

Do female Lake Eyre dragon lizards adjust courtship rejection behaviour under higher predation risk?

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Summary

Female resistance is expected to evolve when mating costs outweigh resistance costs. One potential cost of resistance is increased predation risk; however, the ability to compensate behaviourally may reduce these costs. In the Lake Eyre dragon, *Ctenophorus maculosus*, non-receptive females employ several rejection strategies, including lateral threat displays and flipping over, to prevent superfluous matings. *C. maculosus* rely on cryptic dorsal colouration for protection from predators; however, resisting females are highly conspicuous as they develop orange ventro-lateral colouration, which is emphasised during rejection displays. Furthermore, flipping over may increase vulnerability to predators by decreasing a female's ability to detect predators and to flee. We tested whether females behaviourally compensate for potential increased vulnerability by altering their use of lateral threats and flip-overs under high and low perceived predation risk. The duration of flip-over rejections was significantly lower under high predation but there was no effect of predation risk on the frequency or duration of lateral threats. This suggests that females may compensate for reduced mobility or ability to detect predators rather than increased conspicuousness. Our study confirms that females are able to modulate resistance behaviour in relation to predation risk, potentially altering the trade-off between mating costs and costs of resistance.

Keywords: sexual conflict, female resistance, forced copulation, behavioural compensation, predation risk, lizard.

Introduction

Differences in the reproductive interests of males and females can lead to antagonistic co-evolution between the sexes (Chapman et al., 2003). To optimise their reproductive output, males may employ coercive mating strategies

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(Clutton-Brock & Parker, 1995). When males are capable of forcing copulations, females may suffer significant direct and indirect costs. These costs have been widely studied and can include; increased mortality (Le Boeuf & Mesnick, 1990; Blanckenhorn et al., 2002; Ronn et al., 2006), energetic costs (Watson et al., 1998), increased predation risk (Arnqvist, 1989) and reduced mate choice leading to the production of inferior offspring (Cotar et al., 2008). As a result, in many species, females have evolved counter-adaptations to mitigate these costs (Arnqvist & Rowe, 2002). Specifically, females of many species have evolved behavioural resistance strategies or morphological adaptations to make it difficult for males to force copulation (Arnqvist & Rowe, 1995; Chapman et al., 2003). In species where resistance is observed, females are often successful in preventing forced copulations; however, resistance strategies themselves may carry costs. Consequently, there will be a trade-off between the costs associated with mating and costs of resistance. Female resistance strategies are expected to evolve when the direct and indirect benefits from preventing mating exceed the costs associated with resistance (Muhlhauser & Blanckenhorn, 2002). While the costs of mating have been well documented, the costs of resistance have rarely been quantified.

One potential cost of female resistance is increased predation risk due to decreased mobility (Muhlhauser & Blanckenhorn, 2002), reduced ability to detect predators or increased conspicuousness (Olsson, 1995). Therefore, there is a potential trade-off between resisting males and avoiding predation. This trade-off may be altered if females are able to behaviourally compensate for increased predation risk by altering their resistance behaviour. There is substantial evidence that individuals can flexibly adjust their reproductive behaviour such as mate choice, male-male competition and courtship investment in response to variation in predation risk (Berglund, 1993; Sih, 1994; Candolin, 1997; Kotiaho, 2001). Furthermore, in species with conspicuous mating displays, such as song or bright colouration, males with more conspicuous signals often compensate by being more cautious towards predators (Candolin, 1997; Hedrick, 2000; Cabido et al., 2008) or being better at escaping predator attacks (Lindstrom et al., 2006).

If courtship resistance makes females more susceptible to predation, females may compensate by altering their resistance strategies under different levels of perceived predation risk. As the ability to compensate behaviourally may reduce the overall costs of a trait, it must be taken into account to fully

quantify the costs of female resistance. How variation in predation risk influences female resistance behaviour, however, has yet to be assessed experimentally.

In the Lake Eyre dragon lizard, *Ctenophorus maculosus*, males are highly aggressive and persistently harass both receptive and unreceptive females by chasing and biting them in attempts to force copulation (Olsson, 1995). Males may gain paternity by forcing copulation if females are able to store sperm, as in other small agamid lizards (Uller & Olsson, 2006; Olsson et al., 2009). During copulation, males bite the female on the neck and pin her to the ground. Overly aggressive males may injure or even kill the female with their mating grasp (Olsson, 1995). To mitigate the costs of mating, *C. maculosus* females resist males with three behavioural rejection strategies (Olsson, 1995). Females may attempt to flee from the courting male, perform a threat display or flip-over onto their back, a move that exposes bright orange ventral colouration and prevents forced male intromission. This unique and unusual resistance behaviour is observed only in this species and a species of insect (Arnqvist, 1992). In *C. maculosus*, females develop bright orange ventro-lateral colouration on the throat and abdomen prior to becoming receptive and maintain this colouration until after laying (Mitchell, 1973; Chan et al., 2009). In comparison, males remain relatively cryptic throughout the breeding season. The flip-over and lateral threat rejection strategies emphasise female ventral colouration to varying degrees with ventral colouration fully exposed during the flip-over rejection and partially visible during the threat display due to lateral compression of the female's body and extension of the throat. Both of these rejection strategies could impose a significant predation cost given that *C. maculosus* occurs only on the featureless, dry salt lakes of Australia's arid interior and relies on cryptic dorsal colouration for protection from predators. Its primary anti-predator tactic is to crouch motionless on the salt crust rather than flee into burrows (Mitchell, 1973). The flip-over rejection may also increase predation risk by impairing the lizards' ability to detect a predator. In this study, we investigate whether *C. maculosus* females alter their use of lateral threat and flip-over rejection strategies in response to different levels of perceived predation risk. Specifically, we test the hypothesis that females behaviourally compensate for their increased vulnerability to predators when predation risk is high.

Methods

Study species

The Lake Eyre dragon, *Ctenophorus maculosus*, is an agamid lizard endemic to the three largest dry salt lakes of arid inner South Australia. The average size of adult males is 7 cm snout–vent length (SVL), slightly larger than females which average 6 cm SVL (Mitchell, 1973). The breeding season of *C. maculosus* runs from September to late December (Mitchell, 1973). Females are receptive soon after development of ventral colouration with ovulation occurring at 9–12 days after colouration develops (Chan et al., 2009). Prior to receptivity and developing orange coloration, females signal their reproductive status by performing head-bobs and arm waves to courting males (Chan et al., 2009). Receptive females frequently accept copulation with courting males and very rarely perform rejection behaviours (Chan et al., 2009), however once gravid, females are unreceptive and will consistently reject persistent male courtship and forced copulation attempts by either fleeing, performing a threat display or flipping over onto their backs (Olsson, 1995). Females lay 3–4 eggs 20–25 days after fertilization (Mitchell, 1973). The primary predators of *C. maculosus* are birds of prey, although they are also preyed upon by varanid lizards, which make short forays onto the salt crust from the shore dunes (Mitchell, 1973).

Capture and husbandry

In this experiment, we used 9 females and 22 males captured by hand from Lake Eyre, between 22 August and 7 September 2007 and 8 females captured between 17 September and 3 October 2008. There were no significant differences in the body size (SVL) of females captured in the two years (2007: 56.4 ± 2.07 mm; 2008: 57.2 ± 2.38 mm; $t_{15} = 2.13$, $p = 0.47$).

Captive lizards were housed individually in $61 \times 30 \times 30$ cm glass tanks separated by opaque dividers. The room was maintained at an average temperature of 28°C on a 12:12 day/night light cycle. Each tank had a UV light and heat lamp and contained a layer of sand, salt crust and an area of deep, damp sand required for burrowing and egg laying. Lizards were watered and fed live crickets (*Anchiesta domesticus*) and meal worms (*Tenbrio* spp. larvae) dusted with calcium and vitamins three times a week.

Small agamid female lizards are more likely to become sexually receptive and lay eggs in captivity when housed continually with males than when only

in visual contact (Uller & Olsson, 2005). We ensured females became sexually receptive by periodically exposing them to two males of similar mass and size (SVL) until the female developed ventral colouration, a process referred to as 'priming'. We alternated between two males to ensure females were stimulated and to reduce habituation. For priming, one of the males was introduced to the female's enclosure and left for approximately 4 h a day on alternate days. The two males used for priming were different to those that the female was exposed to in the subsequent experiment. Once females developed ventral colouration, they became receptive to mating and the same males that were used for priming were added to the female's enclosure and left for several hours and any observed copulations were noted. Mated females became gravid approximately 10 days after development of orange ventral colouration (Chan et al., 2009). Only gravid females (i.e., those carrying fertilised eggs), which consistently rejected courting males, were used in this study. We determined that females were gravid by palpation and by their consistent courtship rejection behaviour.

Experimental design

We conducted experiments between 15 October and 12 December 2008. The temperature of the experimental room was maintained at 32°C. We set up a large plastic tub (59 × 38 × 23 cm) with a layer of washed sand covering the base, but not deep enough for lizards to burrow into. Temperature within the tub was constantly monitored and was found to fluctuate between 33.2 and 36.4°C. *C. maculosus* are capable of their full range of movement and activity at 32°C (Mitchell, 1973). We conducted the experiments between 9 am and 12 pm as this is peak activity time for the species (Mitchell, 1973). We exposed gravid, rejecting females to high and low levels of perceived predation risk. For the high perceived predation risk treatment, we exposed females to a taxidermic mount of a brown goshawk (*Accipiter fasciatus*) in flight with wings fully outspread. The hawk hung from clear fishing wire attached to a 1.5 m wooden rod, which allowed us to swoop the hawk over the enclosure without being visible to the lizards. The distribution of *A. fasciatus* includes Lake Eyre (Simpson & Day, 2004), making it a suitable predator cue as it is a potential predator of *C. maculosus*. Females were left in the tub to acclimatise for 10 min before the hawk was swooped over the tub 10 times (back and forth). Generally, females responded to the predator mount

in one of two ways: they would either crouch down and remain motionless or attempt to flee. Following exposure to predation, the females were left for a further 5 min before an unfamiliar male was added to the tub and their interaction video recorded. For the low perceived predation risk treatment, females were not exposed to any predator cue. We refer to this treatment as 'low' predation risk as females were initially cautious when released into novel experimental enclosures suggesting that they may have considered the situation to be risky and, therefore, behaved differently than if they perceived no risk. Females were left in the experimental enclosure for 15 min before the male was added. For each treatment, we recorded the interaction between the male and female for 20 min with a Panasonic SDR-H250 digital video camera.

Each female was exposed to both treatments in random order. 11 and 6 females were randomly assigned high and low predation risk as their first treatment respectively. The same male was used for both treatments to account for any differences in behaviour that may be due to different males. Lizards were given at least two days rest between treatments to minimise stress and minimise the chance females would remember the previous treatment.

We scored female and male behavioural reproductive strategies from the video footage. Male behaviour comprised head-bobs, frog-leaps consisting of a push-up followed by a leap towards the female, bites and forced copulation attempts in which the male would bite the female's neck while forcing her to the ground and aligning his body with hers to allow intromission. Female behaviour primarily comprised two behavioural rejection displays: lateral threat displays in which the female would laterally compress her body and arch her back while elevated on all four legs, sometimes accompanied by walking with a stiffened gait; and flip-overs in which the female would flip onto her back to prevent forced intromission and remain motionless. We recorded frequency of all behavioural strategies, as well as the duration of female lateral threat displays and flip-overs (all log-transformed for subsequent analysis).

We tested whether there was a significant difference between the frequency and duration of female courtship resistance strategies under high and low perceived predation risk using a repeated measures ANOVA (SAS PROC GLMM) with treatment (high or low predation) as the repeated measure and female ID as the subject. To account for any effect of order of treatments,

treatment (high or low perceived predation risk) order (first or second trial) and their interaction were included as fixed effects in the model. As some males were used twice, we included male ID as a random factor in the model. We also tested whether there was a significant difference in male behaviour between the two treatments using the same model structure, except with male behaviour as the dependent variable. Although males were never exposed to any predator cue, they may have been reacting to a difference in female behaviour. In each case, we performed four tests but did not apply Bonferroni correction for multiple tests due to the greater risk of inflating type II error with moderate sample sizes (Nakagawa, 2004).

Results

Male reproductive behaviour

Males courted females with head bobs and frog leaps and harassed them by biting them in an attempt to gain a mating grasp and force copulation. The frequency of male head bobs and frog leaps did not differ significantly between treatments, nor did the frequency of bites or forced copulation attempts (Table 1). Treatment order had no significant effect on the frequency of male head bobs, frog leaps or forced copulation attempts (Table 1). However, there was a significant treatment order effect for bite frequency with males biting significantly more during the females' first treatment ($F_{1,15} = 4.90$, $p = 0.04$, Table 1). With the exception of bite frequency, male behaviour was consistent between high and low predation treatments and first and second trials (see also Table A2 in the Appendix).

Female reproductive behaviour

Females were always successful in resisting male courtship with no forced copulations observed. Females consistently rejected courting males with two types of rejection displays: lateral threats and flip-overs. Of the total time spent resisting courtship, females employed flip-overs an average of 18.8% of the time and lateral threats an average of 73.1% of the time. The remaining 8.1% of the time was spent attempting to flee from the male. As the female's ability to flee was constrained by the enclosure and this behaviour was performed only rarely, we present only results of the lateral

Table 1. Results of two-way ANOVAs testing for an effect of treatment (high or low perceived predation risk), treatment order (first or second) and their interaction on the frequency of male courtship behaviour.

| Male behaviour | Factor | $F_{1,15}$ | p |
|---------------------------|--------------------------|------------|-------|
| Head-bob | Treatment | 0.36 | 0.56 |
| | Order | 2.76 | 0.12 |
| | Treatment \times Order | 0.16 | 0.69 |
| Frog-leap | Treatment | 0.28 | 0.61 |
| | Order | 0.04 | 0.85 |
| | Treatment \times Order | 0.00 | 0.96 |
| Bite | Treatment | 1.10 | 0.31 |
| | Order | 4.90* | 0.04* |
| | Treatment \times Order | 0.53 | 0.48 |
| Forced copulation attempt | Treatment | 3.91 | 0.07 |
| | Order | 3.81 | 0.07 |
| | Treatment \times Order | 0.00 | 0.95 |

* Significant effect.

threat and flipping rejection behaviours. There were no significant differences in the behaviour of females captured in 2007 and 2008 (lateral threat frequency: $F_{1,15} = 0.003$, $p = 0.96$; lateral threat duration: $F_{1,15} = 0.002$, $p = 0.97$; flip-over frequency: $F_{1,15} = 0.005$, $p = 0.94$; flip-over duration: $F_{1,15} < 0.001$, $p = 0.98$). The frequency of rejection displays did not differ significantly between treatments (Table 2). However, females spent significantly less time performing the flip-over rejection when perceived predation risk was high (Figure 1), although the duration of lateral threats was not significantly different between treatments (Table 2). Females performed significantly more flip-overs and lateral threats and also spent significantly more time performing the flip-over rejection during their first trial (lateral threat frequency: $F_{1,15} = 6.53$, $p = 0.02$, flip-over frequency: $F_{1,15} = 5.72$, $p = 0.03$, flip-over duration: $F_{1,15} = 9.04$, $p = 0.01$, Table 2). However, order of treatment had no significant effect on the duration of lateral threats and there were no significant interactions between treatment and order for any of the female behavioural strategies (Table 2; see also Table A2).

Male and female behavioural strategies were highly correlated. The more harassment from the male, the more the female would reject. The relative

Table 2. Results of two-way ANOVAs testing for an effect of treatment (high or low perceived predation risk), treatment order (first or second) and their interaction on the frequency and duration of female behavioural rejection strategies.

| Female behaviour | Factor | $F_{1,19}$ | p |
|--------------------------|--------------------------|------------|-------|
| Lateral threat frequency | Treatment | 2.00 | 0.17 |
| | Order | 6.53* | 0.02* |
| | Treatment \times Order | 2.93 | 0.10 |
| Lateral threat duration | Treatment | 3.03 | 0.10 |
| | Order | 3.28 | 0.09 |
| | Treatment \times Order | 3.60 | 0.07 |
| Flip-over frequency | Treatment | 2.13 | 0.16 |
| | Order | 5.72* | 0.03* |
| | Treatment \times Order | 3.87 | 0.06 |
| Flip-over duration | Treatment | 9.04* | 0.03* |
| | Order | 9.04* | 0.01* |
| | Treatment \times Order | 3.04 | 0.10 |

* Significant effect.

size of males compared to females did not affect behaviour. There were no significant correlations between the ratio of female to male size (SVL) and any of the behavioural strategies (Table A1).

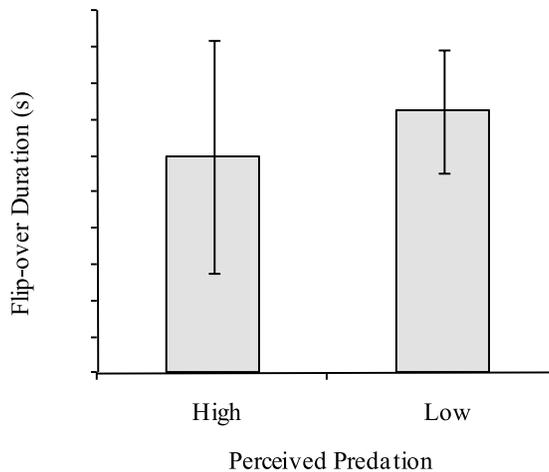


Figure 1. Mean (\pm SE) duration of female flip-over rejections during high and low perceived predation risk treatments.

Discussion

Predation pressure may constrain the evolution of female courtship rejection displays if those displays increase vulnerability to predators. However, females may compensate for increased vulnerability by reducing the frequency or duration of behavioural rejection strategies. We tested whether *C. maculosus* females adjust their resistance behaviour in response to different levels of perceived predation risk. Specifically, we tested the hypothesis that females would behaviourally compensate for their increased vulnerability to predators when predation risk was high. Our study showed that females spent less time performing the flip-over rejection when perceived predation risk was high, suggesting that they may modulate their resistance behaviour in relation to predation risk.

The rejection displays of female *C. maculosus* may increase their vulnerability to predation due to increased conspicuousness. The lateral threat display and flip-over rejections emphasise the bright orange ventro-lateral coloration exhibited by gravid females. The orange colour patches contrast highly with both the adjacent white of the lizards' ventral surface and the grey-brown salt crust of Lake Eyre, and are highly conspicuous to the visual system of both lizards (Chan et al., 2009) and birds (McLean et al., 2010). The lateral threat display is most visible from the side and is, therefore, likely to be most conspicuous to lizards whereas the flip-over behaviour is conspicuous to both lizards and aerial predators. Thus, although lateral threat displays were performed more frequently, the flip-over rejection behaviour is more likely to affect vulnerability to predation. Evidence from other species indicates that more conspicuous individuals sometimes alter their behaviour to compensate for their increased risk of predation (e.g., Fuller & Berglund, 1996; Candolin, 1997; Hedrick, 2000; Cabido et al., 2008). However, a previous study using static models of *C. maculosus* found that although flipped over females are much more conspicuous to birds, they were attacked significantly less frequently than non resisting, cryptic females (McLean et al., 2010) although they were not immune from predator attacks. This may be due to apostatic selection, where predators form a search image of common prey types and are more likely to avoid rare, conspicuous prey types. This form of frequency dependent predation increases foraging efficiency when searching for highly cryptic prey such as *C. maculosus* (Dukas, 2004). If predators are less likely to attack conspicuous orange, flipped over females, females may not need to compensate for their increased conspicuousness.

Besides increased conspicuousness, female resistance may increase vulnerability to predation for other reasons such as reduced mobility or ability to detect predators. In response to reduced mobility or low visibility, animals may increase their vigilance (Metcalf, 1984; Arenz & Leger, 1997; Riginos & Grace, 2008). When predation is high, *C. maculosus* females may spend less time flipped-over, but not alter their lateral display behaviour, because their view is obstructed only when flipped over. While flipped-over, visibility is impaired as the eyes are close to the substrate and the lizard's ability to detect predators is reduced. Flipping over also impairs normal anti-predator behaviour as females either crouched down or fled when exposed to a predator cue, both of which are not possible when flipped-over. A resisting female may, therefore, be vulnerable to predation due to a decreased ability to detect predators and an inability to flee quickly to a burrow should the need arise. It is possible that females flip back over more readily under high predation risk as a means of increasing vigilance and consequently, decreasing predation risk. Thus, females may be compensating for increased vulnerability due to reduced ability to detect predators rather than increased conspicuousness. This hypothesis is consistent with the finding that females did not alter the frequency or duration of lateral threat displays. Lateral threat displays increase conspicuousness because the ventro-lateral orange coloration is clearly visible when females extend their throats and laterally compress their bodies; but these displays are unlikely to affect their ability to detect predators. Consequently, females may be less likely to reduce the frequency or duration of lateral threats when having previously been exposed to a predator cue.

In this study, females were exposed to a predator cue and males were not. It is possible that in the wild, males also alter their behaviour in response to different levels of perceived predation risk. Courtship by *C. maculosus* involves a lot of movement with males performing head bobs and push-ups and frog leaping towards females (Mitchell, 1973). Courtship may, therefore, increase the conspicuousness of males if movement attracts the attention of predators. In other species, males compensate for conspicuous courtship behavioural strategies by decreasing courtship in the presence of predators (e.g., Forsgren & Magnhagen, 1993; Candolin, 1997). It is possible that *C. maculosus* males reduce courtship behaviour or do not court at all when predation risk is high. If males reduce courtship under higher predation risk, females will not resist and hence the flip-over rejection may rarely

be performed when predation risk is high. Nevertheless, our experiments suggest that if males do attempt courtship when there is risk of predation, females are able to modulate their resistance behaviour to reduce risk.

In addition to a significant effect of predation risk, we found a significant effect of treatment order on male biting, the frequency of female lateral threats and the frequency and duration of flip-overs. In the first trial, males attempted to gain mating grasps and copulate with females more persistently, and in response, females resisted with more lateral displays and flip-overs. This may indicate individual recognition, with males reducing their investment in females that they had previously determined to be non-receptive. We allowed a minimum of two days between experiments with the same pair, as in most taxa (apart from mammals) experience effects are short lived (<24 h; reviewed in Hsu et al., 2006). However, there is evidence to suggest that in some species, including reptiles, individuals may recognise and remember each other for periods of up to several weeks (Schuett, 1997; Stuart-Fox & Johnston, 2005). The territories of male Lake Eyre dragons generally overlap the home ranges of one or more females. Males may also encounter unfamiliar females as *C. maculosus* spend long periods foraging (up to 8 hours per day), during which they may travel long distances from their territories (Mitchell, 1973). Given the substantial energy males devote to courtship (and the harsh environment), there may be strong selection for individual recognition to facilitate male courtship investment decisions.

Despite substantial evidence for flexible anti-predator behaviour (reviewed in Lima & Dill, 1990; Lima, 1998) the proximate determinants of behavioural responses to perceived predation risk are often unclear. Our study suggests that in *C. maculosus* a resisting female's compromised ability to detect predators may be more important than her increased conspicuousness in determining her vulnerability to predation and her behavioural responses to perceived risk. Our results also provide experimental evidence for behavioural modulation of female resistance behaviour in relation to predation risk, which may alter the trade-off between costs of resistance and costs of mating.

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Appendix

Table A1. Correlations between female and male behavioural reproductive strategies and female to male size ratio under low perceived predation risk (no predator cue).

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|--|----------|----------|----------|-------|----------|---------|----------|--------|------|
| 1. Flip-over frequency | 1.00 | | | | | | | | |
| 2. Flip-over duration | 0.932*** | 1.00 | | | | | | | |
| 3. Lateral threat frequency | 0.609** | 0.535* | 1.00 | | | | | | |
| 4. Lateral threat duration | 0.431 | 0.388 | 0.840*** | 1.00 | | | | | |
| 5. Head-bob frequency | 0.749*** | 0.745*** | 0.333 | 0.348 | 1.00 | | | | |
| 6. Frog-leap frequency | 0.585* | 0.602* | 0.166 | 0.128 | 0.811*** | 1.00 | | | |
| 7. Forced copulation attempt frequency | 0.844*** | 0.788*** | 0.265 | 0.073 | 0.746*** | 0.622** | 1.00 | | |
| 8. Bite frequency | 0.762*** | 0.730*** | 0.302 | 0.207 | 0.635** | 0.633** | 0.853*** | 1.00 | |
| 9. Ratio (female/male SVL) | -0.261 | -0.199 | -0.074 | 0.255 | -0.248 | -0.265 | -0.385 | -0.250 | 1.00 |

Data are Pearson correlation coefficients ($N = 17$). Significant correlations: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table A2. Female and male reproductive behaviour means, SEs and percentages of total rejection/courtship behaviour during the first and second trials and under high and low perceived predation risk.

| Behaviour | Low predation | | | High predation | | | First trial | | | Second trial | | |
|---------------------------|---------------|-------|-------|----------------|-------|-------|-------------|-------|-------|--------------|-------|-------|
| | Mean | SE | Perc. | Mean | SE | Perc. | Mean | SE | Perc. | Mean | SE | Perc. |
| Female | | | | | | | | | | | | |
| Lateral threat frequency | 7.18 | 1.39 | 71.50 | 6.59 | 1.52 | 61.22 | 9.23* | 1.52 | 64.91 | 4.53* | 1.12 | 68.24 |
| Lateral threat duration | 127.06 | 21.91 | 76.15 | 125.59 | 36.13 | 68.02 | 165.94 | 33.22 | 71.83 | 86.71 | 22.04 | 74.42 |
| Flip-over frequency | 2.76 | 0.58 | 23.00 | 2.71 | 0.98 | 19.70 | 3.53* | 0.96 | 22.56 | 1.94* | 0.54 | 20.17 |
| Flip-over duration | 36.18* | 8.44 | 21.74 | 29.88* | 16.00 | 16.42 | 43.94* | 15.70 | 19.76 | 22.12* | 8.20 | 17.78 |
| Male | | | | | | | | | | | | |
| Head-bob | 30.24 | 5.51 | 59.58 | 35.76 | 6.78 | 71.06 | 39.71 | 7.13 | 65.21 | 26.29 | 4.56 | 65.08 |
| Frog-leap | 6.00 | 1.56 | 9.24 | 6.53 | 1.67 | 10.68 | 6.65 | 1.73 | 8.46 | 5.88 | 1.49 | 11.50 |
| Bite | 7.18 | 1.66 | 23.14 | 6.06 | 1.41 | 12.95 | 8.12* | 1.84 | 19.44 | 5.12* | 1.06 | 16.88 |
| Forced copulation attempt | 4.65 | 1.17 | 8.04 | 2.94 | 0.94 | 5.32 | 4.76 | 1.32 | 6.89 | 2.82 | 0.70 | 6.53 |

Durations are in s ($N = 17$). Significant differences between treatments/trials are indicated by an asterisk (*).