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SEXUAL DIMORPHISM IN BODY SHAPE WITHOUT SEXUAL DIMORPHISM IN BODY SIZE IN WATER SKINKS (*EULAMPRUS QUOYII*)

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ABSTRACT: Sexual dimorphism in body size is often accompanied by shape dimorphism. Shape dimorphism may be selected directly, or may be an indirect result of selection for size dimorphism. To determine whether shape differences are likely to have been directly influenced by selection, the indirect effects of size dimorphism on shape can be removed statistically, the approach of most previous studies, or, alternatively, we can examine the patterns of shape dimorphism in species that are not size dimorphic. Here I describe sexual shape dimorphism in adults and neonates of a lizard that is not dimorphic in body length, the eastern water skink (*Eulamprus quoyii*). In this species, snout–vent length is not significantly different between adult or neonate males and females, but there are significant shape differences between sexes in both adults and neonates. For a given body length, adult males have wider heads, longer limbs, shorter trunk length (the distance between the forelimb and the hindlimb), and greater mass than females. In addition, head width, forelimb length and mass increase significantly more rapidly with body length in adult males than in females, whereas the rate of change of hindlimb length and trunk length with length is not significantly different in males and females. The shape of the body is more similar in neonates than adults, but female neonates have significantly longer trunks than males. The intersexual shape difference in neonate *E. quoyii* suggests that, although growth rate differences among body parts are the main source of differences in shape between adults, the difference between male and female interlimb lengths is present initially. Shape differences present at birth that are preserved until adulthood are less common than growth differences as a source of adult shape differences. The intersexual shape differences among adult *E. quoyii* are similar to those reported for species that are sexually size dimorphic, suggesting that selective forces have influenced body shape in similar ways in both size dimorphic and nondimorphic species, and that allometric relationships alone may not be responsible for shape differences between males and females in size dimorphic species.

Key words: *Eulamprus quoyii*; Head size; Limb length; Lizards; Mass; Natural selection; Sexual selection

SEXUAL size dimorphism is widespread in animals and has a variety of causes, including sexual selection for contest success in males, natural selection for high fecundity in females, and natural selection for diet specialization in either sex (reviewed by Andersson, 1994; Olsson and Madsen, 1998). In addition to size dimorphism, sexual dimorphism in body shape is common (Butler and Losos, 2002; Malhotra and Thorpe, 1997; Olsson et al., 2002; Powell and Russell, 1992). Sexual dimorphism in head size in lizards, in which males have larger heads, may be caused by (i) sexual selection for contest success in males, if males fight or display using their heads, or (ii) selection for mating success, if males grip females with their jaws; or both (Andersson, 1994). In lizards, diets of males and females seldom differ, so that head size differences are likely to be due to sexual selection rather than natural selection for diet partitioning (Stamps, 1983). Another common form of sexual shape dimorphism in lizards is longer trunk length (i.e., the distance between the fore and hind limbs) in females, presumably due to selection for more space to accommodate developing young (Olsson et al., 2002), although improved locomotor performance in crawling over or through litter also may select for longer trunk length (Greer, 1989).

Shape dimorphism also may occur as an indirect result of selection on other traits without being directly selected. For example, where shape is related allometrically to size, selection on size could cause dimorphism (Gould, 1975). Therefore, examining shape dimorphism in species that are not sexually size dimorphic is of interest, because in such species there are no "hidden" effects of size selection on shape. There have been few studies of sexual dimorphism in body shape (Tokarz, 1995), and even fewer studies of the patterns of sexual shape dimorphism in groups that do not also show sexual size dimorphism. Examining shape dimorphism in species without sexual size dimorphism provides an

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alternative to statistical control of size effects, allowing us to describe selection on morphology in the absence of selection for differences in body size.

Studies of size and shape dimorphism typically concentrate on comparisons of adults, but examination of the ontogenetic development of dimorphism can reveal its causes, for example if one sex is larger at birth, it will be larger at maturity if growth trajectories of the two sexes are identical (e.g., Badyaev, 2002; Shine, 1990; Watkins, 1996). Thus, comparing sexual size and shape dimorphism in adults and neonates can help to infer the sources of sexual dimorphism.

Here I explore shape dimorphism in adult and neonate eastern water skinks, *Eulamprus quoyii*. *Eulamprus quoyii* are medium-sized (90–130 mm snout–vent length), viviparous skinks, which are not sexually dimorphic in body coloration (L. Schwarzkopf, personal observations). Adults are site tenacious and possibly territorial (Spellerberg, 1972; L. Schwarzkopf, personal observations). They are probably polygynous (based on the behavior of the closely related species *E. heatwolei*, Morrison et al., 2002), but they are not sexually dimorphic in size (body length, see below). Because polygynous species typically are dimorphic in some way (Andersson, 1994), shape dimorphism in the absence of size dimorphism is interesting to examine in this species.

Materials and Methods

Adults

I conducted a mark-recapture study of *E. quoyii* at Alligator Creek, Mount Elliot National Park (19° 30′ S 146° 47′ E) between March 1994 and December 1996. Skinks were captured by hand, noosing, or with baited sticky traps. Snout-to-vent length (SVL) and tail length (TL) from the vent to the tip of the tail of captured individuals were measured with a plastic ruler. Head width (HW) at the widest point of the jaw, forelimb length (FLL) from the wrist to the point where the limb connects to the body, hind limb length (HLL) from the ankle to the point where the limb connects to the body, and interlimb length (ILL) from posterior to the point of insertion of the forelimb to anterior to the point of insertion of the hind limb were measured with dial callipers to the nearest mm. Individuals were weighed with a Pesola™ spring balance to the nearest 0.5 g. Only measurements made during the first capture of each individual were used for this study.

To meet the assumptions of least squares regression, all variables were logarithmically transformed prior to analysis. Mean SVL of males and females were compared using a *t*-test. I compared shapes of males and females using an analysis of covariance on each character with sex as the factor and SVL as the covariate. A significant interaction term indicates that there are differences between the slopes of the lines for males and females (Sokal and Rohlf, 1981). If there was no significant interaction between sex and SVL in the model, the interaction term was eliminated from the model, pooling interaction effects, and the model was used again including only main effects. This process reveals differences in the intercepts of the regressions for males and females, given that there are no differences between slopes (Sokal and Rohlf, 1981).

Neonates

To determine body size of neonates, I collected 19 gravid females from the Alligator Creek study area within 2 wk of parturition. Females were housed in lidless plastic boxes ($55 \times 33 \times 35$ cm LWH), with a 75-watt globe for heat and light. Each box was lined with paper towel, and provided with a branch as a basking perch and a small cardboard box for shelter. Females were fed crickets, mealworms and commercially prepared cat food three times per wk. Water was provided ad libitum in a dish large enough to allow the female to be completely submerged. These females were allowed to give birth naturally in the boxes, and were checked twice daily to determine if offspring were present. When offspring were first noted, females were not fed, and any remains of food were removed from the box, to prevent offspring from eating until they were weighed. Twenty-four hours after the first neonates were noted, offspring were removed from the boxes, and measured and weighed. Measurements recorded were identical to those reported for adults.

Individual measurements from offspring in litters are not independent, and male and female offspring are not independent within

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TABLE 1.—Means, ranges, and slopes of the relationships of each variable (± SE) with snout–vent length for a series of measurements of body morphology of male and female eastern water skinks, *Eulamprus quoyii*.

Variable	*n* Males	Mean (SE) Males	Range Males	Slope of variable vs. SVL (SE)	*n* Females	Mean (SE) Females	Range females	Slope of variable vs. SVL (SE)
Snout-to-Vent Length (mm)	76	106.2 (1.01)	90–127	—	85	104.6 (0.95)	90–123	—
Head Width* (mm)	76	13.7 (0.16)	10.8–17.0	1.07 (0.07)	85	12.11 (0.10)	10.3–14.7	0.88 (0.04)
Hind Limb Length* (mm)	76	26.6 (0.25)	21.8–31.1	0.85 (0.06)	85	24.55 (0.18)	20.2–28.6	0.63 (0.06)
Forelimb Length (mm)	76	19.25 (0.20)	15.3–23.0	0.82 (0.08)	85	18.08 (0.15)	15.4–21.3	0.66 (0.07)
Interlimb Length (mm)	76	53.69 (0.57)	42.0–65.7	0.98 (0.06)	84†	55.2 (0.58)	44.2–68.9	1.05 (0.05)
Mass* (g)	73††	25.82 (0.92)	14.0–45.8	3.20 (0.19)	82	21.8 (0.63)	11.6–37.0[#]	2.62[#] (0.19) 2.50[##] (0.22)

* Note that means for the sexes for these variables are not directly comparable, because the slopes of the relationships of these variables with body size differ for the sexes.
† Interlimb length of 1 female was not recorded.
†† Mass of 3 males and 3 females was not recorded.
[#] Includes 38 gravid females.
[##] Nongravid females only.

mothers, so comparing offspring was less straightforward than comparing the adults. To accomplish this comparison, I calculated means for each variable for the male and female offspring of each mother, and using these means, I calculated the difference between mean trait sizes of male and female offspring within a mother for each trait. This method generated an independent measure of difference between male and female trait sizes for each mother. If such differences are normally distributed, a mean difference for each trait of zero indicates that there is no significant difference between trait sizes of male and female offspring. A mean that is different from zero indicates a significant difference among trait sizes of male and female offspring. I tested for normal distribution of the differences for each trait using a Wilk's Shapiro goodness-of-fit test for a normal distribution. I compared the means of these differences with zero using *t*-tests. For visual comparison with the adult data, I have displayed the relationships between $\log_{(10)}$SVL and each variable for males and females, separately for each trait.

RESULTS

Adults

Over the period of this study, I captured a total of 85 females and 76 males that were adults (SVL $\geq$ 90 mm, L. Schwarzkopf and M.J. Caley, unpublished data) at the time of first capture. There was no significant difference between mean SVL of males and females ($t = -1.91$, df = 161, $P > 0.24$, Table 1). Head width increased more rapidly with SVL for males than for females. ($F_{1,157} = 5.5$, $P < 0.01$) (Fig. 1*a*). Similarly, hind limb length increased more rapidly with body length for males than for females ($F_{1,157,} = 7.0$, $P < 0.01$) (Fig. 1*b*). For a given SVL, forelimb length was greater in males than in females ($F_{1,158} = 30.5$, $P < 0.0001$, Fig. 1*c*), but there was no significant difference in the slopes of the relationship between forelimb length and SVL for the two sexes ($F_{1,158} = 2.0$, $P < 0.16$, Fig. 1*c*). For a given SVL, interlimb length was greater for females than for males ($F_{1,157} = 43.2$, $P < 0.0001$, Fig. 1*d*), but there was no significant difference in the slopes of the relationship between interlimb length and SVL for males and females ($F_{1,157} = 0.7$, $P > 0.4$, Fig. 1*d*). Finally, mass increased more rapidly with body size for males than for females, both when gravid females were included in the analysis ($F_{1,151} = 5.1$, $P < 0.02$, Fig. 1*e*), and when they were not ($F_{1,113} = 5.9$, $P < 0.02$).

Neonates

The 19 females gave birth to a total of 131 (64 female, 67 male) offspring, with a mean

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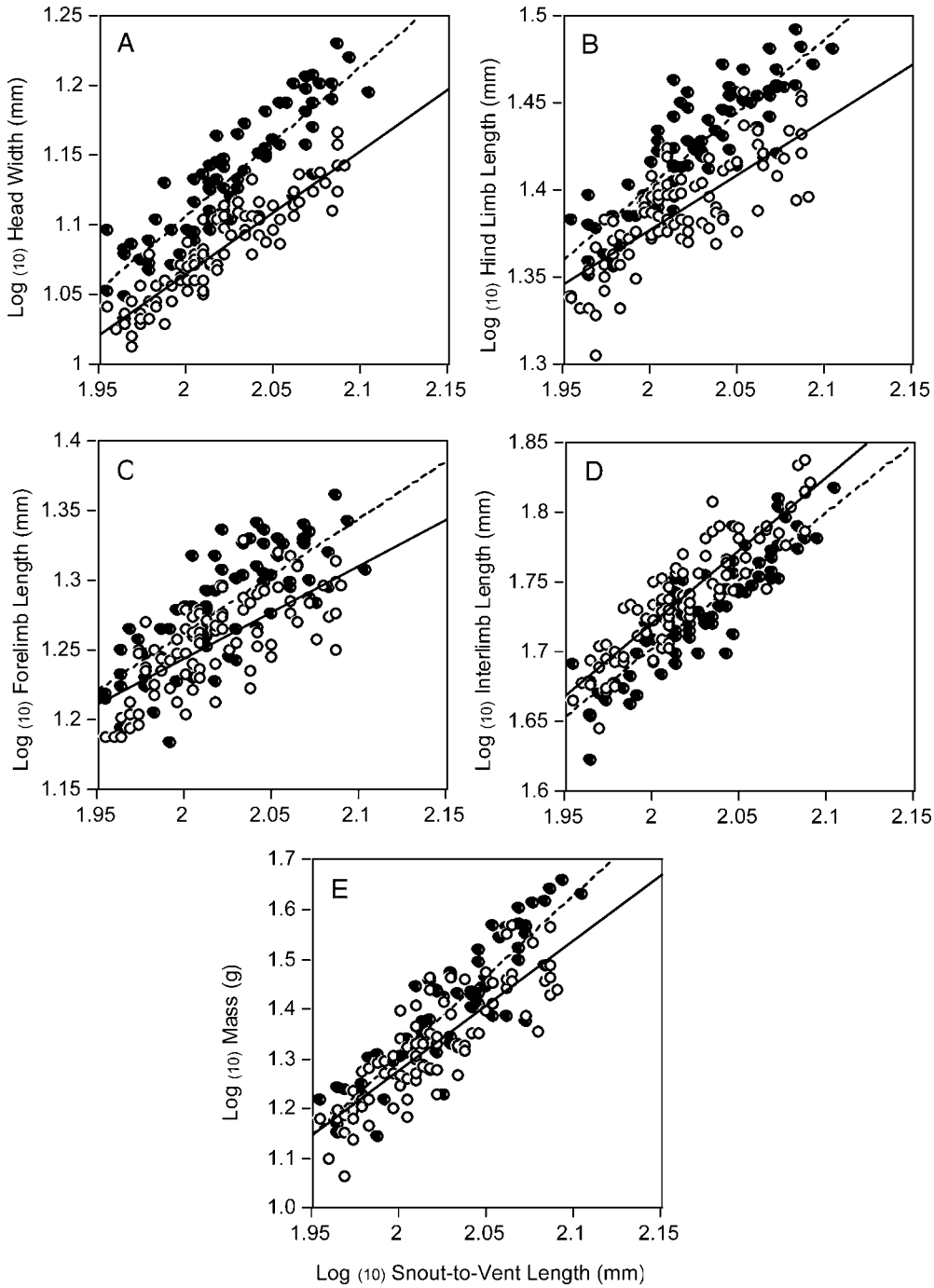


FIG. 1.—The relationships between snout–vent length and other body size measures in adult male and female eastern water skinks (*Eulamprus quoyii*). All variables have been logarithmically transformed. Filled circles and broken lines indicate males; open circles and solid lines indicate females.

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TABLE 2.—Means and ranges of each morphological variable (± SE) for neonate male and female eastern water skinks, *Eulamprus quoyii*. To statistically compare offspring from the same litter, the difference between males and females was calculated for each litter, and the distribution of differences were examined using a Shapiro Wilk test. All these distributions were normal ($P < W$), so *t*-tests were employed to compare the means of these distributions with zero. Only the mean of the distribution of interlimb length differences was significantly different from zero: females have longer interlimb lengths at birth.

	SVL mm (SE)	Head width mm (SE)	Hind limb Length mm (SE)	Fore limb Length mm (SE)	Interlimb Length mm (SE)	Mass (g)
Male Mean ($n = 67$)	38.9 (0.2)	5.5 (0.02)	9.9 (0.06)	7.9 (0.05)	17.8 (0.1)	0.86 (0.02)
Female Mean ($n = 64$)	39.3 (0.2)	5.6 (0.03)	9.9 (0.06)	7.9 (0.05)	18.4 (0.2)	0.90 (0.01)
(x female–x male for each litter) $n = 17$	0.06 (0.3)	0.02 (0.03)	−0.05 (0.08)	−0.08 (0.08)	0.53 (0.2)	−0.001 (0.02)
Shapiro Wilk *W*	0.94	0.97	0.93	0.97	0.96	0.95
$P < W$	0.29	0.81	0.24	0.73	0.63	0.48
t	0.26	0.52	−0.53	−0.93	2.51	−0.06
P	0.8	0.7	0.6	0.36	0.02	0.95

litter size of 6.7 (range 3–10). Two females had female offspring only, the rest had both males and females in their litters. The differences between mean trait values for male and female offspring within litters were all normally distributed (Table 2), and were not significantly different from zero for SVL, head width, hind limb length, or fore limb length (Table 2); mean values for these traits in male and female offspring are very similar (Table 2). There was a significant difference between male and female offspring within litters for interlimb length, female offspring have longer interlimb lengths (Table 2), and the mean value for interlimb length was greater for females than males (Table 2). Further supporting these conclusions, the least squares regression for female offspring SVL versus interlimb length is parallel to, but entirely above that for males, whereas regression lines for all the other traits fall on top of one another (Fig. 2*a–e*).

DISCUSSION

Although male and female adults did not differ in average body length, they differed considerably in body shape. Male head width, forelimb length, and mass increased more rapidly with body length than did those of females, and for a given body length, male hindlimb length was greater than that of females. Females had greater trunk (interlimb) lengths than did males. Male and female neonates also had similar body lengths, but differed from adults in that neonates of both sexes had similar-sized heads and limbs, and weighed approximately the same amount. Female neonates, like female adults, had greater trunk lengths than males.

Both wider heads in males, and greater trunk lengths in females are commonly observed forms of sexual dimorphism in squamates (Andersson, 1994; Olsson et al., 2002). Finding such differences in a species that is not sexually dimorphic in body length suggests that, when they are observed in sexually size dimorphic species, these differences may be due to direct selection on morphology, rather than to indirect selection on overall body size. Thus, the occurrence and pattern of sexual shape dimorphism in *E. quoyii* appears to support the conclusions of many studies that have controlled for sexual size dimorphism statistically (e.g., Olsson et al., 2002; Vitt and Zani, 1996).

Sexual dimorphism in leg length, on the other hand, is less commonly reported in comparisons of male and female lizards, although when it is observed in sexually size dimorphic species (Butler and Losos, 2002; Malhotra and Thorpe, 1997; Powell and Russell, 1992) males tend to have longer limbs than females. Once again, data from *E. quoyii* support the conclusion that there is selection directly on leg length in these species, rather than *via* indirect selection on body size.

Sexual dimorphism in trunk or interlimb length in these lizards deserves special mention because, unlike all the other shape measures, this one does not develop as the sexes grow, but instead is present at birth. Female and male *E. quoyii* have equal numbers of presacral vertebrae (A. Greer, unpublished observations), so the trunk-length difference between the sexes may be due to differences in the

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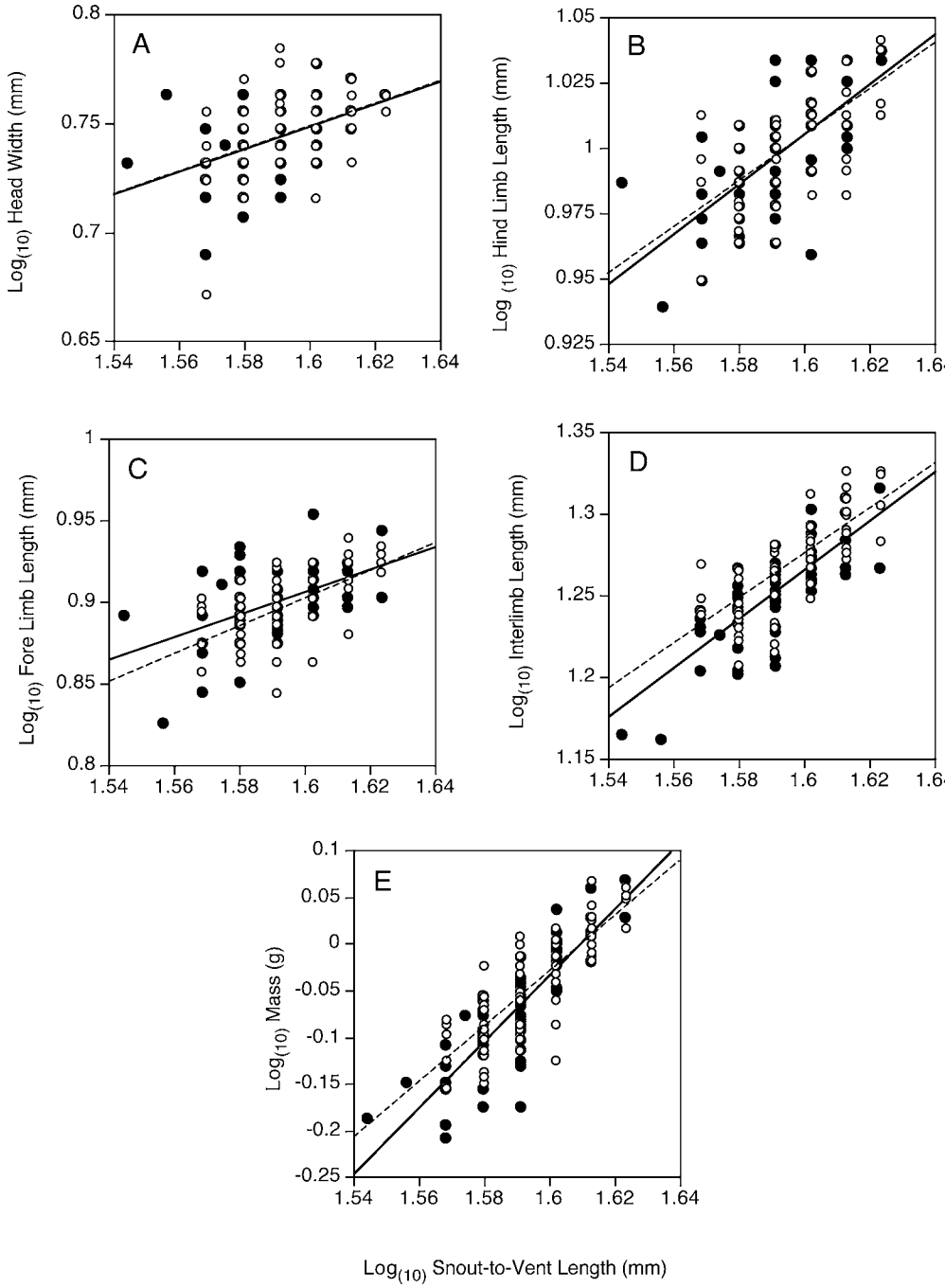


FIG. 2.—The relationships between snout–vent length and other body size measures in neonate male and female eastern water skinks (*Eulamprus quoyii*). All variables have been logarithmically transformed. Filled circles and broken lines indicate males; open circles and solid lines indicate females.

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length of the actual vertebrae, or in the size of the intervertebral cartilages. A morphological difference between males and females at birth is interesting (e.g., Watkins, 1996), as sexual dimorphism in adults usually occurs due to differences in the developmental programs of the sexes after birth (e.g., due to growth rate differences), rather than as "hard-wired" morphological differences between sexes (Badyaev, 2002). It is not, however, clear why this particular difference would be "hard-wired" in this species, but it would be worth examining other species to see if this difference is common at birth in lizards sexually dimorphic for trunk-length as adults.

What, then, is likely to select for differences in the body shape of males and females? Wide heads of males are thought to be due to selection for male fighting and/or mating ability in a variety of taxa (Andersson, 1994). *Eulamprus quoyii* males fight with each other by grasping with their jaws and rolling (Done and Heatwole, 1977; L. Schwarzkopf, personal observations). They also grasp females with their jaws during copulation (Done and Heatwole, 1977; L. Schwarzkopf, personal observations). Despite the difference in jaw width, there is little difference between the diets of male and female *E. quoyii* (Schwarzkopf, 1996; Veron, 1969; L. Schwarzkopf, unpublished data). Thus, the wider heads of male *E. quoyii* are likely to be a sexually selected trait in this species.

The greater mass of male *E. quoyii*, compared to females of a similar SVL, also may be related to superior fighting and/or mating ability. Males may carry more muscle than females of a given size, so they can overpower females during forced copulation, or male rivals during combat.

Similar to *Tropidurus* and some anolines (Malhotra and Thorpe, 1997; Vitt and Zani, 1996), male *E. quoyii* have longer fore and hindlimbs than do females. Longer limbs typically enhance running speed (Irschick and Losos, 1998; cf. Vitt and Zani, 1996), and longer legs may enable males to more effectively chase females prior to copulation. Alternatively, longer legs may allow males to better escape predators, if, for example, their behavior during the breeding season makes them more vulnerable to predation (Butler and Losos, 2002). Differences in leg morphology also may be due to ecological differences between males and females, such as differing habitat usage between the sexes (Butler and Losos, 2002). Although there are no obvious differences in habitat use between male and female *E. quoyii*, subtle differences may still select for differences in morphology, and there is little data on sex specific substrate use in this species.

Longer trunk lengths relative to body size in female lizards are commonly observed (e.g., Butler and Losos, 2002; Olsson et al., 2002), and may provide extra space for eggs or developing offspring (Forsman and Shine, 1996; Olsson et al., 2002; Vitt and Congdon, 1978). There is fecundity selection for longer trunks in female snow skinks (*Niveoscincus microlepidotus*) (Olsson et al., 2002). Longer trunk lengths in *E. quoyii*, a viviparous species, also may be due to selection for increased clutch volume. Alternatively, longer trunk lengths may provide a performance advantage in ground dwelling species active in leaf litter (Greer, 1989). Because *E. quoyii* primarily occupies rock and leaf-litter (Law and Bradley, 1990), there may be selection for body elongation in this species. Currently, however, there are no data on whether males and females differ with respect to leaf-litter use.

Selection on individual body part differences, without selection on body size, is one possible explanation for body shape differences between sexes in species with equal body length. However, it also is possible that different selective pressures, acting on each sex separately, could produce equal body size. It is plausible that sexual selection for large body size in males might produce a proportional increase in mass, head width and leg length, whereas fecundity selection on females produces longer trunks, and thus both sexes are the same length in adulthood, but due to very different selective regimes. To some extent, the data from neonates refutes this hypothesis because female neonates have longer trunks but are not longer in SVL. Thus, selection for longer trunk length apparently can occur without increasing SVL. A comparative study of the evolution of sexual dimorphism in body size and shape among skink species with a range of dimorphism (males longer, females longer, sexes equal), correlated with other factors influencing body size in each

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sex, may help elucidate the factors responsible for sexual size dimorphism in this group.

Developmental rate in ectotherms can influence body shape (Blouin and Loeb, 1991; Burger et al., 1987). If, for example, there was temperature dependent sex determination in this species, as there is in other members of the clade (Robert and Thompson, 2001), differences in developmental rate of males and females due to incubation/gestation temperature may cause differences in body shape. There is, however, presently no evidence for temperature dependent sex determination in *E. quoyii* (M.J. Caley and L. Schwarzkopf, unpublished data), so differences in developmental rate of males and females due to incubation temperature seem unlikely. Instead, it is likely that a combination of natural and sexual selection on body proportions maintains differences between the sexes in these lizards.

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