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Male southern water skinks (*Eulamprus heatwolei*) use both visual and chemical cues to detect female sexual receptivity

Received: 14 December 2004 / Revised: 12 June 2005 / Accepted: 4 July 2005 / Published online: 2 August 2005
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Abstract A wide range of organisms use chemical and visual cues in mate attraction and courtship; however, chemical discrimination relevant to reproduction and the interplay between these two types of communication are poorly understood in reptiles. We experimentally tested the ability of male *Eulamprus heatwolei*, a scincoid lizard, to discriminate between sexually receptive and non-receptive females in two ways. First, we conducted 155 staged encounters between males and females over 29 days to determine the start and the duration of the female receptive period based on the date of copulations. These data suggest that the receptive period lasted for approximately 7 days in late October under controlled laboratory conditions. We also recorded 6,330 individual male and female behaviours during these trials to evaluate the frequency of female courtship and rejection behaviours and the intensity of male courtship behaviour. Female courtship increased sharply during the receptive period and then diminished. The disparity between female courtship behaviours and female rejection behaviours was greatest during the receptive period. Male courtship intensity increased sharply prior to the receptive period, peaked during the receptive period and thereafter declined rapidly. To determine if males were using visual cues, chemical cues or both from females, we conducted an experiment during and after the receptive period wherein male lizards were presented with a choice of two retreat sites treated either with the odour of large sexually receptive females, odour of small sexually non-receptive females or no odour (control). Males preferred the scent of females over the odourless control, and analysis using a special form of a generalized linear model, the Bradley–Terry model, showed a clear order of retreat site preferences, with large sexually receptive females

favoured over small non-receptive females over the odourless control. We speculate that males use vision to find females and then use their chemosensory ability to chemically evaluate female sexual receptivity once the pair are in close proximity.

Keywords Behavioural ecology · Mating system · Chemical ecology · Courtship

Introduction

Detecting the reproductive status of potential sexual partners is a crucial component of sexual behaviour in most animals (Johnston 1980). For receptive females, it is important to have access to males, particularly in species with a short mating period (Cooper and Vitt 1986). For males, an ability to distinguish between sexually receptive and non-receptive females allows them to concentrate breeding efforts at times when they are most likely to be successful (Landauer et al. 1977; Cooper 1995; Stoddart 1980). Courting a female that is not sexually receptive is costly because it takes time and energy away from other important activities, and it exposes males to a greater predation risk (Brodie 1989). Thus, males with the means to distinguish between sexually receptive and non-receptive females may enjoy greater fitness, and there should be selection on males for this ability.

In reptiles, female reproductive status may be advertised via visual (morphological or behavioural), tactile or chemical cues. Advertisement via chemical cues is probably the least costly of these alternatives because chemical cues are often a by-product of other processes associated with physiological changes during reproduction. However, little is known about the role that chemical cues play in communicating important reproductive information in reptiles (Cooper 1996). This is surprising, since most squamate reptiles have well-developed chemosensory systems (Schwenk 1995).

In snakes, chemical communication is essential for the display of normal reproductive behaviour. For example,

Communicated by R. Oliveira

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cutting the vomeronasal nerve prevents courtship, mating and recognition of sex in the adder snake (*Vipera berus*; Andren 1982) and the garter snake (*Thamnophis* spp.; Noble 1937; Kubie et al. 1978; Gartska and Crews 1986). The importance of chemical communication in reproduction is less clear in lizards (Simon 1983). Traditionally, it has been believed that lizards rely heavily on visual cues for most social interactions. This notion is based on studies of highly territorial, sexually dimorphic taxa such as *Sceloporus* and *Anolis*, which exhibit elaborate push-up and/or dewlap displays (Duvall 1979; Stamps and Krishnan 1994; Sheldahl and Martins 2000). Studies on less visually oriented taxa suggest a greater importance of chemical signals in social interactions. Evidence suggests that chemical cues may be important for sex recognition in a number of skinks (Duvall et al. 1980; Cooper and Vitt 1986) and geckos (Greenberg 1943; Brillet 1993), but not in the more visually oriented iguanid lizards (Ferguson 1966; Duvall 1979, 1981). Only a few studies have examined the detection of female receptivity in lizards, and only one study has investigated whether males can detect female receptivity via chemical cues (Cooper 1995). Cooper found that males of the broad-headed skink (*Eumeces laticeps*) were able to distinguish between post-reproductive females and postreproductive females injected with estrogen to induce receptivity. The role of visual systems in the reproductive behaviour of lizards is even more poorly known (Lopez et al. 2004).

As part of a larger project on the role of chemical communication in the ecology of lizards (Head et al. 2002), we examined the role that visual and chemical communication plays in the male detection of sexually receptive females in the Australian southern water skink, *Eulamprus heatwolei*. Staged mating encounters before, during and after the female sexual receptive period and male retreat site experiments were used to determine the ability of the male to detect female sexual receptivity via chemical and visual cues. In contrast to Cooper's (1995) study, we used naturally occurring receptive and non-receptive females and also two complementary experimental approaches.

Methods

Eulamprus heatwolei is a medium-sized (<110 mm maximum snout vent length [SVL]) diurnal skink distributed in the mountainous regions of southeastern Australia. They are semiterritorial, with some males defending home ranges and others roaming over the landscape (Morrison et al. 2002; Stapley and Keogh 2004, 2005). Mating occurs in spring after emergence from hibernation, and parturition occurs 3–4 months later. Lizards were collected in late September and early October 2000 from the Tidbinbilla Nature Reserve (Canberra, ACT, Australia; 800 m elevation). This capture period occurred immediately after spring emergence and before mating began. The lizards were brought back to the Australian National University where they were measured, weighed and sexed via hemipene eversion. Males were housed in plastic boxes (43×32×23 cm)

and females in glass terrariums (45×60×45 cm). All cages contained a bark substrate, a water bowl and shelter. Cages were kept in a naturally lit room, and a 40 W-light bulb at one end of the cage allowed lizards to bask and thermoregulate naturally. The light bulb was on between 0900 and 1600 hours, and temperatures in cages ranged from 33°C under the light bulb to 25°C at the opposite end of the cage. Lizards were provided with food (tenebrio larvae and dog food) and water ad libitum.

Staged encounters

We used staged encounters between seven potentially sexually receptive females and seven adult males to determine the start and length of the female receptive period under laboratory conditions and also to observe the sexual behaviour of males and females. Only large females (>85 mm) were used to ensure sexual maturity (Schwarzkopf 1993). Because female water skinks often skip years for reproduction (Schwarzkopf 1993), the reproductive status of the females could not be determined with certainty until after the staged encounters.

Daily staged encounters began on 8 October and finished on 6 November. For each staged encounter, an adult male was introduced into the home cage of a female once each day between 1000 and 1400 hours. Pairs were chosen randomly, but each of the seven males saw each of the seven females only once per 7-day period. Each encounter lasted for 10 min or until an attempted copulation. If copulation was attempted, the encounter was terminated and lizards were separated.

During the staged encounter, we recorded the behaviour of both males and females. For males, we observed and recorded any male courtship behaviour then rated the male's behaviour to give a single score of "courtship intensity" for each encounter (Table 1). While attempted copulation often meant that males did not display as long as males with lower courtship intensity scores, attempted copulation was a more intense (and obvious) behaviour and was considered as the best indicator of female receptivity because female cooperation was required. These scores were then averaged across males.

For females, we recorded the frequency of a wider range of behaviours, including both courtship and rejection of males. For female courtship of males, we noted the following behaviours (for descriptions of behaviours, see Carpenter and Ferguson 1977): head bobbing, tail wagging, tail arching, female follows male, female nudges male, female head rests on male, female with head up, female with neck arched, female on top of male, female walks over male, female pushes up, female runs under male, female stands high, female tongue-flicks male and female throat extended. For female rejection of males, we noted the following behaviours: female walks or runs away from male, female attacks male, female bites male, female burrows in substrate, female charges male, female chases male, female flips male and female somersaults. Because it was much more difficult to determine the sexual "intensity"

Table 1 Courtship scoring system for staged encounters between males and females in *Eulamprus heatwolei*

Courtship intensity	Criteria
0	Male showed no interest in female
1	Male initially examined female (i.e. approached and sometimes tongue-flicked) and then showed no interest
2	Male displayed, i.e. head bobbing, throat extension, lateral compression and neck arching, for less than 5 min
3	Male displayed, i.e. as above, plus biting on the neck (a typical lizard precursor to mating), for more than 5 min
4	Male unsuccessfully attempted copulation with female rejection (i.e. male bit female's neck and tried to mount female but she moved away)
5	Male successfully attempted copulation with female cooperation

of these behaviours due to lack of knowledge about female courtship in lizards, we conservatively weighted all female behaviours equally and simply recorded the frequency of each behaviour in each staged encounter. These data were then combined across all females, and we used analysis of variance (ANOVA) to test for differences in the frequency of these behaviours between the prereceptive, receptive and postreceptive periods as determined by the distribution of encounters resulting in copulation.

Retreat site selection experiment

We conducted a series of retreat site selection experiments that were designed to test the hypothesis that adult males can differentiate between sexually receptive and non-receptive females based only on chemical cues. A total of 13 males, including the seven males that were used in the staged encounters, were used in the retreat site choice experiment. We had no way of determining female sexual receptivity a priori, and so we had to use large females and smaller sexually immature females to make sure that we were using females in each reproductive category. Schwarzkopf (1993) showed that females <85 mm were always sexually immature. We used 13 females to provide odour for the retreat sites, and this number included seven large females (87–96 mm SVL) from the staged encounters and six small females (75–82 mm SVL); however, one large female originally classed as receptive (87 mm) was discovered through the staged encounters to be non-receptive (she did not allow copulation), and so trials in which this female was compared to another non-receptive female were discarded. This resulted in the inclusion of trials from six large females and six small females for analysis.

Retreat sites consisted of two ceramic tiles (11×11 cm) randomly placed at either end of a male's home cage. Tiles were treated in one of three ways: (1) placed with a large sexually receptive female for 24 h; (2) placed with a small sexually non-receptive female for 24 h; or (3) not placed with a female (control). Tiles were used in three discrimination tests: large receptive female tiles vs control; small non-receptive female tiles vs control; and large receptive female tiles vs small non-receptive female tile. All tiles

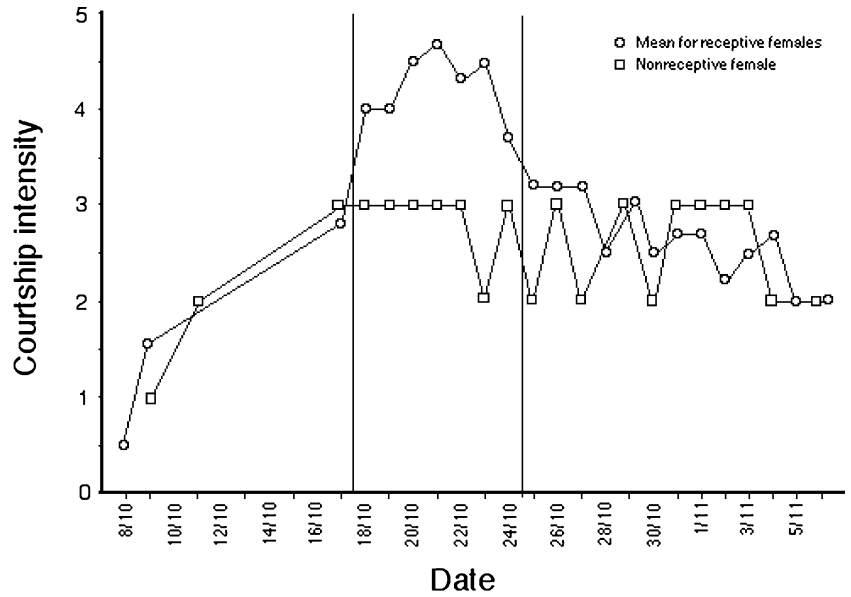
were washed with detergent and dried before being reused. Retreat site choice trials were conducted between 19 October and 5 November. On each night, five receptive vs non-receptive, six non-receptive vs control and one receptive vs control trials were conducted. Tiles were placed at opposite ends of the male's cage in the evening (1700 hours). Early the next morning, we recorded the tiles under which the male slept. The few trials where males slept under the bark substrate were discarded.

Results

Staged encounters

We conducted a total of 155 staged encounters over a 29-day period and recorded 6,330 individual behaviours. Trials involving the female that did not allow copulation for the duration of the experiment were classed as non-receptive (21 trials), while trials involving females that allowed copulation at some time during the experiment were classed as receptive (134 trials). Attempted copulations were observed only between 18 October and 24 October (what we hereafter define as the "receptive period"). Male courtship intensity increased sharply prior to the receptive period and declined gradually afterwards (Fig. 1). Of the 42 encounters during this period, 26 resulted in an attempted copulation with female cooperation. Males showed interest in and courted the non-receptive female even though she never allowed mating. The frequency of female courtship behaviours increased sharply during the receptive period and then diminished in the postreceptive period (ANOVA, $F[2, 6,229]=4.95$, $P=0.007$; Fig. 2). Female rejection behaviours also increased in the receptive period and then increased again in the post-receptive period (ANOVA, $F[2, 6,325]=11.877$, $P<0.0001$; Fig. 2). It is not surprising that both female courtship and rejection behaviours increased during the receptive period as there was much more interaction between males and females during this time. Importantly, the disparity between female courtship behaviours and female rejection behaviours was greatest during the receptive period (Fig. 2).

Fig. 1 Mean male courtship intensity for staged encounters over a 28-day period. The two vertical lines indicate when females were sexually receptive to males



Retreat site selection experiment

Initially, retreat site data were divided into two periods—during and after the female receptive period (as determined by the staged encounters)—to look for differences in male retreat site choice relative to female reproductive condition. Male choice of receptive or non-receptive females between these two periods was not significantly different (55 vs 42, $\chi^2=1.735$, $df=1$, $P=0.188$), so we pooled the data and tested for differences against the control. Our small samples sizes mean that statistical power is an issue, but our data do show that males chose small non-receptive females over the control (38 vs 20, $\chi^2=5.586$, $P=0.018$) and, while not statistically significant, the ratio of male choice for large receptive females to the control was similar (12 vs 6, $\chi^2=2.0$, $P=0.157$).

We were also interested in overall preferences between odour treatments, and so we used the Bradley–Terry model,

a type of general linear model specifically designed for experiments consisting of multiple paired comparisons (linked paired comparisons) (David 1988). In addition to providing a statistical test of choice, it allows the treatments to be ordered according to preference, provides a single overall test rather than multiple independent tests and accounts for repeated measures (Imrey et al. 1976; De’ath and Moran 1998; Head et al. 2002; Stapley 2003). A likelihood ratio test was used to determine whether data conformed to the Bradley–Terry model (David 1988). We were able to reject the model of no preference for our data ($\chi^2=8.2696$, $df=2$, $P=0.025$) and accept the Bradley–Terry model, which fitted the data well ($\chi^2=0.0593$, $df=1$, $P=0.224$). Because the data were not significantly different from the Bradley–Terry model, they showed that males displayed an ordered hierarchy of preferences (De’ath and

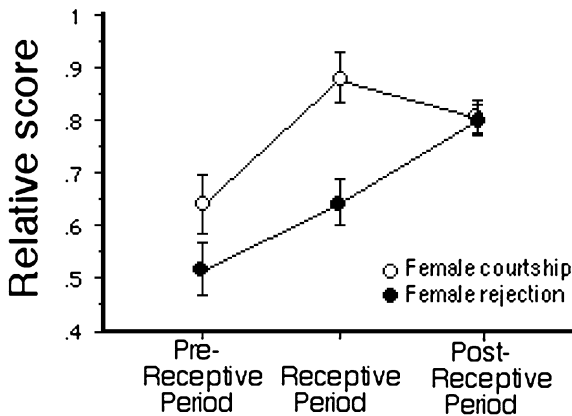


Fig. 2 Mean female courtship scores and female rejection scores with standard errors for the prereceptive, receptive and postreceptive periods. Female courtship decreased and female rejection increased after the postreceptive period. See the text for details of statistical analyses

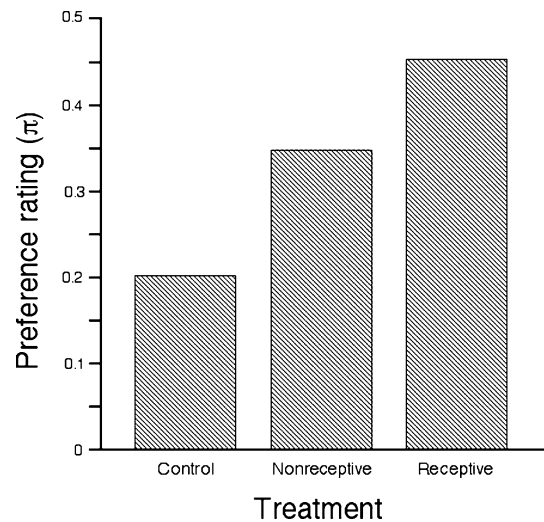


Fig. 3 Male preference ratings for females as obtained from the Bradley–Terry model, showing that males prefer to sleep under the tiles treated with receptive female odour over non-receptive females over odourless control

Moran 1998). Males chose retreat sites treated with the chemical cues of large receptive females, most often followed by small non-receptive females and, finally, the control, but the differences between preferences for receptive and non-receptive females were small (Fig. 3). Our trials were also, necessarily, confounded by female body size, and so we cannot clearly demonstrate that males are able to chemically distinguish between receptive and non-receptive females based on chemical cues alone, but males do show a preference for the odour of female conspecifics, in general, over an odourless control.

Discussion

This study is one of only two studies that examine the role of chemical communication in the detection of female sexual receptivity in lizards and the only study to use naturally occurring receptive females. We also augment our study with a detailed behavioural analysis to examine the role of female courtship and rejection behaviours in the detection of female sexual readiness by males. Our staged laboratory encounters demonstrate that the female receptive period is short in *Eulamprus heatwolei* and that, while males tend to court females even when not receptive, female cooperation and behavioural cues are needed to elicit copulation during the courtship process. Our retreat site study demonstrates that, while male *Eulamprus heatwolei* prefer large over small females, the ability to discriminate between receptive and non-receptive females via chemical cues may be weaker. This pattern remained the same in trials during and after the female receptive period.

Length of female receptive period

We have clearly demonstrated that the period of time over which females will allow copulation is quite short. Under controlled laboratory conditions, females allowed copulations for approximately 1 week. This period is likely to be longer in nature because of the more variable weather conditions (Penguilly 1972; Crews 1978; Wilson 2001), and we have demonstrated this in a female mate choice experiment on *Eulamprus heatwolei*, which took place in outdoor enclosures. In those studies, we have documented a maximum spread of 16 days between matings with different males that resulted in offspring in a single clutch (Wilson 2001; Keogh, unpublished data). The short receptive period in spring is not surprising given that *Eulamprus heatwolei* is an alpine lizard with a short reproductive season, and this environment should lead to a strong selective pressure for efficient visual or chemical means of locating receptive partners. It has been suggested that species with short receptive periods may be more reliant on chemical cues in detecting sexually receptive females than those with long receptive periods (Cooper and Vitt 1984), but our data show that visual signals are also important in this species.

Visual detection of female receptivity

Most studies that have looked at the detection of female receptivity in lizards have shown morphological cues to be important for the male assessment of female reproductive condition (e.g. in agamids, LeBas and Marshall 2000; chamaeleonids, Cuadrado 1998; iguanids, Zucker and Boeklen 1990; phrynosomatids, Vinegar 1972). Many of these studies have shown a change in female coloration associated with the breeding season. For some species, this color change has been shown to simply aid in sex recognition (Cooper and Vitt 1984), while, in other species, it may play a part in the male detection of female receptivity—signaling that either the female is willing (Cuadrado 1998; Medica et al. 1973; LeBas and Marshall 2000) or unwilling (Ferguson 1976) to mate. Behavioural cues are also important to males for locating females and detecting female receptivity in some lizard species. For example, *Anolis garmani* and *Tropidurus delanonis* actively indicate that they are willing to mate by posturing conspicuously prior to copulation (Trivers 1976; Werner 1978).

Morphological cues are not likely to play a large role in detecting the female reproductive status in *Eulamprus heatwolei*. Unlike the species mentioned above, *Eulamprus heatwolei* exhibits only a subtle sexual dimorphism and no obvious morphological signs of receptivity, such as color change. While only large females (SVL > 85 mm) are reproductively active, SVL is not reliable for indicating female receptivity because mature females do not necessarily breed every year (Schwarzkopf 1993). Instead, our data clearly show that female visual signals in the form of both courtship and rejection are very important and, in large part, determine male response. Measures of male interest in our experiment indicate that males court all females regardless of their receptivity status and that females are able to resist males. The intensity of male courtship behaviour increased only during the female receptive period when females themselves greatly increased courtship behaviours. Rejection behaviours increased during the receptive period as well, but this was not surprising because females were much more active in all behaviour types during this time. Importantly, female courtship behaviour declined in the postreceptive period, but rejection behaviour continued to rise.

Chemical detection of female receptivity

The use of chemical communication in intraspecific interactions is widespread throughout reptiles; however, the use of chemical cues in the detection of female receptivity has been shown only for snakes (Andren 1982; Noble 1937; Gartska and Crews 1986; Kubie et al. 1978; Shine and Mason 2001) and one skink species (Cooper 1995). Our results are slightly different from those found for the North American skink *Eumeces laticeps*, which were able to distinguish between reproductively active and post-reproductive females via chemical cues (Cooper 1995). In *Eulamprus heatwolei*, this ability appears to be more subtle

than in *Eumeces laticeps*. This finding may reflect methodological differences between our study and that of Cooper (1995). Cooper (1995) injected postreproductive females with oestrogen to induce receptivity. By contrast, we used naturally occurring receptive and non-receptive females, thus providing natural levels of chemical stimuli.

Our study demonstrates that male *Eulamprus heatwolei* preferred to sleep under the tiles treated with the odour of large receptive females over small non-receptive females over odourless control, but the difference between receptive and non-receptive females was small. That male preference for these tiles does not differ before and after the receptive period suggests that the chemical cues used by males may be associated with body size rather than with reproductive status per se. Our data do clearly show, however, that males preferred to sleep under the tiles with female odour (regardless of size) over an odourless control. This does not necessarily mean that males cannot chemically distinguish between sexually receptive and non-receptive females. Because we had to use small sexually immature females for our non-receptive class, our results are confounded by female body size. We already have shown that chemical cues are important in this species in the detection and discrimination between potential predators (Head et al. 2002) and in kin recognition (Head et al., unpublished data), so we know that chemical cues are used heavily in *Eulamprus heatwolei*.

We speculate that the degree to which males distinguish between receptive and non-receptive females via chemical cues may depend, at least in part, on the social organization and mating system of a species (Johnston 1980). For example, species in which the sexes are not normally in regular contact or have large home ranges might be more dependent on olfactory cues than more gregarious species such as *Eulamprus heatwolei*. For example, *Eumeces laticeps* generally occur at much lower densities and are less territorial than *Eulamprus heatwolei*, possibly making chemical detection of female receptivity even more important in this species (Cooper 1995). While some male *Eulamprus heatwolei* defend home ranges, others roam throughout the landscape, covering large distances and overlapping many male and female home ranges (Morrison et al. 2002). In many territorial species, male reproductive success is dependent on the size of the territory and how many female home ranges it overlaps. In *Eulamprus heatwolei*, floating males may obtain up to half of all paternities, and proximity to females does not predict paternity (Morrison et al. 2002; Stapley and Keogh 2004, 2005). We speculate that males use their visual ability to find females but then rely on chemical cues to assess the receptivity of females once the pair are in close proximity.

Acknowledgements The manuscript was improved by the constructive criticisms of Mike Bull, Sharon Downes, members of the Keogh Laboratory and two very helpful reviews. For help in the field, laboratory and workshop, we thank J. Stapley, S. Dennis, E. Wilson, A. Muir and B. Phillips. For help with the statistical analyses, we thank A. Cowling (ANU Statistical Consulting Unit). All work carried out as part of this project was done under the approval of the Australian National University Animal Experimentation Ethics Committee (F.BTZ.01.99) and with research permits from Environment ACT (permit number LT1999008). We thank the staff at Tidbinbilla Nature Reserve for all their help and cooperation and the Australian Research Council for grants to J.S.K.

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