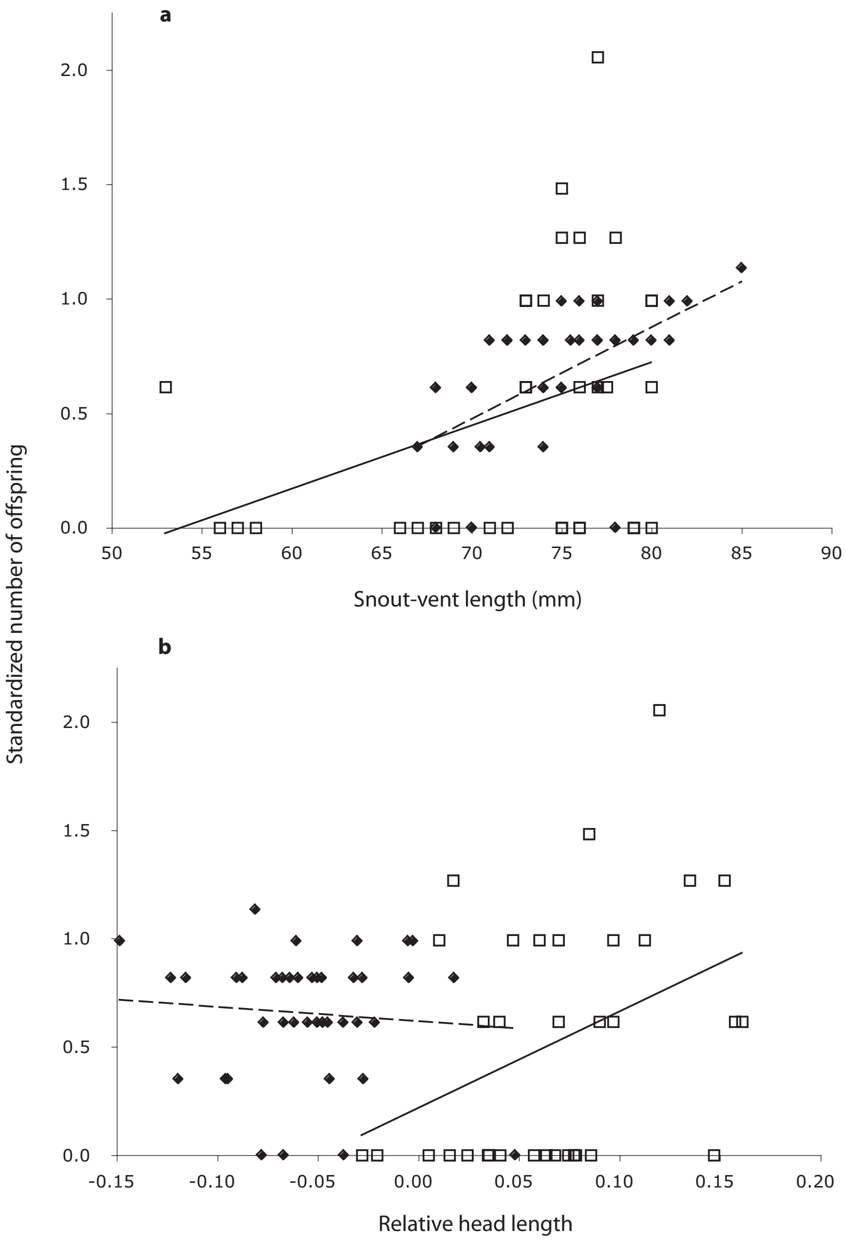

Fig. 1. Relationships between morphology and reproductive success in Blue Mountains water skinks, *Eulamprus leuraensis*: number of offspring (standardized within each sex) as the measure of reproductive success, compared with (a) snout–vent length and (b) relative head length (residual score from linear regression of head length against a Principal Components axis designed to assess overall body size).

1977, 1983). At one extreme, males grow much larger and more colourful than conspecific females, and defend well-defined territories by overt visual displays and male–male rivalry (e.g. many iguanids and agamids: Calsbeek & Sinervo 2004; Radder *et al.* 2005, 2006). At the other extreme, males and females are difficult to distinguish morphologically, overt behavioural displays are subtle or lacking, and many individuals lack site fidelity (e.g. many skinks: Greer 1989; Cogger 2000; Stapley & Keogh 2004). Understanding the selective forces at work in such a diverse array of mating systems will require studies not only on 'classic' territorial defence systems, but also on social systems within more cryptic species for which behavioural studies are logistically prohibitive.

Fortunately, molecular methods of paternity assignment provide an additional source of data on reproductive success, free of many of the biases inherent in behaviour-based measures of male mating success (Eizaguirre *et al.* 2007; Griffith 2007; Uller & Olsson

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2008). Few such studies have been conducted on squamate reptiles compared with birds and mammals, but already the data reveal interspecific differences in processes such as the form and intensity of selection on sexually dimorphic traits (see below). Some broad features of the mating system likely will prove to be consistent among all or most lizards, for example, variance in reproductive success likely is higher in males than in females, and multiple paternity is common (Olsson & Madsen 1998; Uller & Olsson 2008; see Morrison *et al.* 2002 for data on the congeneric *Eulamprus heatwolei*) – but many other aspects vary even between closely related species (Greer 1989; Vitt & Pianka 1994; Pianka & Vitt 2003). Below, we consider our results on *E. leuraensis* in the light of existing data on sexual selection in lizards.

Darwinian theory predicts that in cases where males and females within a population differ in some phenotypic trait, selective forces are likely to differ between the sexes also. The most obvious such trait is mean adult body size, and indeed there appears to be a strong link between mating systems and sexual size dimorphism (SSD: Ord *et al.* 2001). For example, males often grow much larger than females in lizard species in which males defend territories (Stamps 1977, 1983, 1997) whereas females often exceed males in mean adult body size in taxa in which overt male–male rivalry is lacking (Stuart-Smith *et al.* 2008). SSD also may be linked to mode of sex determination in some lineages, with temperature-dependent sex determination more common in agamid species with a male bias in mean adult body size (e.g. Harlow & Taylor 2000). Our data on *E. leuraensis* reveal no overall disparity in mean adult SVL, despite maturation at smaller sizes in males than females. This pattern is common in Australian scincid species (Greer 1989). *Eulamprus* is an interesting genus in terms of SSD, with males attaining larger mean adult body sizes than conspecific females in some taxa (*E. heatwolei*, *E. kosciuskoi*, *E. tympanum*; Done & Heatwole 1977a; Greer 1989; Morrison *et al.* 2002) but not others (*E. quoyii* – Schwarzkopf 2005; and *E. leuraensis* – present study). Intriguingly, modes of sex determination map perfectly onto this dichotomy, with offspring sex affected by maternal body temperatures in *E. heatwolei and E. tympanum* (Robert & Thompson 2001; Langkilde & Shine 2005) but not in *E. leuraensis* or *E. quoyii* (Borges-Landaez 1999; Caley & Schwarzkopf 2004; Dubey & Shine, unpubl. data 2009).

A lack of SSD does mean that body size is irrelevant to individual reproductive success. Instead, our data show that larger body size enhances reproductive output both in females (via fecundity selection, presumably reflecting the greater space available to accommodate offspring within a larger body: Shine 1992; Du *et al.* 2005) and in males (via sexual selection). The proximate mechanisms by which larger body size enhances male reproductive success in *E. leuraensis* remain unclear, because mating systems within congeneric species are complex (Morrison *et al.* 2002; Stapley & Keogh 2005) and we lack behavioural data. Nonetheless, agonistic encounters are frequent in both captive and wild *Eulamprus* (Rawlinson 1974; Done & Heatwole 1977a,b), including *E. leuraensis* (unpubl. data 2009). Given a consistent pattern for larger body size to enhance success in such contests (Vitt & Cooper 1985; Censky 1995; Olsson & Madsen 1998), it seems likely that larger males benefit from their abilities either to vanquish rival males, or to subdue females. Behavioural studies to clarify these issues in *E. leuraensis* would be of great interest.

In contrast to mean adult body size, body shape differs significantly between male and female *E. leuraensis*. Most obviously (even to the naked eye), adult males have larger heads than do adult females of the same overall body size. The same kind of sexual dimorphism is widespread in lizards, including other skinks (Vitt & Cooper 1985; Greer 1989; James & Losos 1991; Clemann *et al.* 2004; Schwarzkopf 2005), and generally has been attributed to the advantages of larger gape and more powerful jaws in battles with rival males or in retaining a grip on females during mating (*Gallotia galloti* – Huyghe *et al.* 2005; *Anolis carolinensis* – Lailvaux *et al.* 2004; *Lacerta vivipara* – Gvozdik & Van Damme 2003). The same kinds of explanations may apply to *E. leuraensis*. A larger relative head size did not enhance reproductive output in females, but was associated with strong increases in mating success in males (Fig. 1b). Two other traits were sexually dimorphic in *E. leuraensis* (relative interlimb distance and relative limb length), as is commonly the case in lizards (e.g. Olsson *et al.* 2002; Schwarzkopf 2005; Ross *et al.* 2008) but neither of these was associated with significant sexual divergence in fitness consequences within our dataset. Analysis of a much larger sample size of Tasmanian snow skinks (*Niveoscincus microlepidotus*) detected a sex difference in the relationship between interlimb length and reproductive output, as predicted by Darwinian theory (Olsson *et al.* 2002).

One intriguing result from our analyses was a positive correlation between reproductive output and relative hindlimb length, in both sexes. Plausibly, leg length might affect locomotor ability (speed and/or agility), enhancing lizard fitness through higher performance in capturing prey, escaping predators, and evading or chasing conspecifics. As for the other patterns detected by our genetic analyses, behavioural data are needed to identify the proximate mechanisms linking phenotypic traits to reproductive success. More generally, it would be instructive to know how variation in male morphology influences behavioural tactics (e.g. territorial *vs.* 'floater' males, as in *E. heatwolei*: Stapley & Keogh 2005), and in turn, reproductive success. The comparison between these two congeneric species would be of

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great interest, because *E. heatwolei* and *E. leuraensis* are two of the few lizard species for which genetic data on reproductive success of free-ranging males has been quantified. Remarkably, the link between male body size and mating success is non-existent in the former species (Morrison *et al.* 2002; Stapley & Keogh 2005), but strong in our own study (Fig. 1a). That divergence in the phenotypic determinants of reproductive success across closely related taxa – as well as substantial intrageneric diversity in traits such as mean body sizes (Cogger 2000), thermal biology (Spellerberg 1972), reaction norms of embryogenesis (Caley & Schwarzkopf 2004), agonistic behaviour (Done & Heatwole 1977a,b) and sex-determining modes (Robert & Thompson 2001; Langkilde & Shine 2005; Dubey and Shine unpubl. data 2009) – suggests that scincid lizards of the genus *Eulamprus* may provide excellent model systems with which to explore the selective forces operating on free-ranging lizards.

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