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Original Article

Social interactions generate mutually reinforcing selection for male aggression in Lake Eyre dragons

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Fighting ability is generally assumed to predict male reproductive success; yet the mechanisms responsible for this relationship are seldom known. Competitively superior males may monopolize access to females, be preferred by females, invest more into courtship, or employ more coercive mating tactics. Differentiating these alternatives is essential to understand the interaction between male–male competition and female mate choice, and their influence on the evolution of male traits such as aggression. We tested whether male fighting ability, body size, courtship, or coercive behavior in intersexual interactions predict copulation success in the Australian Lake Eyre dragon lizard, *Ctenophorus maculosus*. Males with superior fighting ability had higher mating success; however, male harassment (biting and chasing) was a much stronger predictor of copulation, likely because aggressive males are able to overcome female resistance. Better fighters also copulated for longer, which may increase sperm transfer and/or fertilization success. Conversely, courtship effort (head-bobs) decreased copulation success, but only for small males. Females were no less likely to reject males with higher fighting ability, suggesting that females do not prefer these males. Furthermore, males with superior fighting ability were no more or less likely to court or harass females. Instead, both fighting ability and aggression towards females independently increased mating success, potentially generating mutually reinforcing selection on male aggression.

Key words: courtship, fighting ability, lizard, male–male competition, sexual coercion, sexual conflict.

INTRODUCTION

Male fighting ability is generally assumed to predict male reproductive success because males that win contests can monopolize access to females by excluding rivals (Le Boeuf 1974; Dixon et al. 1993; Reichard et al. 2005; Engelhardt et al. 2006). However, competitively superior males may also have higher reproductive success because they are preferred by females (e.g., Horne and Ylönen 1996; Pizzari and Birkhead 2000; Kortet and Hedrick 2005) or because they employ more coercive mating tactics (e.g., Shine and Mason 2005). Therefore, selection on male aggression and associated traits potentially depends on how male competitive ability relates to male behavior towards females (courtship and coercive behavior) and how they each influence male mating or reproductive success. Specifically, male behavior in intra- and intersexual interactions can determine whether male–male competition and female mate choice exert mutually reinforcing or opposing selection on male traits such as aggression (Berglund et al. 1996; Hunt

et al. 2009; Okada et al. 2014). Although several studies have examined the relationship between male fighting ability and female preference (e.g., Horne and Ylönen 1996; Pizzari and Birkhead 2000; Kortet and Hedrick 2005) or reproductive success (reviewed in Ellia 1995), few have specifically quantified male behavior in different contexts (contests, courtship) and how it influences female behavior and male copulation success (but see Okada et al. 2014; Wells et al. 2014).

Females may prefer males that win contests (e.g., Breed et al. 1980; Alatalo et al. 1991; Horne and Ylönen 1996; Doutrelant and McGregor 2000), and gain both direct and indirect fitness benefits from mating with them, when fighting ability predicts a male's viability (Cox and Lebouf 1977), his ability to provide resources to females (or their offspring; Andersson 1994; Candolin and Voigt 2001) or the attractiveness of his sons (Wedell and Tregenza 1999; Taylor et al. 2007). Such a preference may develop because females observe male competitive performance directly ("eaves-dropping"; Cox and Lebouf 1977; Aquiloni et al. 2008) or because better fighters (presumably better "quality") also invest more into courting females (Andersson 1994). Alternatively, females may either show no preference for competitively superior males (Sorenson and

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Derrickson 1994; López et al. 2002; Shackleton et al. 2005; Stapley 2008) or avoid mating with them (Forsgren 1997; Ophir and Galef 2003; Bierbach et al. 2013) if traits associated with dominance in male–male contests, such as larger body size or increased aggression, negatively impact female fitness or reproductive output. For example, mating with males with higher fighting ability may carry direct costs such as increased risk of injury, reduced fecundity or reduced life span, or indirect costs due to genetic incompatibilities (reviewed in Qvarnström and Forsgren 1998).

The costs of mating can be particularly high when males with higher fighting ability are more coercive and coercive behavior towards females improves male mating success. This will create mutually reinforcing selection for aggressiveness, large body size, and/or exaggerated weaponry (Arnqvist and Rowe 2005). For example, in North American garter snakes, *Thamnophis sirtalis parietalis*, large body size increases the ability of males to obtain coercive copulations as well as being advantageous in intrasexual contests (Shine and Mason 2005). Shine and Mason (2005) argue that selection for the ability to forcibly inseminate females (rather than male competition) is the primary mechanism driving body size evolution in this species. However, the opposite is likely in other systems: coercive behavior towards females or risk of injury during copulation could be a by-product of selection for high aggression or large armaments due to male competition. For example, male competition favors extremely large body size in elephant seals, *Mirounga* spp., and as a consequence, females are sometimes accidentally crushed to death during mating (Clutton-Brock and Parker 1995; Galimberti et al. 2000). Dominant males, however, are often not the most coercive. In many species, it is the subordinate (or “sneaker”) males that rely on coercive strategies to obtain matings (reviewed in Wong and Candolin 2005). Both situations (either dominant or subordinate males employing coercive mating tactics) may generate antagonistic coevolution between the sexes. Therefore, to understand the interaction between male competition and female mate choice, and its implications for sexual conflict, it is important to disentangle the relationship between male fighting ability, courtship investment, coercive mating behavior, and reproductive success.

Here, we investigate the relationship between male behavior in intra- and intersexual interactions and mating success in the Lake Eyre dragon, *Ctenophorus maculosus*. The species is a small (≤ 70 mm snout to vent length [SVL]), sexually dimorphic agamid lizard that occurs only on the arid inland salt lakes of South Australia (Mitchell 1973; Pedler and Neilly 2010). Male Lake Eyre dragons are larger than females, highly aggressive and engage in escalated contests over territories (Mitchell 1973; Olsson 1995b). Contest success is predicted by maximum bite force and contest winners perform significantly more aggressive behaviors than losers, but fighting ability is not related to body size, mass, head shape, or prior contest experience (McLean and Stuart-Fox 2015). Competitively, superior males presumably defend larger territories, which overlap the home ranges of a greater number of females (Olsson 1995b), but do not provide resources such as food (which is ephemeral and unpredictable: wind-blown arthropods and, to a lesser degree, ants; Mitchell 1973; Olsson 1995b) or oviposition sites. Both sexes mate multiply and neither sex provides parental care. Males persistently court females with head-bobs (Chan et al. 2009) and harass females by chasing and biting them (particularly on the head and neck) in an attempt to gain a mating gasp, after which males can utilize their larger size to force intromission (Olsson 1995a). Forced copulations can result in serious injury to females or even death during particularly fierce interactions (Olsson 1995a). In response, females

perform rejection behaviors including lateral threat displays (similar to the male’s aggressive lateral display) and flipping onto their back to reveal bright orange ventrolateral coloration and prevent copulation (Olsson 1995a; Chan et al. 2009).

We staged encounters between male and female lizards, in a laboratory setting, to investigate the relationship between male traits (including fighting ability measured previously from male–male contests) and behavior during male–female interactions and how these in turn predict mating success. The fighting ability of each male was estimated based on the outcome of contests conducted as a tournament (where each male faced multiple opponents; McLean and Stuart-Fox 2015). We predicted that better fighters would have greater mating success, as fighting ability is likely to reflect male quality. If this is due to female preference for dominance in male contests, females should be less likely to reject males with higher fighting ability. Additionally, if males are employing alternative mating strategies, we expected to find a relationship between fighting ability and male behavior towards females, and for this behavior to influence mating success. Lastly, if both male–male and male–female interactions generate mutually reinforcing selection on male aggression, we expected both male fighting ability and male aggression towards females to increase mating success.

METHODS

Study species and husbandry

The Lake Eyre dragon, *C. maculosus*, is currently known from Lake Eyre, Frome, Torrens, and Callabonna in South Australia (Mitchell 1973; Pedler and Neilly 2010). In this study, we used 63 adult lizards (34 females and 29 males) captured by hand from Lake Eyre (28.95–29.05°S, 137.65–137.76°E), between 22 August 2007 and 29 September 2008, and kept in captivity at The University of Melbourne, Victoria, Australia. Lizards were housed individually in 61 × 30 × 30 cm (length × width × height) glass tanks, separated by opaque partitions, containing a layer of sand and salt crust to mimic natural habitat. The room was maintained at an average temperature of 28 °C on a 12:12 h day: night light cycle and heat lamps were suspended above each tank to produce a heat gradient for thermoregulation. Lizards were misted with water for hydration and fed live crickets (*Anchieta domesticus*) and mealworms (*Tenebrio* spp. larvae) every second day. All animals were above the minimum SVL at sexual maturity (48 mm for females and 54 mm for males; Mitchell 1973), with females ranging from 48.5 to 63.0 mm and males ranging from 60.2 to 70.2 mm. Only receptive females, during their first or second reproductive cycle for the year, were used in this study. Females are receptive 0–12 days after the onset of orange ventral coloration and accept male courtship and copulation during this time (Chan et al. 2009). All research methods used in this study were reviewed and approved by the Animal Ethics Committee of The University of Melbourne.

Behavioral trials

Courtship trials were conducted during the breeding season (September–November) in 2007 and 2008 between 0900 and 1300 h (peak activity time of the species; Mitchell 1973). Females were placed into male tanks and encounters were videotaped using a Panasonic SDR-H250 digital camera. Females were removed from the tank immediately after mating occurred or after approximately 50 min without a successful copulation. This gave the lizards time to start interacting (mean \pm standard error [SE] latency until

initiation was 11 ± 0.98 min), while copulation was unlikely to occur after 50 min. The mean (\pm SE) duration of courtship trials was 27 (± 1.17) min, ranging from 1 to 50 min. We assigned males so that no female was paired with the same male more than once within a reproductive cycle. To minimize stress, individuals were only used in one trial per day and on no more than 2 consecutive days. Trials were monitored and stopped if there was risk of serious injury and all lizards were checked over following the trials. We conducted a total of 112 behavioral trials, with individual lizards participating in 1–8 trials. We excluded 15 trials in which there was no interaction between the lizards (e.g., one of the individuals hid for the duration of the trial), resulting in 97 trials which were used in the subsequent analysis.

We scored male and female behavior from the video footage using J-watcher ver. 0.9 (Blumstein and Daniel 2007). For males, we recorded the number of head-bobs (pronounced nodding movement of the head; “courtship”) and the total duration of bites as a measure of male “harassment.” Given that males bite females on the neck during copulation, we only included the duration of bites prior to copulation. Females signal their unwillingness to mate by fleeing from the male and performing head-bobs, arm-waves (slow, circular rotation of the forelimb), lateral threat displays, and flip-overs. Therefore, we combined the total duration of these behaviors as a measure of female “rejection” intensity (Chan et al. 2009). These were converted to behavior per minute by dividing the duration/frequency by activity time, which was the total duration of the trial minus any time either individual spent hiding beneath the salt crust. In trials where copulation occurred, we also recorded copulation duration.

Male traits

For each male, we measured SVL (to the nearest 0.1 mm), as body size is a known predictor of mating success in multiple lizard species (e.g., Tokarz 1985; Pratt et al. 1992). Relative fighting ability was determined based on the outcomes of male contests performed in a tournament design, where each male was matched against multiple opponents. Contests were staged in a neutral arena and videotaped for 15 min, by which time there was a clear winner and loser. The loser was the male that withdrew from the contest and/or fled from their opponent. The tournament consisted of a total of 78 contests, involving 32 males (29 of which were used in the current study), with each male participating in 4–7 contests. Relative fighting ability scores were calculated based on which males beat and were beaten by which other males using the Bradley-Terry2 package (BTabilities; Firth 2005) in R (R Development Core Team 2010). A more detailed description of these methods is reported elsewhere (McLean and Stuart-Fox 2015).

Statistical analysis

We first examined the intercorrelation among male traits and behavior in male–female interactions using Pearson correlations (PROC CORR SAS ver. 9.3). We tested whether individual male traits (SVL and fighting ability) or male behavior during interactions (courtship and harassment; both per minute) predicted: 1) whether or not copulation occurred, 2) the duration of copulation when it did occur, 3) whether or not females performed rejection behavior, and 4) the intensity of female rejection behavior when it was performed (i.e., the combined duration of arm-waves, head-bobs, fleeing, lateral threat displays, and flip-overs, standardized as behavior per minute) using generalized linear mixed models

(glmer, lme4 package, R; Bates et al. 2015). In all models, SVL, fighting ability, male courtship (number of head-bobs per minute), and male harassment (duration of biting per minute) were the independent variables (predictors). Given the order of magnitude difference between some variables, and the inclusion of interaction terms, all predictors were mean centered and scaled to have a standard deviation of 1. We also included interaction terms between SVL and male harassment, SVL and male courtship, fighting ability and male harassment, and fighting ability and male courtship as we predicted that males may behave differently depending on their size or fighting ability. Additionally, we included 2 random factors, female ID and male ID, in all models to account for repeated use of individuals.

For models 1 and 3 (whether or not courtship and rejection occurred), we specified a binary distribution and a logit link function. For models 2 and 4 (duration of copulation and intensity of rejection, when they occurred), we specified a normal distribution. We examined the probability distribution of the response variables (qqPlot, car package, R; Fox and Weisberg 2011) and log transformed the duration of female rejection behavior per minute (model 4) to meet model assumptions of normality. To determine the best fitting models for each of the response variables, we employed an all subset model selection approach (dredge, MuMIn package, R; Bartoń 2015; total of 256 models per response variable) based on corrected Akaike’s information criterion (AIC_C). Models with AIC_C differences (ΔAIC_C) < 2 are considered to be essentially as good as the best model; however, models with ΔAIC_C values above this threshold should generally not be discounted (Symonds and Moussalli 2001; Burnham and Anderson 2002; Richards 2005). For each response variable, the cumulative AIC_C weights for models with $\Delta AIC_C < 2$ were between 0.41 and 0.49, equating to 41–49% confidence that the best model was included in this subset. Therefore, to increase the probability of retaining the best model, we considered models with $\Delta AIC_C < 4$ (cumulative AIC_C weights = 0.65–0.82; Tables 2–5). From this subset of models, we calculated model-averaged coefficients along with their 95% confidence intervals and measured the relative importance of each variable (RIV) by summing the normalized AIC_C weights across all models in which a given variable was present (Symonds and Moussalli 2001). Finally, we calculated R^2 values for the fixed effects (marginal R^2) and the fixed and random effects combined (conditional R^2 ; Nakagawa and Schielzeth 2013; r.squaredGLMM, MuMIn package, R) to determine the total variance explained by each of the global models, as recommended by Symonds and Moussalli (2001).

RESULTS

We did not detect significant relationships between any of the predictor variables examined (Table 1). Copulation occurred in 43 of 97 (44.33%) trials. The global model for copulation success had a marginal R^2 of 0.983 and a conditional R^2 of 0.983, indicating a very good fit to the data and little variance explained by the random variables (male ID and female ID). Successful copulation was more likely when males performed more harassment behavior. Male harassment was a significant predictor in all models within the top-model set (models with $\Delta AIC_C < 4$; Table 2). The interaction between SVL and courtship also appeared in all of the top models (RIV = 1.00) and was significant in 5/8 models. The relationship was such that increased courtship effort (head-bobs per

minute) decreased the likelihood of successfully copulating for small males, while it did not affect the mating success of large males (Figure 1). Additionally, fighting ability had a high relative importance (RIV = 0.90; Table 2) and was a significant predictor of copulation success in 3/6 models, such that males with higher fighting ability had greater copulation success. However, the parameter estimate for harassment behavior (model-averaged coefficient = 8.246) was an order of magnitude larger than that for fighting ability (model-averaged coefficient = 0.928). Although all remaining interaction terms appeared in models in the top-model set, they had low relative importance (RIV = 0.17–0.41) and were not significant predictors in any of the models.

The global model for copulation duration had a weaker fit to the data with a marginal R^2 of 0.315 and a conditional R^2 of 0.459. When copulation occurred, fighting ability, male courtship, and male harassment (the latter 2 per minute) were the most important predictors of copulation duration (all RIV = 1.00; Table 3). Fighting ability and courtship were significant predictors in 8/9 and 7/9 models respectively, while the relationship between harassment and copulation duration was not significant in any of the models. Therefore, males with higher fighting abilities copulated for longer, while increased courtship effort decreased copulation duration. SVL and the interactions between SVL and courtship, fighting ability and courtship, and fighting ability and harassment all had high relative importance (RIV = 0.78–0.96) but were not significant predictors in any of the top models (Table 3).

Copulation occurred in 20/70 (28.6%) trials in which females performed rejection behavior, as opposed to 23/27 (85.2%) trials in which they did not. The global model for whether or not rejection occurred explained approximately half of the total variance with a marginal R^2 of 0.474 and a conditional R^2 of 0.518. For all of the top models, male courtship was a significant predictor of whether or not females rejected (RIV = 1.00; Table 4), and the relationship was such that males that courted more were more likely to be rejected by females. Just 3 variables (SVL, Courtship, and their interaction) consistently featured in the top-model set for female rejection intensity; however, we were cautious in our interpretation of these results as the global model explained only a small proportion of the total variance with a marginal R^2 of 0.199 and a conditional R^2 of 0.416. The top models indicated that the interaction between SVL and courtship was a significant predictor of rejection intensity (Table 5). Therefore, the effect of male courtship on the intensity of female rejection behavior was dependent on male body size, with courtship increasing rejection intensity when males were large but not when they were small (Figure 2). All other variables were either absent

Table 1
Correlations among male morphological and performance variables and behavior in male–female interactions (29 males in 97 trials)

	SVL	Fighting ability	Male courtship	Male harassment
SVL	—	0.405	0.558	0.055
Fighting ability	0.085	—	0.360	0.018
Male courtship	−0.060	−0.094	—	0.021
Male harassment	−0.196	0.240	0.235	—

Pearson correlation coefficients are below the diagonal and P values are above the diagonal. No relationship were significant after false discovery rate correction for multiple tests (Verhoeven et al. 2005).

from the top-model sets or had low relative importance and were not significant (all RIVs \leq 0.37; Tables 4 and 5).

DISCUSSION

As predicted, males with greater fighting ability were more likely to copulate, and in particular, copulated for longer. This did not appear to be due to female preference because females were no less likely to reject males with higher fighting ability. We found no evidence that males were employing alternative reproductive tactics because male traits were unrelated to their behavior towards females. Specifically, males with higher fighting ability or larger males were no more or less likely to court or harass females. Instead, male fighting ability and harassment behavior independently predicted mating success, suggesting mutually reinforcing selection for male aggression in both male–male and male–female interactions.

The longer copulation time observed for competitively superior males is likely to influence reproductive success. Longer copulations result in greater fertilization in multiple taxa (e.g., Thornhill and Alcock 1983; Andrés and Cordero 2000; Pilastro et al. 2007), including reptiles (Olsson and Madsen 1998; Olsson 2001b), and can influence cryptic female choice (Andrés and Cordero 2000), prevent females from remating (Alcock 1994), or allow time to remove the sperm of rival males (Siva-Jothy 1987) or transfer a larger quantity of sperm (Engqvist and Sauer 2003). This is particularly likely when females store sperm, as is the case for Lake Eyre dragons (Mitchell 1973). Therefore, males with higher fighting ability not only monopolize access to females by defending larger territories (Olsson 1995b), they may also have a higher fertilization rate.

Fighting ability was not associated with differences in male behavior in male–female interactions, and there was no relationship between fighting ability and female rejection behavior, suggesting that females are not showing a preference for males that win contests. This is consistent with the apparent rarity of female choice in lizards (Olsson and Madsen 1995; Tokarz 1995; Olsson and Madsen 1998), including the congeneric species *Ctenophorus fordi* (Olsson 2001a). Instead, harassment behavior (chasing and biting) was strongly associated with an increase in copulation success, which may reflect the greater ability of aggressive males to overcome female resistance. Importantly, however, although harassment increased copulation success in a laboratory setting, a coercive mating strategy may be less successful under natural conditions in the wild. This is because behavioral trials were conducted in a small enclosure, which may restrict the ability of females to flee from males. Nevertheless, the artificial setting of trials would not explain the relationship detected between fighting ability and copulation duration.

Sexual coercion is most commonly used as an opportunistic tactic by subordinate males with limited access to females (reviewed in Wong and Candolin 2005) and there are relatively few examples of dominant males using sexual coercion as their primary mating strategy (e.g., Le Boeuf and Mesnick 1991; Wells et al. 2014). One such species is the brush turkey, *Alectura lathami*, in which dominant, mound-holding males consistently harass females while subordinate males do not (Wells et al. 2014). Wells et al. (2014) suggest that brush turkeys use aggression as their default response to social interactions due to the agonistic nature of most social encounters in the species. Similarly, in the Lake Eyre dragon, it appears that aggression in male–male contests (which frequently escalate to physical combat including prolonged biting) and male–female interactions (in the form of harassment) both increase mating success, thus both contexts generate selection for male aggression.

Table 2
Parameter estimates for each of the top models ($\Delta AIC_C < 4$) for copulation success (whether or not copulation occurred; model 1; $N = 97$)

Copulation success model	Intercept	SVL	FA	Court.	Har.	EA × Court.	FA × Har.	SVL × Court.	SVL × Har.	k	AIC _C	ΔAIC_C	AIC _C weight
1	0.715	1.837	1.110	-7.810	8.010			5.164		8	83.8	0	0.27
2	1.113	2.574	1.017	-7.395	8.423			4.532	2.533	9	84.6	0.8	0.43
3	0.814	1.765	0.888	-7.552	8.066		-0.588	4.918		9	86.1	2.3	0.54
4	0.596	1.930	1.161	-8.126	7.993	0.320		5.432		9	86.2	2.38	0.62
5	1.308	2.529	0.777	-7.091	8.665		-0.620	4.206	2.637	10	86.9	3.11	0.68
6	0.997	2.645	1.074	-7.686	8.390	0.305		4.747	2.518	10	87	3.26	0.73
7	1.925	2.520		-5.724	9.178			3.077	3.316	8	87.4	3.61	0.78
8	1.374	1.287		-5.786	8.132			3.461		7	87.5	3.75	0.82
Model-averaged coefficient	0.961	2.113	0.928	-7.447	8.246	0.052	-0.105	4.730	1.092				
2.5% CI	-1.275	0.194	-0.213	-12.41	3.580	-2.790	-3.679	0.177	-1.242				
97.5% CI	3.444	3.995	2.179	-1.943	13.06	3.347	2.207	9.305	6.916				
RIV	1.00	1.00	0.90	1.00	1.00	0.17	0.18	1.00	0.41				

Predictor variables include: SVL, fighting ability (FA), male courtship behavior per minute (Court.), and male harassment behavior per minute (Har.) as well as interaction terms. All predictor variables were mean centered and scaled to have a standard deviation of 1. For each model, the number of parameters (β), AIC_C, ΔAIC_C , and cumulative AIC_C weight are provided. Model-averaged estimates, along with their 95% confidence intervals (CIs), and the RIVs were calculated based on this subset of models. Variables with a significant ($P < 0.05$) effect on copulation success are in bold.

Table 3
Parameter estimates for each of the top models ($\Delta AIC_C < 4$) for copulation duration (model 2; $N = 43$)

Copulation duration model	Intercept	SVL	FA	Court.	Har.	EA × Court.	FA × Har.	SVL × Court.	SVL × Har.	k	AIC _C	ΔAIC_C	AIC _C weight
1	36.88	0.985	9.047	-12.06	-2.963	-5.120	-5.313	-0.675	1.171	12	367.8	0	0.21
2	36.61	1.139	9.372	-12.07	-3.464	-5.440	-5.149	-0.816		11	368.1	0.32	0.39
3	36.63	1.232	9.132	-12.58	-2.843	-4.704	-5.210		1.191	11	369.7	1.94	0.47
4	34.67	2.865	9.044	-16.11	-2.038		-4.712	4.152	1.472	11	369.8	2	0.54
5	34.88	1.324	8.026	-13.80	-2.369	-4.002	-5.019	1.834	0.590	11	370.2	2.4	0.60
6	36.30	1.476	9.477	-12.70	-3.343	-4.959	-4.411	4.367		10	370.3	2.48	0.66
7	34.16	3.258	9.441	-16.50	-2.630		-4.411	1.772		10	370.4	2.67	0.72
8	34.75	1.402	8.236	-13.82	-2.647	-4.171	-4.817			10	370.6	2.86	0.76
9	36.31		9.194	-12.31	-3.707	-5.188				9	371.4	3.59	0.81
Model-averaged estimate	36.04	1.437	9.062	-13.10	-2.945	-4.157	-4.359	0.592	0.607				
2.5% CI	27.00	-6.714	0.906	-25.01	-10.59	-14.13	-13.24	-13.52	-5.171				
97.5% CI	44.66	9.899	16.89	-1.596	4.842	4.305	3.074	15.74	7.438				
RIV	0.96	1.00	1.00	1.00	1.00	0.84	0.86	0.78	0.53				

Predictor variables include: SVL, fighting ability (FA), male courtship behavior per minute (Court.), and male harassment behavior per minute (Har.) as well as interaction terms. All predictor variables were mean centered and scaled to have a standard deviation of 1. For each model, the number of parameters (β), AIC_C, ΔAIC_C , and cumulative AIC_C weight are provided. Model-averaged estimates, along with their 95% confidence intervals (CIs), and the RIVs were calculated based on this subset of models. Variables with a significant ($P < 0.05$) effect on copulation duration are in bold.

Table 4
Parameter estimates for each of the top models ($\Delta AIC_C < 4$) for whether or not females performed rejection behavior (model 3; $N = 97$)

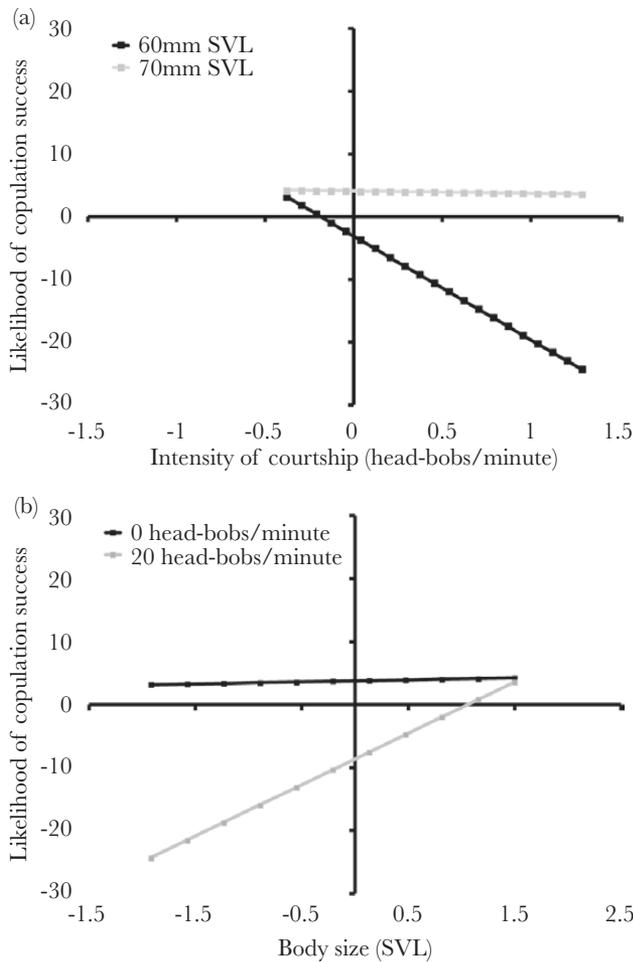
Rejection model	Intercept	SVL	FA	Court.	Har.	FA × Court.	FA × Har.	SVL × Court.	SVL × Har.	k	AIC_C	ΔAIC_C	AIC_C weight
1	1.576			3.351						4	111.4	0	0.19
2	1.561			3.271	-0.270					5	112.4	0.96	0.30
3	1.563		-0.304	3.387						5	112.7	1.23	0.41
4	1.575	-0.223		3.409						5	113.1	1.64	0.49
5	1.557	-0.288		3.334	-0.313					6	113.7	2.27	0.55
6	1.510		-0.168	3.289		1.158				6	114.1	2.68	0.60
7	1.563		-0.231	3.330	-0.221					6	114.1	2.69	0.65
8	1.565	-0.214	-0.302	3.438						6	114.4	2.93	0.69
9	1.739		-0.158	3.575	-0.116		-0.372			7	114.8	3.39	0.73
10	1.529	-0.063		3.207						6	115.0	3.55	0.76
Model-averaged estimate	1.570	-0.062	-0.091	3.352	-0.086	0.075	-0.017	0.034					
2.5% CI	0.713	-0.859	-0.861	0.796	-0.761	-1.439	-0.994	-1.895					
97.5% CI	2.427	0.425	0.439	5.910	0.270	3.770	0.235	3.417					
RIV		0.29	0.37	1.00	0.35	0.07	0.05	0.04	0.00				

Predictor variables include: SVL, fighting ability (FA), male courtship behavior per minute (Court.), and male harassment behavior per minute (Har.) as well as interaction terms. All predictor variables were mean centered and scaled to have a standard deviation of 1. For each model, the number of parameters (k), AIC_C , ΔAIC_C , and cumulative AIC_C weight are provided. Model-averaged estimates, along with their 95% confidence intervals (CIs), and the RIVs were calculated based on this subset of models. Variables with a significant ($P < 0.05$) effect on rejection behavior are in bold.

Table 5
Parameter estimates for each of the top models ($\Delta AIC_C < 4$) for rejection intensity (behavior per minute; model 4; $N = 70$)

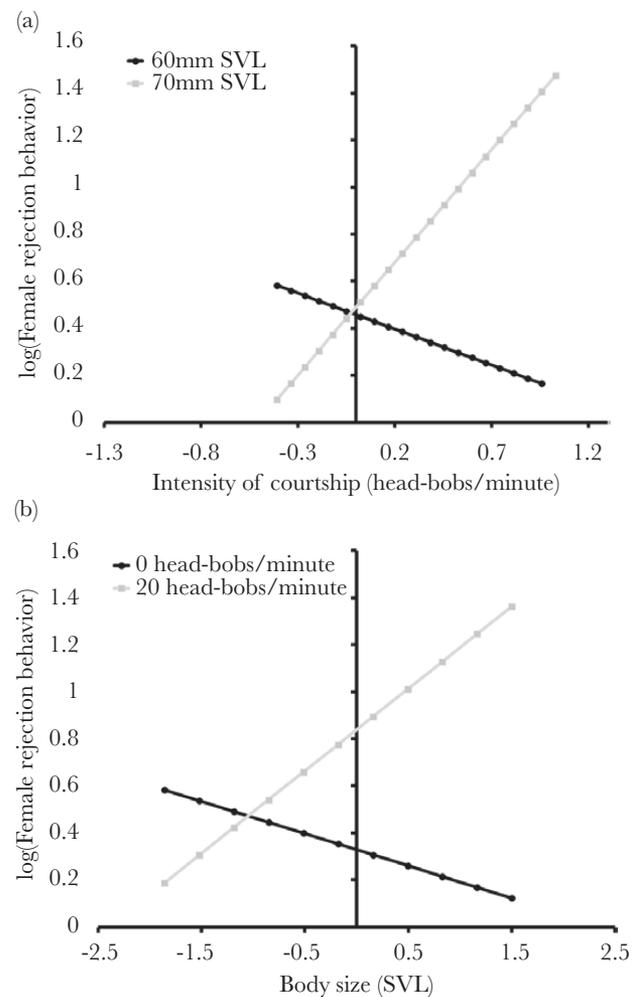
Rejection intensity model	Intercept	SVL	FA	Court.	Har.	FA × Court.	FA × Har.	SVL × Court.	SVL × Har.	K	AIC_C	ΔAIC_C	AIC_C weight
1	0.490	0.017		0.394						7	64.60	0.00	0.41
2	0.491	0.014	0.021	0.390						8	66.90	2.32	0.53
3	0.490	0.018		0.397	0.009					8	67.10	2.53	0.65
Model-averaged estimate	0.490	0.017	0.004	0.394	0.002			0.376					
2.5% CI	0.381	-0.072	-0.072	0.132	-0.101			0.170					
97.5% CI	0.592	0.105	0.114	0.635	0.102			0.584					
RIV		1.00	0.20	1.00	0.18	0.00	0.00	1.00	0.00				

Predictor variables include: SVL, fighting ability (FA), male courtship behavior per minute (Court.), and male harassment behavior per minute (Har.) as well as interaction terms. All predictor variables were mean centered and scaled to have a standard deviation of 1. For each model, the number of parameters (k), AIC_C , ΔAIC_C , and cumulative AIC_C weight are provided. Model-averaged estimates, along with their 95% confidence intervals (CIs), and the RIVs were calculated based on this subset of models. Variables with a significant ($P < 0.001$) effect on rejection intensity are in bold.

**Figure 1**

(a) The effect of male courtship on copulation success dependent on male size (SVL) and (b) the effect of SVL on copulation success dependent on courtship intensity (number of head-bobs per minute). The equation of the slope is: copulation success = $1.026 + 2.087(\text{SVL}) - 7.311(\text{Court.}) + 4.662(\text{SVL} \times \text{Court.})$. SVL and courtship were mean centered and scaled to have a standard deviation of 1.

Copulation duration was shorter when males increased their courtship effort and females were more likely to reject (flee, perform arm-waves, head-bob, lateral threat displays, and flip-overs) males that courted more. Additionally, small males that courted more were less likely to successfully copulate, while this had no effect on the mating success of large males. This is unlikely to be due to female preference for larger males as there was some indication that females increased their rejection intensity towards larger males the more they courted, therefore larger males may again be better able to overcome female resistance. Why, then, do small males court? Firstly, they may be unable to defend a territory that overlaps with female home ranges or to force copulation. Olsson (1995b) suggests that only 16% of male Lake Eyre dragons can successfully defend territories while the remainder are “floaters.” Secondly, courtship effort may influence cryptic female choice and/or maternal investment (Uller and Olsson 2008). Courtship effort is an honest signal of male quality in multiple species (e.g., Knapp and Kovach 1991; Östlund and Ahnesjö 1998). Consequently, females may find courtship effort more attractive than fighting ability (Wong 2004; Stapley 2008), which may influence cryptic female choice. For example,

**Figure 2**

(a) The effect of male courtship on female rejection intensity (behavior per minute) dependent on male size (SVL) and (b) the effect of SVL on female rejection behavior dependent on courtship intensity (number of head-bobs per minute). The equation of the slope is: rejection intensity = $0.490 + 0.016(\text{SVL}) + 0.393(\text{Court.}) + 0.375(\text{SVL} \times \text{Court.})$. SVL and courtship were mean centered and scaled to have a standard deviation of 1.

female flour beetles, *Tribolium castaneum*, bias paternity in favor of males that court more (Edvardsson and Arnqvist 2000). Further work investigating the relationship between male mating success and reproductive output is needed to determine whether cryptic female choice also occurs in Lake Eyre dragons.

In the Lake Eyre dragon, sexual coercion increases the risk of injury to females (Olsson 1995a) and constrains female choice, which is expected to generate sexual conflict over mating (Chapman et al. 2003). However, females may also gain direct or indirect benefits from mating with more aggressive males that counterbalance the costs associated with male harassment (Cordero and Eberhard 2003; Pizzari and Snook 2003; Kokko 2005). Given that male Lake Eyre dragons do not provide resources to females, or parental care, it is unlikely that mating with aggressive males directly benefits females. One possibility is that females gain indirect genetic benefits, such as producing better quality offspring (e.g., Norris 1993) or more aggressive sons that go on to sire more offspring (e.g., Wedell and Tregenza 1999). For example, Head et al. (2005) propose that elevated offspring fitness outweighs the substantial survival costs

associated with mating with more attractive males in the house cricket, *Acheta domesticus*. Importantly, however, theory suggests that it is rare for indirect benefits to outweigh the direct costs of mating (reviewed in Cameron et al. 2003). Therefore, assessment of offspring fitness and reproductive output, in relation to father behavior, is needed to elucidate how this apparently costly mating system is maintained.

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