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Facultative sex allocation in the viviparous lizard *Eulamprus tympanum*, a species with temperature-dependent sex determination

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Abstract

Females of the Australian scincid lizard *Eulamprus tympanum* can manipulate the sex of their offspring in response to gender imbalances in the population using temperature-dependent sex determination. Here we show that when adult males are scarce females produced male-biased litters and when adult males were common females produced female-biased litters. The cues used by a female to assess the adult population are not known but presumably depend upon her experience throughout the breeding season. Maternal manipulation of the sex ratio of the offspring in *E. tympanum* illustrates a selective advantage of temperature-dependent sex determination in a viviparous species.

Introduction

Most animals produce equal numbers of sons and daughters, although the ability to choose the sex of the offspring may be an advantage in changing environments with different selective pressures on males and females (Hamilton 1967; Trivers and Willard 1973; Charnov 1982). Such a choice could enhance fitness by skewing the sex ratio of the offspring towards the sex with the best reproductive success (Trivers and Willard 1973; Werren and Charnov 1978). Temperature-dependent sex determination (TSD), where the temperature of development determines the sex of the offspring produced, is widespread among oviparous (egg-laying) reptiles and may provide a mechanism for mothers to choose the sex of their offspring through nest-site selection (Bull 1980). However, maternal manipulation of the sex of their offspring by nest-site selection is controversial and may be implausible because many oviparous reptiles with TSD are long-lived with late maturation, so that any nest-site decision would need to predict the population sex ratio many years into the future when those offspring mature (Rosenburg and Niewiarowski 1998). Many studies that have linked maternal manipulation by nest-site selection have used repeatability of microenvironment or non-random selection of nest sites as evidence (Vogt and Bull 1984; Schwarzkopf and Brooks 1985; Janzen and Morjan 2001) without monitoring other potential limiting factors such as predators; hence, repeatability of nesting microenvironments may reflect a response to other consistent driving pressures of nest-site selection rather than heritability (Spencer and Thompson 2003). These concerns would not apply to fast-maturing, short-lived species, and the exciting recent discovery of a viviparous (live-bearing) lizard that is relatively short-lived, fast-maturing and can manipulate the sex of its offspring directly by TSD (Robert and Thompson 2001) means that this species, and others with similar life histories, could gain selective advantages from manipulating the sex of their offspring. TSD provides the mechanism for *Eulamprus tympanum*, an Australian skink, to directly alter population sex ratios through active thermoregulation, rather than by nest-site selection as in oviparous species. The mother's basking behaviour throughout

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pregnancy directly controls the thermal conditions experienced by the developing embryo and hence the sex of the offspring (Robert and Thompson 2001). Gestation temperature has a highly significant effect on sex, with warmer temperatures giving rise to male offspring (Robert and Thompson 2001).

In this study, we altered the sex ratios experienced by pregnant females to test the hypothesis that females use TSD to adjust the sex ratio of their offspring in response to sexual imbalances within the population.

Methods

Pregnant females ($n = 12$) were collected from Kanangra Boyd National Park (33°55′64.3″S, 150°3′6.9″E; elevation 1300 m) immediately following ovulation and mating (ovulation was evident by palpation for eggs and recent mating by fresh mating scars) and were assigned to laboratory enclosures (450 mm × 350 mm) with either a high proportion of males (3 males to 1 female) or all females (4 females). Lizards were able to thermoregulate, with the enclosures providing a thermal gradient (20–40°C) for 8 hours per day, falling to 20°C overnight. In addition, a 'low male' treatment was conducted where females ($n = 6$) were maintained singly in enclosures (3.5 m in diameter × 450 mm in height) in the field at the site of collection. The thermal regime experienced under field conditions varied with weather conditions. As part of another study, miniature temperature data-loggers (Robert and Thompson 2003) were attached to females to measure thermal behaviour; the resulting average temperatures ranged from 9°C overnight to 31°C throughout the day (K. Robert, unpublished data). The sex of the resulting offspring ($n = 72$) was determined by palpation for the presence or absence of hemipenes on the day of birth (Harlow 1996).

Results

The proportion of males to females in the three experimental treatments was significantly different (heterogeneity $\chi^2 = 22.53$, d.f. = 2, $P < 0.0001$). Females maintained in female-only groups produced more male than female offspring (Fig. 1) and 11 of the 12 litters were male-biased (Table 1). In contrast, females maintained with males produced offspring of mixed sexes (Fig. 1) and 4 of the 6 litters were female-biased (Table 1).

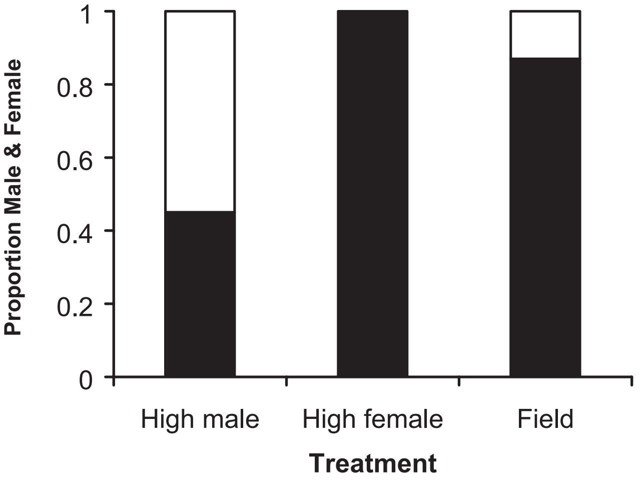

Fig. 1. Influence of the sex ratio of the adults on that of the offspring in the viviparous skink *Eulamprus tympanum*. Females maintained for the duration of pregnancy in populations with males ($n = 6$) gave birth to mixed sexes ($n = 27$; 12 male and 15 female) whereas those maintained in populations lacking males under laboratory conditions ($n = 6$) gave birth only to male offspring ($n = 22$ male) and under field conditions ($n = 6$) gave birth predominantly to male offspring ($n = 23$; 20 male and 3 female). Black portions of the bars represent male offspring; white portions represent female offspring.

Table 1. Comparison of sex ratios within litters for females maintained in either 'low male' populations (n = 12 females) or 'high male' populations (n = 6 females)

Litter size	Treatment			
	'High male' populations		'Low male' populations	
	Male offspring	Female offspring	Male offspring	Female offspring
2	–	–	2	0
3	–	–	3	0
	–	–	3	0
	–	–	3	0
	–	–	2	1
4	1	3	4	0
	3	1	4	0
	3	1	4	0
	–	–	4	0
	–	–	2	2
5	1	4	5	0
	2	3	–	–
	2	3	–	–
6	–	–	6	0
Total	12	15	42	3

Discussion

Ecological theory predicts a population to be in equilibrium when reproductive resources are divided evenly between the production of sons and daughters (Fisher 1929). However, there are ecological and social circumstances when producing one sex over the other has an advantage; for example, in response to local mate competition (Hamilton 1967; Werren 1980), local resource competition (Clark 1978; Clutton-Brock and Lason 1986; Komdeur *et al.* 1997), local resource enhancement (Schwartz 1988; Komdeur *et al.* 1997) and sex-specific fitness (Trivers and Willard 1973). In natural systems where it is common for populations to suffer unpredicted periods of exceptional mortality or survival, one sex can be affected more because of behavioural or physiological differences (Werren and Charnov 1978). Any facultative sex ratio response needs to recognise the scarcity of one sex in order to overproduce that sex in the next generation; the sex ratio of the offspring will vary inversely with that of the adults (Werren and Charnov 1978). This report links maternal sex allocation with the sex ratio of the population (or of the adults); however, the mechanism by which females recognise a shortage of one sex over the other is not understood (and is under further investigation). One possibility is that proposed by Olsson and Shine (2001) for viviparous snow skinks, *Niveoscincus microlepidotus*: females facultatively adjust the sex ratio of their offspring depending upon their experience during the mating season. Those females courted and mated by many males would perceive the adult male population to be plentiful and would, in turn, overproduce female offspring in an attempt to balance the sex ratio of the population (Olsson and Shine 2001). The maternal manipulation of the sex ratio of the offspring in *E. tympanum* illustrates a selective advantage of TSD in a viviparous species and further studies will help identify the mechanisms used by females to recognise a shortage of one sex over the other. TSD extends across such a diverse group of species that no one explanation for its selective advantage would be possible; however, maternal effects potentially play an adaptive role in many of these species.

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