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Male dwarf chameleons assess risk of courting large, aggressive females

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Conflict between the sexes has traditionally been studied in terms of costs of mating to females and female resistance. However, courting can also be costly to males, especially when females are larger and aggressively resist copulation attempts. We examined male display intensity towards females in the Cape dwarf chameleon, *Bradypodion pumilum*, in which females are larger than males and very aggressive. We assessed whether aggressive female rejection imposes potential costs on males and whether males vary their display behaviour with intensity of female rejection, female size or relative size differences. Males persisted in courtship after initial female rejection in 84% of trials, and were bitten in 28% of trials. Attempted mounts were positively associated with males being bitten. Males reduced courtship with increased intensity of female rejection. Male courtship behaviour also varied with female size: males were more likely to court and approach smaller females, consistent with the hypothesis that larger females can inflict more damage. These results suggest that, in addition to assessing female willingness to mate, male dwarf chameleons may use courtship displays to assess potential costs of persistence, including costs associated with aggressive female rejection, weighed against potential reproductive pay-offs associated with forced copulation.

Keywords: mating costs; sexual conflict; antagonistic coevolution; female rejection

1. INTRODUCTION

Conflict of interest between the sexes has broad-ranging evolutionary consequences for behavioural strategies, mating systems, mate choice and even speciation (Holland & Rice 1998; Parker & Partridge 1998; Gavrilets 2000; Gavrilets *et al.* 2001). When the costs of mating for females outweigh the direct or indirect benefits received, females may evolve strategies to resist attempted copulations because the optimal number of matings for females is generally less than that for males (Parker 1979). In turn, males evolve strategies to circumvent female resistance or rejection, which can lead to an evolutionary arms race (Holland & Rice 1998; Arnqvist & Rowe 2002). Male attempts to circumvent female resistance are often manifested in elaborate means of enticing females to mate, persistent courtship and/or high levels of female harassment and attempted forced copulations (Pilastro *et al.* 2003; Shine *et al.* 2003).

Most studies to date have examined the costs of mating and sexual conflict in terms of costs to the female and the evolution of female resistance strategies (e.g. Watson *et al.* 1998; Stutt & Siva-Jothy 2001; Muhlhauser & Blanckenhorn 2002; Shine *et al.* 2004). However, courtship can be costly for both sexes (Wong & Jennions 2003). Male courtship costs may include direct energetic costs and indirect opportunity costs (e.g. lost foraging opportunities) or increased predation risk, but can also include physical injury, an extreme case of which is sexual cannibalism in certain arthropods (Arnqvist & Henriksson 1997). Owing to costs of mating, males are expected to maximize efforts towards females that will provide maximum reproductive pay-offs, often manifested in a preference for larger females (Werner & Lotem 2003; Wong & Jennions 2003). However, in systems where males are smaller than females and females respond aggressively, courting large females may be risky. Female behaviour may serve not only as a cue to receptiveness, but may also provide cues to potential risk involved in intensifying courtship. This is especially true for taxa, such as dwarf chameleons, in which males vigorously court females, the great majority of mating attempts are resisted and copulation is sometimes coercive (Arnqvist & Rowe 2002; Pilastro *et al.* 2003; Shine *et al.* 2004).

Male dwarf chameleons (*Bradypodion* spp.) assess female willingness to mate by courting every female encountered with vigorous headshakes, lateral displays and approaches. Encounter of a receptive female is rare as these chameleons have asynchronous reproduction, are live-bearing with long gestation (approximately three months) and at any one time, 40–80% of females are gravid (Burrage 1973). Females are receptive only for short periods when recently ovulated, and they store sperm, reducing the need to mate after each litter is born (Burrage 1973). Unlike some egg-laying chameleons (Cuadrado 2000), female *Bradypodion* spp. show no change in coloration with receptive state or when gravid. Thus, males must assess female willingness to mate with courtship displays and, in the great majority of cases, females respond with aggressive rejection behaviours, including violent swaying, open mouth threat displays, chasing and biting (Burrage 1973; D. M. Stuart-Fox, personal observation). Females are larger than males, although males do sometimes attempt forced copulations, which can result in injury to the male when the female responds aggressively by biting (Burrage 1973; D. M. Stuart-Fox, personal observation). In the wild, biting results in skin abrasions and scarring as well as more serious injury such as surface wounds (Burrage 1973; D. M. Stuart-Fox, personal observation).

Here, we examine male display intensity towards females in the Cape dwarf chameleon, *Bradypodion pumilum*, to assess whether males vary their display behaviour according to potential costs associated with female resistance. Specifically, we asked the following questions. (i) Is female rejection potentially costly to males? (ii) Does male display behaviour vary with

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Table 1. Description of male and female chameleon behaviours.
(Mean, standard error (s.e.) and range (raw counts) of each behaviour performed per trial.)

sex	behaviour	description	mean ± s.e.	range
male	headshake	short, rapid, discrete side-to-side shakes of the head, usually combined with bright coloration and body laterally compressed	39.14 ± 2.24	0–146
	headshake-approach	as above, but including approach of female	18.55 ± 1.77	0–118
	grab/attempt mount	precedes mounts: the male grabs the female's torso	0.21 ± 0.04	0–4
	mount	male on female's back, holding the female, the male attempts to wrap his tail around the female's tail base for hemipene insertion	0.03 ± 0.01	0–1
female	LC	laterally compressed combined with dark or contrasting coloration	0.82 ± 0.10	0–8
	LCS	as above and swaying/rocking from side to side (often rapidly/violently)	1.03 ± 0.10	0–7
	LCSO	as above, combined with open mouth threat	3.14 ± 0.21	0–12
	aggressive approach	approaching the male while displaying LCS or LCSO or chasing the male with open mouth threat	1.65 ± 0.13	0–8
	bite	biting the male	0.55 ± 0.09	0–10
	initiate	the female initiates the interaction with a rejection behaviour	0.19 ± 0.03	0–1

female aggressive rejection behaviour? (iii) Does male display intensity vary with female size or relative size difference between males and females?

2. MATERIALS AND METHODS

(a) *Study system*

We captured adult Cape dwarf chameleons by hand from the Stellenbosch region, South Africa (33°56′S, 18°52′E) during April 2003, over-wintered them to ensure females were not recently mated and conducted experiments the following Spring (21 September–6 November 2003). They were subsequently (November 2003) released at their site of capture. Males were housed individually and females in same-sex pairs in enclosures (40×40×80 cm) with a live shrub. Enclosures were in constant temperature (CT) rooms with Osram L36W/72-965 Biolux fluorescent lights and day–night light and temperature cycles approximating (or slightly warmer than) their natural environment (April–May: day 28 °C 13 h, night 15 °C; June–August: day 23 °C 12 h, night 10 °C; September–November: day 28 °C 14 h, night 15 °C). Chameleons were misted daily and fed on live gut-loaded crickets three times per week.

(b) *Experimental design*

Snout–vent length (SVL, mm) was measured at the beginning and end of the trial period and the mean used to represent size at the time of the experiments. The sizes (mean SVL ± s.e.) of individuals used in this study were: female 83.5 ± 1.7 mm, range: 66.8–96.8 mm, $n = 21$; male 79.6 ± 1.4 mm, range: 73.7–88.7 mm, $n = 13$. We avoided using very small males to maximize the probability of males consistently displaying to females. In natural populations, females are on average 112% of male size ($n = 65$ males, 86 females; Burrage 1973).

Trials were conducted in an arena (60×20×50 cm) with a horizontal dowel stick fixed lengthwise (60 cm) 30 cm above the floor as a perch and two vertical dowel sticks at 15 cm from either end, joined to the horizontal perch. The arena was in a CT room under the same conditions described above: 28 °C is slightly higher than the mean but within the range of active body temperatures in the field (mean = 22.4 °C, range = 3.6–39 °C; Burrage 1973). A male was placed at one end of the perch and a female at the other, then the two were allowed to interact. Contests were observed from outside the room through a small glass window in the door, and male and female behaviours (table 1) noted. Males display using short, rapid shakes of the head, which can easily be counted. Female behaviours, such as swaying (S) with mouth open (O) and body laterally compressed (LC), tend to be continuous—therefore we counted the number of discreet bouts (separated by > 5 s).

Each of 13 males was presented with 20 or 21 females over the course of six weeks, enabling us to assess whether the same male varied display behaviour towards females depending on female size or rejection behaviour. We conducted seven trials a day between 09.00 and 12.00 h. Thus females were presented with a male every 3 days (three sets of seven randomly chosen females used on a rotating basis) and males were used on average every second day and never twice on the same day. We randomized the order of presentation of the females to each male to account for the possibility that males may alter courtship investment based on the female they saw last (Wong *et al.* 2004). Interactions lasted 7 min. Pilot experiments had shown that within 7 min (almost always less), males had stopped displaying and retreated when females showed clear rejection displays, or else attempted to mount.

(c) *Statistical analysis*

We tested whether males differed in their display rate towards females depending on female aggressive behaviour, size or relative size difference using a general linear mixed model (PROC MIXED in SAS v. 9.1) with repeated statement (female ID). This analysis takes proper account of dependency (correlated error structure) of responses of individual males (subjects) to the same set of females (Littell *et al.* 1998). Explanatory variables were male SVL, female SVL, the difference between male and female SVL and the frequency of each female behaviour (table 1). Counts of male and female behaviours were log-transformed to meet model assumptions. We employed stepwise model selection with a criterion for retaining a variable within the model of $p < 0.1$.

Eleven of the 13 males displayed consistently. The other two males displayed in less than 20% of trials so data for these individuals were discarded on the basis that they were unresponsive. One of the males was hyper-aggressive and attacked females (as in male–male interactions) in 11 trials, rather than performing courtship displays. These trials were discarded, reducing sample size for this male to nine. Five trials were terminated (to prevent insemination) after 2 min owing to successful mounting and were also discarded. Overall, 205 trials were retained for statistical analysis.

3. RESULTS

Males persisted in courtship after initial female rejection (see table 1 for a list and definition of female behaviours) in 84% of trials. Male courtship (number of headshakes) was significantly positively associated with the number of female rejection displays (lateral display with contrasting coloration, swaying and open month threat, LCSO) and lack of female initiation of the interaction (table 2). Male courtship with approach was negatively associated with female size (SVL) but positively associated with the least aggressive type of female rejection behaviour (lateral display with contrasting coloration, LC) and lack of female aggressive initiation (table 2). Thus, males were more willing to court and approach females that were smaller, displayed only mild rejection behaviour and/or did not initiate aggressively. Increased courtship towards smaller females was not owing to smaller females being less aggressive: female size was

Table 2. Factors associated with male courtship.
(Effects of male and female size (SVL), difference in SVL and female rejection behaviours (LC, LCS, LCSO, aggressive approach, bite, initiate) on male display behaviour (headshake, headshake approach, grab/attempt mount). Only variables retained after stepwise selection are presented. All three models met convergence criteria and were significantly better than the null model (null model likelihood ratio test: $p<0.000\,1$ for all three models). The factor 'initiated' is binary therefore the coefficient estimate is for initiated = 0, that is, when the female did not initiate aggressively.)

dependent variable	factor	coefficient estimate	$F_{\text{d.f.}}$	p
headshake	LC	0.241	$2.87_{1,192}$	0.092
	LCSO	0.41	$17.16_{1,192}$	<0.000 1
	initiated (0)	0.494	$27.73_{1,10}$	0.000 4
headshake-approach	♀ SVL	−0.023	$15.32_{1,191}$	0.000 1
	LC	0.447	$6.12_{1,191}$	0.014
	initiated (0)	0.469	$15.54_{1,10}$	0.003
grab/attempt mount	aggressive approach	−0.126	$18.66_{1,191}$	<0.000 1
	bite	0.231	$32.00_{1,191}$	<0.000 1
	initiated (0)	0.062	$7.79_{1,10}$	0.019

uncorrelated with female aggressive behaviour (Pearson correlation: LC $r=-0.19$, $p=0.42$; LSC $r=-0.01$, $p=0.98$; LCSO: $r=-0.09$, $p=0.69$; aggressive approach: $r=-0.15$, $p=0.52$; bite: $r=-0.18$, $p=0.44$; initiated: $r=-0.35$, $p=0.12$; $n=21$ females). Number of male attempted mounts was negatively associated with female aggressive approaches and positively associated with female biting and lack of female aggressive initiation (table 2). That is, males were less likely to try to mount females if females approached aggressively or initiated the interaction with an aggressive display and females tended to respond to males attempting mounts by biting. Males were bitten in 58 out of 205 trials (28%).

We observed mounting (as opposed to grabbing/attempted mounting) in only 11 trials (5.4%), 5 of which (2.4%) were successful. In the unsuccessful attempts, females struggled and bit, whereupon the male retreated. Although in three cases females showed some rejection behaviours, in none of the five trials with successful mounts did females initiate aggressively, bite the male or approach the male aggressively.

4. DISCUSSION

Our results show that male dwarf chameleons vary their courtship intensity with intensity of aggressive female rejection, which is potentially costly to males. In the great majority of trials, males persisted in courtship after females displayed initial rejection, suggesting that males are not only assessing female receptive status. As a result of male persistence, female rejection almost always intensified, often to the point of biting (28% of trials). Males were bitten during all unsuccessful mounts, whereupon they would invariably retreat. In addition, male dwarf chameleons courted less and attempted to mount less frequently if females initiated with aggressive rejection and/or approached aggressively with open mouth threat. Conversely, males were more likely to court and approach females when females displayed the least aggressive rejection behaviour. That males consistently varied courtship behaviour with the intensity of female rejection suggests that males assess costs associated with female aggressive rejection in courtship decisions.

Male courtship behaviour also varied with absolute female size: males of all sizes were more likely to headshake and approach smaller females; a behaviour that always preceded attempted mounting. That males increased courtship intensity towards smaller females may appear paradoxical at first, given that larger females have larger litters (Burrage 1973). This result is also contrary to the findings of previous studies showing increased male courtship intensity or male preference for larger females (e.g. Shine *et al.* 2001; Werner & Lotem 2003); however, in these studies, females were not reported to dominate or inflict injury on males. In dwarf chameleons, large females may be able to inflict more damage through biting than small females, for males of any size. Thus, absolute rather than relative female size may reflect potential cost of injury to the male. Males retreated in all 58 trials in which females bit males, regardless of whether the male was larger. As courting large females may be riskier, male dwarf chameleons may be more willing to approach, persist in courtship and attempt copulation with smaller females.

In systems where females store sperm, males may gain reproductive pay-offs from forced copulation, even when females are not receptive. Males must weigh such potential reproductive pay-offs against potential costs. Male decisions on whether to intensify or abandon courtship after females show initial rejection are probably a complex function of multiple types of cost such as metabolic costs, opportunity costs and increased predation risk (Wong & Jennions 2003). Our results suggest that the risk of injury from aggressive female rejection may also represent an underappreciated cost of courtship for males of some species. This study highlights the need to not only consider female mating costs and resistance strategies in studies of sexual conflict, but also trade-offs in male mating decisions, including potential costs of aggressive female rejection.

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