Evolutionary Ecology **15:** 129–141, 2001.

Research article

No female mate choice in Mallee dragon lizards, *Ctenophorus fordi*

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Received 29 August 2000; accepted 30 September 2001

Co-ordinating editor: V. Kaitala

Abstract. Aspects of sexual selection were studied in a sexually monomorphic Australian agamid lizard (*Ctenophorus fordi*), in particular with respect to the sensory exploitation hypothesis. In enclosure trials, females were offered the choice between 'large' vs. 'small' males and, in a different experiment, males with 'blue' vs. 'normal' head color. The rationale for these experiments was: firstly, to establish if females actively solicit copulations; secondly, if so, do females solicit copulations non-randomly with respect to male size (because large males may have access to food resources); thirdly, if male coloration is manipulated to match traits of congeneric, conspicuous and sexually dimorphic species, do females show preference for this novel trait (in accordance with the sensory exploitation hypothesis). The corresponding manipulations were also made in a free-living population where the distribution of females on the home ranges of color-manipulated males were monitored. Blue-headed males were accepted as mating partners both in the staged mating trials and in the natural population. Females appeared not to express any kind of active or passive mate choice (rejection); in only one out of 62 trials did a female approach a male herself rather than being approached by the male(s). There was no discrimination against any male category regardless of size or color within a female's receptive period and the manipulation of male head color in the natural population did not result in spatial re-distribution of females. Thus, a female appears to mate unselectively within her receptive period. Rejection behaviors were used only outside of the receptive period to communicate, to all males, that the female is not receptive.

Key words: lizards, mate choice, novel trait, sexual selection

Introduction

In a recent review of sexual selection and sperm competition in reptiles, T. Madsen and myself (Olsson and Madsen, 1998) called for more experimental tests of female choice in reptilian species. Our survey showed that very few studies have convincingly demonstrated that female reptiles discriminate among sexual partners, which there is no a priori reason to expect since female choice is widespread in both the animal and plant kingdoms (Andersson, 1994).

Our own work on sand lizards (*Lacerta agilis*) (Olsson and Madsen, 1995) showed that in spite of a positive relationship between a sire's age and the hatching success of a clutch, hence, satisfying a basic premise of the 'good genes' hypothesis, females did not mate selectively with older or larger males. Furthermore, our review revealed that most reptile species mate more than once and with more than one partner (Appendix A in Olsson and Madsen, 1998). Thus, any pre-copulatory mate choice made by the female is compromised, 'traded up' and/or re-evaluated in subsequent matings. Thus, an experimental test situation should preferably evaluate both active and passive choices, and consistency in choice when a female is offered multiple partners. I know of only one study where this condition is (nearly) satisfied (Cooper and Vitt, 1993) and that is also the only experimental work I am aware of that convincingly demonstrates female choice in a reptilian species, namely on body size in the scincid lizard *Eumeces laticeps*.

To the best of my knowledge, experimental manipulation of male phenotypes have never been attempted in natural, reptilian populations in order to investigate female mating behavior. However, Hews (1993) manipulated food resources on territories of male *Uta palmeri* and concluded that females re-distributed themselves in accordance with prey abundance, i.e., compromising any previously made mate choices. Thus, female mate choice is a complex behavior incorporating discrimination between the 'quality' of partners and resources and can be expressed both actively and passively. Passive choice by mate rejection recently led Holland and Rice (1998) to suggest that extravagant male traits may evolve via a coevolutionary arms race between the sexes where males with 'too small' traits under-stimulate females that, hence, refuse to mate. Reptiles, in particular lizards, may provide a useful taxon in which to test sexual selection hypothesis based on female mate rejection because in many species females have evolved behaviors specifically for this purpose. For example, in the Lake Eyre dragon (*Ctenophorus maculosus*), non-receptive females develop two bright orange ventral patches exposed to an approaching male when she flips over onto her back, leaving the male no possibility to mate with her (Mitchell, 1973; Olsson, 1995). Similarly easy-to-identify female mate rejections are widespread in lizards (Carpenter and Ferguson, 1977; Olsson and Madsen, 1998).

The crucial question from a sexual selection perspective, however, is whether females use active or passive choice in order to deter some but not all males and, if females are choosy, what male trait(s) do they base their choice upon. In the last decade, the sensory exploitation hypothesis has gained considerable support, suggesting that pre-existing biases in sensory organs or in the neural processing of signals result in some partners being preferred over others (Ryan, 1999). This hypothesis thus predicts that traits phenotypically manifested in species in the tops of phylogenetic trees have evolved as a result of sensory biases and this trait preference is shared with less advanced species that have not yet evolved the trait itself (Ryan, 1998). In the present manipulation study, I used a blue color occurring in strongly sexually dimorphic species in Australian agamid lizards, such as *C. pictus* and *C. decresii* (Cogger, 1994), to test whether females in the monomorphic Mallee dragon (*C. fordi*) show preferences for partners of this color. I deliberately avoided red (which also occurs in related sexually dichromatic species) because it is normally developed in response to carotenoid intake (Olson and Owens, 1998). Thus, a mate preference for red could be indicative of, for example, male territory quality rather than reflect female sensory bias alone, and by using blue I was hoping to avoid this confounder in the test of the sensory exploitation hypothesis.

This study comprises two parts, one laboratory experiment in which females were offered the choice between males of different color morphs and size classes, and one manipulation experiment of male coloration in a natural population with subsequent monitoring of female spatial distribution in relation to male treatment. The aim of the study was: (i) to establish whether females actively solicit matings from males; (ii) to look for female preferences in terms of male body size and a novel trait (blue head color) which occurs in dimorphic closely related taxa; (iii) to perform staged mating trials not only as a ‘snap-shot’ observation during the mating season, but to do this for long enough to detect how the use of the rejection behavior changes throughout a female’s reproductive cycle, and (iv) to look for congruence and differences between any female preferences in the captive population and male mating success in the wild.

Methods

Study species

The Mallee dragon (*C. fordii*) is a small (up to 4 g, ca. 50 mm snout-vent length), agamid lizard from arid Australia. Less than 10% survive more than 1 year in both sexes (Cogger, 1974, 1978). Thus, an estimate of a male’s mating success represents that of his life-time. Mallee dragons are sexually monomorpic in size and in color, with the exception of a vague, darkening line on the chest which appears to be more pronounced in males (Cogger, 1978; Olsson, unpublished). Females have a remarkably conspicuous rejection behavior during which they press the chest to the ground while raising their hind legs straight into the air, resulting in a 45° angle of the body towards the ground, head down. Thus, female receptivity is easily established based on presence/absence of rejection postures (Cogger, 1978). Indeed, this was one of the reasons for selecting this species for a study with passive mate choice (rejection of some but not all males) as a target question. Once a female is receptive, she mates passively without any attempt to interrupt the copulation (Cogger, 1978; Olsson, unpublished).

The Mallee dragon is a ground-dweller relying on tussocks of the spinifex grass (*Triodia scariosa*) for its existence (Cogger, 1978). The tussocks form half-moon shaped 'pillows' of sharp, spiny grass up to ca. 1 m in diameter, which the lizards use for perching and basking in mornings and afternoons, and shelter in the mid day sun and at night. In August, the annual cohort from the (normally) two clutches in the previous spring/summer emerges from hibernation (June-mid August; Cogger, 1974, 1978), and the mating season begins.

Laboratory study

The study site was situated on the Yathong Nature Reserve in central NSW, Australia (145°35′; 32°35′). The experiment in captivity took place in October, i.e., approximately in the middle of the reproductive period (Cogger, 1978). All lizards were caught by noose or by hand outside of the study population and placed in outdoor enclosures (1.2×1.2 m^2) with a tussock of *Triodia* in its middle, in which the lizards could take refuge upon any disturbance. The lizards were then left for ca. 2 weeks to acclimatize before the trials began. Males were kept separately from females with four males in each enclosure. The females were kept until a first clutch was laid and then fed ad libitum to induce a new ovarian cycle and receptivity. Once the trials commenced, the same individual females were re-tested in female choice trials over a period of ca. 3 weeks as they progressed from pre-receptivity through their receptive period to post-receptivity (10 October–2 November). The lizards were fed meal worms (*Tenebrio*) and termites ad libitum and had water available at all times. Since the set-up of the enclosures mimicked the natural habitat of the lizards in detail, their behavior over the day followed closely the chronology of behaviors in the natural population. For example, in mornings and afternoons the lizards basked out in the open while at mid day and night they retreated into the center of the *Trioida* tussock, indicating that the thermal environment closely mimicked that in the wild (Cogger, 1978). The lizards had access to shade in the *Triodia* bush and/or along the circumference of the enclosure at all times of the day.

Female preference for male phenotypes was tested in an outdoor arena (1.2×2.4 m^2), divided into three compartments by two perspex walls that formed a triangular center compartment allowing the female to observe both males simultaneously. At the outset of the experiment I decided against using mere position of the female in the test cage as my criteria for 'active mate choice' (for example, being closer to one male; Baird *et al.*, 1997). Instead, I found it more satisfactory to base this judgement on a nominal variable ('preference', vs. 'no preference'). I therefore sawed a 27.5 × 5 cm 'gate' at ground level in the center of each perspex wall, hinged so that only the female in the center compartment could enter into the outer male compartments. I tested the experimental set-up by letting a male stay in the center compartment and a female in a peripheral compartment and he immediately entered the female's compartment via the hinged perspex gate. This test was repeated with >15 males that all successfully entered the females' compartments. Thus, the weight or the friction of the gate posed no constraint on entering a peripheral compartment. Using this design, I aimed to evaluate active choice based on two criteria "approach/no approach" of perspex, and 'entering/no entering' of a male's compartment.

The experimental categories outlined above are heretoforth referred to as 'size trials' and 'color trials', respectively. In captivity, I staged trials using two different male color morphs, blue and controls, accomplished by painting male heads with tattoo paint (Spuck Baulding, New York). Developed for the human skin, this paint is biologically inert and harmless to the lizard's skin. Every second male was 'painted' with a brush on its head as control. In the color trials, male size was kept within error of measurement (1 mm), whereas in the size trials, the size difference between males was equal to or more than two mm (ca. 5% of the mean). The average snout-vent length of participating males in the color trials was 47.5 mm (±1.9, SD) for blue males and 47.2 mm (±2.1, SD) for controls, and in the size trials 48.7 mm (±1.1, SD) for 'large' males and 44.8 mm (±1.3, SD) for 'small' males. Female mean snout-vent length was 46.4 mm (±3.1, SD).

At the time of the trial, a female was positioned in the center of the three-compartment test cage. In each peripheral compartment there was a small *Triodia* plant and a male, randomly assigned to either of the peripheral male compartments. If a female had not responded by approaching a perspex wall within 15 min the trial was interrupted. In all trials, males and females displayed towards each other by head bobbing, confirming that they could see each other through the perspex. In most cases, non-receptive females displayed their characteristic rejection posture already at this stage. Thus, female reluctance to approaching a male was not a result of not perceiving his presence. Once a trial was completed, i.e., a female had been assigned to an active choice category ('choosy', 'not choosy'), the female was introduced to each male in random order into their respective compartment. The rationale for this was to see whether a female would reject a male which she had not expressed preference for, i.e., asking whether she was consistent in her mate choice also at the level of copulation.

When the experiments were completed the lizards were released back into the wild at their places of capture. All lizards fed well in captivity and were in good condition at release.

Field study

As the activity season began in early September, the lizards were captured by hand or by noose and measured snout to vent (SVL) and total length to the nearest 1 mm and weighed to the nearest 0.1 g. Every third male was painted 'blue' and 'controls' as outlined for the laboratory experiments above. In addition to these treatments, I also used one 'black' treatment in the wild (Tattoo paint, Spuck Baulding, New York), in order to exaggerate the vague sexual dimorphism in chest stripe; the reason this was never used in the staged experiments was simply that I judged the sample sizes too small to include this treatment in the experimental design. I also painted a number and sex ID on the lizards' backs (because early in the season, prior to ovarian enlargement, males and females are indistinguishable) before they were released at the place of capture. The whole procedure from capture to release took less than 5 min. Females were measured and marked using the same protocol as for males, except for the male color manipulation. The lizards were then monitored for positions in a 220 × 70 m grid, marked along both orthogonal axes every 10 m with color-coded poles to facilitate monitoring of lizard grid-positions. Once the study period was completed in late November, male and female home ranges were plotted using the convex polygon method.

Results

Laboratory experiment

In all, 17 females participated in the staged experiments. Three of these females never showed rejection behaviors towards males, but the males stopped their mating attempts after the initial sexual chase and/or nape bite that precede copulation (Cogger, 1978). These females were significantly smaller than the remaining females (48.0 ± 0.54 SE, vs. 42.9 ± 0.96 SE; $t = 3.90$, $p = 0.0007$) and all had relatively small follicles (ca. 1–2 mm). Thus, even though they undoubtedly would have reproduced later in the season, males were apparently reluctant to copulate with these females at this early stage of ovarian development. I therefore excluded them from the analysis.

Only in one trial out of 62 did a female approach the perspex separating her compartment from that of a male (a female approached a blue male, stopping 5 cm from the perspex wall). However, in no trial did a female enter a male's compartment. In the wild, females were never observed to actively approach displaying males (see below) and their behavior in captivity, hence, agreed with the apparent reluctance to actively solicit matings in the wild. Males invariably approached the perspex subsequent to noticing a female. A female, however, only displayed back to the male using head bobbing or just laid down (apart from in the one instance mentioned above). Mating followed in 25 of the 62 introductions of females to males (in 31 color trials and 31 size trials), in nine of these only with one male and in the remaining trials with both males. Mating of rejecting females occurred in three cases following male coercion.

All females participated in both trial series, but some only mated in one of the experimental categories. To some degree this is likely to be explained by the short receptivity period (ca. 2 days).

At the onset of my analyses, I decided to use a single observation per female to avoid pseudoreplication (the first voluntary mating per female). However, as the trials progressed, it became increasingly apparent that female receptivity was determined by the stage of her reproductive cycle rather than by the identity of her potential partners. Thus, because females almost invariably either mated with no male or both males, repeat observations should not pseudoreplicate a female 'choice' for a certain male category. Therefore, I also present test statistics for all trials in each category and tests on pooled data for both trial series (i.e., with 'size' and 'color' trials pooled for analysis, Table 1).

I set out to test three null hypothesis with respect to female reproductive behavior (Table 1; all tests are binomial tests):

Hypothesis 1: *Active choice: females do not actively solicit matings from males.*

In seven color trials, none of the females approached either of the males. One female moved in the direction of a blue male but never approached the perspex;

Table 1. Results of mate choice experiment

Hypothesis	Category	Observation	
		Single (per female)	All
1[a]	Male coloration	1 out of 7 ($p = 0.062$)	1 out of 11 ($p = 0.011$)
	Male body size	0 out of 7 ($p = 0.008$)	0 out of 11 ($p < 0.001$)
	All trials combined	1 out of 14 ($p < 0.001$)	1 out of 21 ($p < 0.001$)
2[b]	Male coloration	1 out of 7 ($p = 0.062$)	1 out of 11 ($p = 0.006$)
	Male body size	1 out of 7 ($p = 0.062$)	1 out of 11 ($p = 0.006$)
	All trials combined	2 out of 12 ($p = 0.019$)	2 out of 21 ($p < 0.001$)
3[c]	Male coloration	1 out of 7 ($p = 0.062$)	1 out of 10 ($p = 0.011$)
	Male body size	1 out of 7 ($p = 0.062$)	2 out of 8 ($p = 0.145$)
	All trials combined	2 out of 12 ($p = 0.019$)	3 out of 18 ($p = 0.004$)

All tests are one-tailed binomial tests of directional predictions.

[a] **Hypothesis 1** *A sexually receptive female (confirmed by voluntary mating) does not actively solicit matings.*

[b] **Hypothesis 2** *A receptive female does not express mate preference by rejecting only one of two potential partners.*

[c] **Hypothesis 3** *A receptive female may compromise her first 'choice' by remating.*

to make the test maximally conservative I have scored this as an occurrence of ‘choice’. That same female then mated with both males, hence, compromising any ‘choice’ that she may initially have made. In the size trials, no female out of seven approached either of the males ($p = 0.008$). Thus, with both experiments pooled together, a female only approached a male in a single instance out of 14 (one trial per female, $p < 0.001$), but never pursued to enter his compartment. In all trials combined (in which females mated voluntarily), a female approached but never entered into a male’s compartment in one trial out of 21 ($p < 0.001$; Table 1).

To sum, a null hypothesis of no active choice cannot be rejected. Therefore, it was also impossible to test for female choice between male categories.

Hypothesis 2: *Passive choice: a female does not express’ mate preference by rejecting only one of two potential partners.*

Rejection of only one of the males occurred in one of seven trials in each treatment ($p = 0.062$ in each series). Both these instances took place as the females were crossing from being non-receptive to receptive or vice versa. For the pooled data (one observation per female), two females out of 12 rejected one of the males ($p = 0.019$). When allowing for multiple observations per female, females rejected one of the males in two of 21 trials ($p < 0.001$).

To sum, a null hypothesis of no passive choice via mate rejection cannot be rejected.

Hypothesis 3: *Once mated, a female may compromise her pre-copulatory ‘choice’ by remating.*

A single female out of seven in each trial series rejected one of the males and then also refused to mate with the rejected male after having mated with the ‘preferred’ male ($p = 0.062$). When the data were pooled for both series, two females out of 12 refused re-copulation ($p = 0.019$). In all trials combined where females showed any receptive behavior, females refused to re-copulate in three trials out of 18 ($p = 0.004$).

To sum, the null hypothesis that females may compromise pre-copulatory ‘choices’ by repeat matings with multiple partners cannot be rejected.

In summary, all males but one mated during the experiments and a female often rejected an individual male outside of her period of receptivity but then mated him when receptive. Out of 62 trials involving 14 females and combinations of 15 males, females only showed single rejections in three cases, whereas they rejected both males in 30 trials, all starting or ending a female’s series of trials. Also, females did not consistently reject a small male after a large male, or vice versa, or a blue male after a control, or vice versa. Thus, there was no indication of a consistent 'trading up' of partners' quality by females.

Field study

In the field study 10 males in each experimental category (black, blue) and nine control males were studied over the 10 week study period lasting over two female reproductive cycles (double-clutching is the norm in Mallee dragons; Cogger, 1974, 1978). Males had an average home range size of 1401 m^2 (±401, SD), whereas the corresponding figure for females was 418 m^2 (±592, SD). Thus, males had a home range size more than three times the size of females. Judging from Table 2, there appears to be a substantial difference in home range size between blue males and controls. However, this result is largely the effect of a large home range of a single male, as is also indicated by the large variance in home range sizes of blue males (more than twice as variable as for controls). Because females mate multiply and regardless of male size and coloration, I assumed that a male mated with all females within his home range. I therefore calculated a reproductive success score for each male, so that a female shared with other males was devalued by her number of potential partners (i.e., a male's RS score was calculated as (1/no of female partners) summed over all his females). A more fine-grained estimate of male reproductive success would be a genetic marker of paternity. However, the present study focus' on pre-copulatory female choice and therefore female re-distribution on the home ranges of males are more informative then would be results potentially confounded by post-copulatory mechanisms, such as sperm competition and cryptic female choice (Eberhard, 1996; Birkhead and Møller, 1998). I then looked for differences in the number of partners and in the reproductive success score among the male color categories using Kruskal–Wallis non-parametric analysis of variance.

There was no difference among treatments in number of observations per male, snout-vent length, mass, number of partners per male, reproductive success score, or home range size (Table 2; $0.10 < \chi^2 < 0.67$; $0.41 < p < 0.995$; d.f. = 2). To make a direct comparison of mating success scores possible

Table 2. Descriptive data for males in the study population at the Yathong nature reserve

Treatment	Mass (g)	SVL (mm)	Observations	Home range size (m^2)	Partners	RS Score
Black ($n = 10$)	3.57 (±1.64)	44.3 (±3.97)	11.5 (±6.13)	1385 (±309)	4.3 (±2.9)	0.84 (±0.58)
Blue ($n = 10$)	3.05 (±0.72)	45.3 (±4.29)	12.7 (±5.38)	1810 (±520)	4.7 (±2.9)	1.04 (±0.58)
Control ($n = 9$)	2.95 (±0.99)	44.0 (±5.33)	9.67 (±3.04)	1008 (±246)	4.0 (±3.0)	0.85 (±0.67)

'RS Score' denotes cumulated 'female scores' per male, where a 'female score' = (1/number of visiting males on her home range), i.e., devaluing her fitness value to a male in proportion of expected shared paternity.

between the enclosure trials and the field data I also repeated my analysis while excluding 'black' males from the data set. However, again there was no difference between 'blue' and 'control' males in their mating success score or in their number of partners (Wilcoxon two-sample test, $\chi^2 = 0.81$ and 0.24, $p = 0.37$ and 0.62, respectively; d.f. = 2). Because of this I pooled the color categories to look for relationships between male morphology and reproductive success. However, there was no relationship between neither mass nor SVL and a male's number of partners or reproductive success score ($r_s = -0.20$, $p = 0.32$, $r_s = -0.20$, $p = 0.32$; $r_s = 0.15$, $p = 0.44$, $r_s = 0.13$, $p = 0.52$, respectively; $n = 29$). Again, this agrees with the outcome of the enclosure trials. There was, however, a strong correlation between home range area and a male's number of partners and with his reproductive success score, also when number of observations were controlled for in a Spearman's partial correlation coefficient analysis (Proc Corr, SAS Institute, 1990; $r_s = 0.77$, $p = 0.0001$, and $r_s = 0.71$, $p = 0.0001$, respectively, $n = 29$).

I observed three matings in the wild, one in each category of the two painted males, and one of a control male. They all conformed well with our observations of captive animals and with previous descriptions of Mallee dragon mating behavior (Cogger, 1978) in being short (<25 sec), not preceded by courtship, and not superceded by post-copulatory mate guarding.

Discussion

Agamids (and iguanids) are among the most visually oriented of all lizards (Cooper, 1989). Still, female Mallee dragons do not select mates based on body size or on a novel trait (males of course still could but this is outside the scope of this study). This result is strong and congruent between the laboratory trials and the field experiment. Receptive females almost entirely refrain from approaching conspecific males, while passively accepting copulation when receptive. Indeed, Noble and Bradley's pioneering observation that 'lizard females are passive lovers' (Noble and Bradley, 1933) is re-confirmed in Mallee dragons. Furthermore, females most often compromise any pre-copulatory choice that could have been made by copulating repeatedly with different partners and do not consistently 'trade up', for example, by only re-mating with a larger male. Furthermore, in the few cases when females showed directional rejections of single males, these were not consistent with respect to male phenotype. A simple explanation to the female indifference to the color manipulations is that they cannot perceive wavelengths within the manipulation range, but this is challenged by findings in other lizard species (Swiezawska, 1949). Furthermore, assuming some function of conspicuous colors in males of closely related dichromatic species (e.g., status signaling), female indifference seems much more likely than constraints on perception.

If female receptivity was triggered by the male phenotype in Mallee dragons, one would expect to see shifts in behavior, such as 'receptive-rejective-receptive', through a female's receptive period. However, no such pattern exists in this series of data, and I am not aware of any case in which this has been reported (Olsson and Madsen, 1998).

In summation, my data strongly suggest that a female reaches a stage close to ovulation at which she becomes receptive. At this point, she mates multiply and indiscriminantly with any and all males on her home range, whereafter she rejects males using her characteristic rejection posture (Cogger, 1978).

From the perspective of sexual selection theory, the crucial question then becomes 'Why have females not evolved preferential mating with larger males or those with exaggerated traits'? The following three alternative hypotheses would be plausible explanations:

(i) Predation: This hypothesis suggests that predation prevents conspicuous color morphs from evolving and, hence, that females would have evolved 'chosiness' if males first evolved variation in conspicuous colors on which female choice could be based (i.e., in opposition to sensory exploitation). Although predation from large predatory lizards (*Varanus gouldii*) is likely to be substantial in this population (Olsson, pers obs,), there was no difference in the number of observations per lizard between treatment groups. Assuming similar relative rate of detection of the male color categories in man and predators, equal observation rate is inconsistent with differential predation pressures. However, the realism of this assumption may be doubtful. Furthermore, one of the most brightly colored of all lizard species (and strongly sexually dimorphic), *C. pictus*, occupies the same habitat.

(ii) Time constraints: In an annual species, females are likely to be under strong selection to complete reproduction with a minimum of time waste, since they only have a single season to reproduce. Thus, this may constrain the evolution of mate choice and other forms of complex communication systems. Although there is little data available at present, at least two annual species (and at least in some populations) exist in brightly colored morphs, *Urosaurus ornatus* (Thompson and Moore, 1991; Thompson *et al.*, 1993; Zucker, 1994) and *C. pictus*, (Peter Harlow and Gregg Johnstone pers. com.). At least *U. ornatus* have evolved an intricate communication system based on male coloration (Thompson and Moore, 1991). Thus, there is no support of this hypothesis although data are too meager to reject it.

(iii) Sperm competition/sperm choice: This hypothesis suggests that females may create a selection scenario through some post-copulatory rather than precopulatory mechanism (e.g., Stearns, 1987; Eberhard, 1996). Thus, males may compete also at an intra-uterine level for fertilisation opportunities, for example, by evolving large testes or by interfering with other males ejaculates via copulatory plugs (Birkhead and Møller, 1998). Furthermore, females may be able to bias a males' probability of paternity depending on his genotype. I have no data in support of either of these hypotheses but both are currently under further investigation.

In sum, I find no support for pre-copulatory choice on male color or size in Mallee dragon females. Female rejection behavior occurs in the overwhelming majority of cases outside of a female's receptive period. Any preference that may have been expressed in this way in my study was not consistently directed towards a given male morph and is not congruent with current understanding of epigamic selection.

Acknowledgements

I am grateful to the Australian Research Council and Jubileumsfonden Göteborg who provided financial support for this work. I am especially grateful to Peter Harlow and Rick Shine for continued support and discussions throughout this project, and to Janne Kotiaho for comments on a previous version of the manuscript.

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