Female's courtship threshold allows intruding males to mate with reduced effort

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Female decision rules can influence the nature and intensity of sexual selection on males, but empirical demonstrations of rules underlying choice are rare. We hypothesized that female choice is largely based on a courtship duration threshold in the Australian redback spider (*Latrodectus hasselti*) because females kill males before copulation is complete (premature cannibalism) and reduce their paternity if courtship is brief. We used published data to infer that the female's threshold is approximately 100 min of courtship. We support this hypothesis by showing that premature cannibalism is common when the male's courtship duration is below this threshold, but is infrequent and unrelated to duration once courtship exceeds the threshold. We then ask whether females discriminate the source of courtship when rival males compete, as this will determine the effect of the threshold on male competitive tactics. We staged competitions where 'resident' males initially courted females in the absence of competition, exceeding the courtship threshold before 'intruding' males were introduced. Intruding males mated rapidly but were not prematurely cannibalized by females, in contrast to cases where competition starts before the threshold is surpassed. This suggests females do not distinguish which male satisfies the threshold, allowing intruders to parasitize the courtship efforts of residents. To our knowledge, such exploitation of mating efforts by rival males mediated by a female choice threshold has not been demonstrated elsewhere. Ironically, this female choice threshold and the attendant possibility of courtship parasitism may lead to selection for lower-quality males to recognize and seek out (rather than avoid) webs in which competitors are already present.

Keywords: sexual selection; male–male competition; residency; mate choice; threshold; cannibalism

1. INTRODUCTION

Male mating success can depend on traits that increase success in combat or scramble competition, such as condition, weaponry or body size (Huntingford & Turner 1987). However, context may also affect male success, and such effects may be independent of or interact with phenotypic traits such as size. One important contextual determinant of success is residency status; this can be important in systems where 'intruding' males may attempt to mate with females with which a 'resident' male is currently associated (Davies 1978; Krebs 1982; Otronen 1984; Thornhill 1984). In some cases, resident males may be more likely to win contests regardless of differences in phenotypic traits such as size (Maynard Smith & Parker 1976; Hammerstein & Parker 1982; Leimar & Enquist 1984; Enquist & Leimar 1987; Grafen 1987). In the majority of studies of residency effects, males defend territories or females directly, but competition is temporally displaced from courtship behaviour and mating. In these systems, residents that win in competition are left with exclusive access to females and their mating success increases (e.g. Kruse & Switzer 2007; reviewed in Kemp & Wiklund 2001). In some systems, however, courtship and competition occur simultaneously (Baker 1983; Uzendowski *et al.* 1993; Tauber & Eberl 2002; Wong 2004; Stoltz *et al.* 2008). There may

be drastic changes in courtship during competition (e.g. atypical courtship, Baker 1983; alteration of courtship songs, Tauber & Eberl 2002; reduction in courtship effort, Wong 2004; Stoltz *et al.* 2008) and this can affect female choice when courtship is used to assess males. Female mate choice may thus be influenced by the process of male–male competition. Interactions between choice and competition can have important consequences for the evolution of male traits (reviewed in Hunt *et al.* 2009). In many systems, understanding how female preferences are affected by the interplay between residency, male phenotypic traits and courtship effort is critical for understanding selection on male traits in nature (Hunt *et al.* 2009).

Effects of residency on female mating patterns may depend on decision rules used by females and how these relate to courtship. Two of the most commonly examined decision rules for female choice are sample-based ('best of *n*') and threshold-based rules (Janetos 1980; Wittenberger 1983; Real 1990; Valone *et al.* 1996; Wiegmann *et al.* 1996). Sample-based decisions are comparative and require assessing a number of potential mates, the best of which is then chosen for copulation (Valone *et al.* 1996). In contrast, under threshold rules, any potential mate that exceeds the female's threshold is acceptable, and this criterion does not depend on whether others of higher quality may be available (Valone *et al.* 1996). Thus, while best-of-*n* rules should yield directional selection on male phenotypes, threshold

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rules may be more likely to give rise to stabilizing selection (Wiegmann *et al.* 1996). Moreover, male mating success may be more strongly linked to residency when females use thresholds rather than best-of-*n* rules, as any resident male exceeding the threshold will be an acceptable mate.

We hypothesized that such scenarios may have a different outcome when courtship and competition occur simultaneously (e.g. Wong & Candolin 2005; Stoltz *et al.* 2008, 2009; Hunt *et al.* 2009). If females do not discriminate the source of stimulatory courtship signals, threshold criteria may allow males to exploit courtship effort of rivals. Threshold criteria could then lead to reduced selection on male traits that are normally important for mating success. Such exploitation was suggested in red spotted newts (*Notophthalmus viridescens*), where males may intercept receptive females from courting rivals, but this report is anecdotal and females' decision rules are unclear (Verrell 1982). While there are documented examples of cooperative courtship behaviour (e.g. in birds: McDonald & Potts 1994; Lank *et al.* 2002; Krakauer 2005; Cockburn *et al.* 2008) and 'sneaker' male tactics with minimal courtship (Parker 1990; Taborsky 1998), threshold-based exploitation would differ in that (i) parasitic males would not necessarily expend courtship effort and would decrease (rather than increase) the fitness of their rival, and (ii) the success of the sneaking tactic would be a step function, dependent on whether the threshold had been satisfied by a resident.

Thresholds are either rare in nature or difficult to demonstrate (Valone *et al.* 1996; but see Ivy & Sakaluk 2007; Parri *et al.* 1997). However, threshold decision rules of choosy females (e.g. Parri *et al.* 1997) may allow exploitation by rival males in spiders. In redback spiders (*Latrodectus hasselti*), rival males compete by simultaneously courting the female, and several observations suggest a courtship duration threshold may be an important basis for female choice. Courtship duration may reflect male quality (see Knapp & Kovach 1991; Tregenza *et al.* 2006; Stapley 2008; Kasumovic *et al.* 2009) as courtship occurs after a period of mate searching during which almost 90 per cent of males die owing to predation and depleted energy reserves (Andrade 2003). Males typically do not contact females or attempt mating until at least 2 h of courtship are completed, despite the risk that rivals may arrive and usurp their mate (Forster 1995; Andrade 1996). In addition, although some males copulate after relatively brief courtship, females employ two cryptic mechanisms that decrease paternity of these males (e.g. Stoltz *et al.* 2008, 2009; see Snow & Andrade 2005). First, there is an inverse relationship between the courtship duration of the first male to mate and the number of copulations the female accepts from a rival (Snow & Andrade 2005; Snow *et al.* 2006; Stoltz *et al.* 2009). Second, females often kill and cannibalize smaller, rapidly copulating males prior to completion of a normal mating (premature lethal cannibalism; Stoltz *et al.* 2008), which reduces paternity by 50 per cent under sperm competition (Snow & Andrade 2005; see also Prenter *et al.* 2006). In contrast, larger, longer-courting males mate normally. Thus, female choice is apparently linked to courtship effort as well as male size (Stoltz *et al.* 2008, 2009; see also Prenter *et al.* 2006), and selection imposed by females may have resulted in males that

attempt mating only after satisfying the female's threshold duration of courtship.

In this study, we use published data (Stoltz *et al.* 2008, 2009) to derive a putative courtship duration threshold for female choice in redback spiders. We then test whether premature lethal cannibalism (i.e. female cryptic choice *sensu* Eberhard 1996) depends on this threshold by comparing female responses to males that attempt mating before or after the threshold is reached. Next, we investigate whether intruding males can exploit the reproductive effort of resident males that have met the courtship demands of females. We predict that (i) whereas courtship duration will determine female responses below the threshold, there will be no relationship between duration and premature cannibalism once courtship exceeds the threshold (e.g. a step function in female discrimination); (ii) premature cannibalism of mating males will be less frequent if mating occurs after residents court past the estimated threshold, compared with contexts in which mating is first attempted before the courtship threshold is reached; and (iii) once a resident meets the courtship duration threshold, intruding males that rapidly 'sneak' copulations will not suffer the female-imposed penalties documented when there is no period of resident courtship (Stoltz *et al.* 2008, 2009).

2. MATERIAL AND METHODS

(a) Study animals

Spiders were from an outbred laboratory population of *L. hasselti* started with spiders collected from Sydney, Australia in 2007. Spiderlings were reared communally until the fourth instar, after which they were housed in separate cages (Amacs Plastics Products Ltd) to ensure that they had not mated at the time of trials (males mature at the fifth instar, females at the seventh to eighth instar). The spiders were kept in a temperature-controlled room at 25°C and 12:12 light:dark cycle. Males were fed fruit flies (*Drosophila* sp.) twice a week and females were fed crickets (*Acheta domesticus*) once a week. All trials were conducted under the dark cycle illuminated by red light as *L. hasselti* are nocturnal.

(b) Mating trials

Females that had matured within the previous two months (females survive for up to 2 years in the laboratory; Andrade & Banta 2002) were placed in mating arenas (35 × 30 × 15 cm) for 48 h and allowed to build webs on metal frames prior to the introduction of males. Trials were 6 h in length and filmed using Panasonic low light black and white cameras (WV BP330) with macro zoom lenses (Navitar Macro-Zoom 7000) and JVC Professional Super VHS recorders (SR-TS1U). Male spiders were weighed (Ohaus Explorer electronic balance), leg lengths were measured (mean patella + tibia of both front legs) and males were marked with a small spot of non-toxic paint on the dorsal side of their abdomen (BioQuip Products, Inc.) 1 h prior to a trial. Males were briefly anaesthetized with CO₂ for less than one minute prior to paint marking.

In our trials, one lone male (resident) was allowed to court a female for a period that approached the proposed courtship duration threshold (see below). We then introduced a rival (intruder) that was relatively larger, size-matched or relatively smaller than the resident. Crossing relative size with residency status was intended to allow us

to determine whether these factors or some interaction affected female choice, since relative size had previously been identified as an important variable (Stoltz *et al.* 2008, 2009). Pairs of males of similar weight (mean weight difference = 0.17 mg, 3.4% of mean body weight; $n = 22$) or different weight (mean weight difference = 2.97 mg, 67.4% of mean body weight; larger intruder male $n = 20$, smaller intruder male $n = 20$) were randomly chosen from among all males that matured within the previous 14 days.

(i) *Estimating and applying the courtship duration threshold*

To derive a putative courtship duration threshold for female choice we used a logistic regression on data from a previously published study (Stoltz *et al.* 2008). In this study, size-mismatched rival males were simultaneously paired with a female and the first male to mate was less likely to be prematurely cannibalized if he courted for a longer period of time prior to the first copulation (Stoltz *et al.* 2008). A binary logistic regression relating the occurrence of premature cannibalism (dependent variable) to courtship duration prior to the first copulation (independent variable) was significant (model $\chi^2 = 5.145$, $n = 27$, d.f. = 1, $p = 0.023$; figure 1):

$$\ln\left(\frac{p}{1-p}\right) = B_0 + \text{Court}, \quad (2.1)$$

where p is the probability of premature cannibalism, $B_0 = 1.002$ and Court the courtship duration (min).

To estimate the courtship threshold for choice, we identified the inflection point of the logistic curve (see Emlen 1996; Andrade 1998; Hosmer & Lemeshow 2000), where the outcome predicted by the model shifts between categories (premature cannibalism versus no premature cannibalism). To do this, we set the p -value to 0.5 and found Court = 100 min. Two s.d. on either side of this putative threshold value (83–125 min) captures 95 per cent of the variance in this estimated courtship duration threshold (figure 1). The model predicts premature cannibalism by females is likely when courtship duration is shorter than this threshold and correctly predicts 88 per cent of the occurrences of premature cannibalism in the published dataset (Stoltz *et al.* 2008).

In our test of this threshold, each trial began when a randomly chosen (resident) male was introduced to the web from a dragline at the furthest point from the female. These males would commence phase one of courtship, which is comprised of exclusively web-based vibrations and no direct contact with the female (Forster 1992, 1995). Phase one typically lasts about 150 minutes from when one male courts in isolation (Forster 1995; Stoltz *et al.* 2008) to when the male contacts the female's abdomen (Forster 1995; Stoltz *et al.* 2008). We allowed residents to complete phase one before introducing a rival as this ensured courtship duration approached or exceeded the proposed threshold before the initiation of competition. Thus the second male (intruder) was placed on the web via a dragline immediately after the resident male contacted the female's abdomen. When single males are courting, this contact marks the start of the second phase of courtship, which usually includes a combination of vibratory behaviour on the female's abdomen and on the web. During the third phase of courtship, males typically remain on the female's abdomen and attempt copulation (see Forster 1995 for more details).

We noted total courtship duration prior to mating, the occurrence of premature cannibalism by females, which

Figure 1. Frequency histogram showing the relationship between premature cannibalism (yes = black, no = grey) and total courtship duration in redback spiders (data from Stoltz *et al.* 2008; $n = 27$). A logistic regression predicts females are unlikely to prematurely cannibalize males that attempt mating if total courtship exceeds 100 min (bold vertical line; dotted lines = 95% confidence interval). Average total courtship duration prior to the first copulation is also indicated on the x -axis for single males (black triangle; adapted from Stoltz *et al.* 2008), competing males introduced simultaneously (grey triangle; adapted from Stoltz *et al.* 2009) and competing males in which a resident courts prior to introduction of a rival (white triangle; this study).

male(s) mated and the number of copulations achieved by each male. In redbacks, a normal mating comprises two copulations (Forster 1995; Andrade 1998). During each copulation, the male deposits a sperm plug in one of the female's two sperm storage organs (Snow *et al.* 2006). Males that copulate twice can achieve close to 100 per cent paternity under sperm competition, but males that mate only once (i.e. due to premature cannibalism) will attain a maximum of 50 per cent paternity when sperm from the two organs mix at fertilization (Snow & Andrade 2005; Snow *et al.* 2006).

(c) *Analysis*

To test the threshold hypothesis, we compare results of these residency trials to results of previously published trials on the same laboratory population of spiders. In those trials, size-matched or size-mismatched rival males were introduced to females' webs simultaneously, and thus the putative courtship threshold was not reached prior to the initiation of competition (Stoltz *et al.* 2008, 2009). This is justified because procedures for both experiments were identical with the exception of the timing of introduction of the rival males. We also compare our new data to trials in which single males court females (Stoltz *et al.* 2008) as this provides a baseline for understanding female responses to male courtship in the absence of competition.

Statistical analysis was performed using SPSS v. 13.0 or online statistical software (www.graphpad.com for contingency tests). Data that violated the assumption of a normal distribution were log transformed. If the log-transformed data did not produce a normal distribution, non-parametric statistics were used. Statistical tests are two-tailed with

mean $\pm$ s.e. reported. Sample sizes vary for some tests because behavioural details were missed in some trials.

We ensured there was no bias in the females selected for the study. The weight of the females was similar whether the resident was size-matched to the intruder (292.17 ± 11.55 mg), was the larger male (279.56 ± 18.55 mg) or was the smaller male (276.73 ± 13.26 mg; $F_{2,59} = 0.33$, $p > 0.05$).

3. RESULTS

The time of first contact with the female's abdomen by the resident (i.e. the time at which we introduced the intruding male) was after 75 ± 6 min. of courtship, regardless of the relative size of the competitor ($F_{2,58} = 0.67$, $p = 0.52$). In addition, regardless of the relative size of competitor ($F_{2,53} = 0.98$, $p = 0.38$), the first copulation occurred approximately 2 h after the start of the trial ($F_{2,53} = 0.98$, $p = 0.38$), well above the 95% confidence interval for the estimated choice threshold (figure 1).

(a) Evidence for a courtship duration threshold

To test our threshold hypothesis we asked whether premature cannibalism depended on courtship duration when competition interrupted courtship before the threshold was reached (males introduced simultaneously; data from Stoltz *et al.* 2008, 2009), but was independent of courtship duration when females experienced a period of exclusive courtship exceeding the threshold (these trials and single-male matings; data from Stoltz *et al.* 2008). We used a separate logistic regression examining premature cannibalism of the first male to mate (dependent variable) as a function of courtship duration, male size and the context of competition (i.e. no competition, Stoltz *et al.* 2008; simultaneous competition, Stoltz *et al.* 2008, 2009; or competition after a residency delay, current study). Male size had no effect but there was a significant interaction between courtship duration and context of competition (Wald = 4.47, $p = 0.03$; figure 2). This arises because the occurrence of premature cannibalism for lone males and simultaneously introduced competing males was negatively related to total pre-copulatory courtship duration (Stoltz *et al.* 2008, 2009), but, as predicted, there was no effect of total courtship duration when mating occurred after a resident had satisfied the estimated courtship threshold (log $t_{53} = 0.15$, $p = 0.88$; figure 2).

Second, regardless of residency, size or courtship duration (figure 3), the first male to mate achieved more copulations than his rival in 64 per cent (36/56) of cases, and equalled his rival in 34 per cent of cases across all trials (compared with only one case where the rival copulated more often than the first male to mate; Wilcoxon signed-rank test for related samples: $Z = -5.31$, $p < 0.001$). Females typically mated once or twice with the first male to mate (mean $\pm$ s.e. number of copulations = 1.39 ± 0.07) and often did not mate at all with his rival (mean $\pm$ s.e. number of copulations = 0.43 ± 0.08). The effect is still strong if the data are separated according to the relative size of competitors (matched: $Z = -2.961$, $p = 0.003$; mismatched: $Z = 4.42$, $p < 0.001$). Overall, residents were more likely to achieve the first copulation, but this

Figure 2. Relationship between total courtship duration prior to the first copulation by either male and whether males were prematurely cannibalized (black bars) or not (grey bars) across different competitive contexts (no competition, Stoltz *et al.* 2008; when a competitor is simultaneously introduced, Stoltz *et al.* 2008, 2009; or if the rival was introduced after a delay, current study).

Figure 3. Duration of courtship following rival introduction as a function of the size and residency status of the first male to mate. First-mating males were smaller residents (SR) or intruders (SI), larger residents (LR) or intruders (LI), or size-matched residents (MR) or intruders (MI).

result was driven by trials in which smaller males were residents (table 1).

(b) Exploitation of reproductive effort of residents by intruding males

Although premature cannibalism is unrelated to total courtship duration in the resident–intruder trials, this is not because all males provided an extended courtship. Rather, intruder males invested very little in courtship. Copulation by the first male to mate occurred after an extremely brief courtship if that male was an intruder rather than a resident in the matched-size treatment (log $t_{18} = 2.12$, $p = 0.05$; figure 3). Similarly, smaller intruding males in mismatched trials tended to copulate sooner than larger residents (log $t_{15} = 1.91$, $p = 0.08$; figure 3), although larger intruding males did not show this effect (log $t_{17} = 0.32$, $p = 0.75$; figure 3).

Table 1. Proportion of male redback spiders that obtained the first and second copulations in competitive trials as a function of their residency status and relative size.

relative size of resident	copulation	status of copulating male		copulation did not occur	statistic	p-value
		resident	intruder			
all pooled	first	64% ($n = 36$)	36% ($n = 20$)	6	$\chi^2 = 4.57$	0.03
	second	58% ($n = 21$)	42% ($n = 15$)	26	$\chi^2 = 1.00$	0.32
smaller	first	74% ($n = 14$)	26% ($n = 5$)	1	$\chi^2 = 4.26$	0.04
	second	64% ($n = 7$)	36% ($n = 4$)	9	$\chi^2 = 0.82$	0.37
larger	first	59% ($n = 10$)	41% ($n = 7$)	3	$\chi^2 = 0.53$	0.47
	second	45% ($n = 5$)	55% ($n = 6$)	9	$\chi^2 = 0.09$	0.76
matched	first	60% ($n = 12$)	40% ($n = 8$)	2	$\chi^2 = 0.8$	0.37
	second	64% ($n = 9$)	36% ($n = 5$)	8	$\chi^2 = 1.14$	0.29

Given that small intruders mate without significant investment in courtship, we examined how residency and size affected the likelihood of premature cannibalism of first-mating males by females. If females favour the individual male that satisfied the courtship threshold, residents should have lower rates of premature cannibalism. However, size-matched males that mated first were no more likely to be cannibalized prematurely when they were residents (2/12 cannibalized) than when they were intruders (3/8 cannibalized; likelihood ratio = 1.01, d.f. = 1, $p = 0.3$). Similarly, in size-mismatched trials, there were no significant effects of size, residency or interactive effects on the likelihood of premature cannibalism of the first-mating male (logistic regression model $\chi^2 = -23.546$; d.f. = 3, $p = 0.058$; interaction t -ratio = -0.022 , $p = 0.982$). Moreover, despite the fact that they provided very brief courtship (figure 3), smaller intruding males that mated first were never cannibalized by females (0/7 trials).

4. DISCUSSION

We show that female redback spiders use threshold-based mate-choice decisions based upon the duration of courtship provided, and intruding males can parasitize the courtship efforts of residents once courtship demands of females are met. Intruding males are able to mate with females after providing extremely brief courtship (figure 3), and first-mating males are not penalized by premature cannibalism (figure 2) since the courtship threshold has been surpassed by resident males. Thus females apparently do not distinguish which male is the source of stimulatory courtship. We identify the threshold as approximately 100 min of courtship, after which the likelihood of premature cannibalism is decreased (figure 1). These results show that, although the ability to provide a prolonged courtship is typically important to male success, the female's mate-choice mechanism is susceptible to circumvention of this requirement by smaller males.

In redback spiders, male competition greatly affects courtship, and the context in which competition occurs can influence cryptic female choice. In the absence of competition, female response to males depends on courtship duration and females limit paternity of rapidly mating males through premature lethal cannibalism (Stoltz *et al.* 2008). When competition and courtship occur simultaneously, mating occurs well before the

lower limit of our predicted courtship threshold for choice (figure 1; see Stoltz *et al.* 2008, 2009), and females respond by limiting male mating opportunities with a severity that depends on courtship investment (Stoltz *et al.* 2008, 2009). In contrast, this study shows that when a resident male courts for a period approaching the putative threshold, female penalization of males (premature cannibalism, decreased mating frequency) is no longer predicted by courtship duration (figure 2). Instead, intruding males can mate rapidly, and, regardless of which male provided the initial courtship, premature cannibalism is rare (figure 2). The first male to mate almost always equals (34% of trials) or exceeds (64% of trials) the mating frequency of his rival (total: 98% of trials). This means that intruders can parasitize the courtship effort of residents by mating rapidly without penalty (figures 2 and 3). Thus, males unlikely to surpass a threshold may do better if they seek a parasitic association with another male. Effectively, this means that there may be selection for smaller males or those in poor body condition to seek out, rather than avoid, competitive situations in nature. This may explain previous studies that show clustering of males with relatively few females despite the availability of other receptive females that remain uncontested (e.g. Kotiaho *et al.* 2004; Kasumovic & Andrade 2009).

For a redback male to maximize fitness, it is critical to achieve the first copulation in each of a female's paired independent sperm storage organs (Snow & Andrade 2005; Snow *et al.* 2006). Thus, females that cannibalize males after the first copulation and prevent a second copulation will severely limit their paternity (Snow & Andrade 2005; Stoltz *et al.* 2008). Our results show that a threshold close to 100 min of courtship reduces the likelihood of such premature cannibalism when rival males compete to copulate (figure 1). The mean rate of premature cannibalism is lowest (10%; Stoltz *et al.* 2008) when males are not competing and devote considerable effort to courtship, making contact with females after 150 min and copulating after 226 min (far exceeding threshold demands predicted by our model; figure 1; see Stoltz *et al.* 2008, 2009). In the competitions staged in this study, males provided 75 min of exclusive courtship prior to the introduction of a rival and the first copulation typically occurred after approximately 2 h (figure 2; high end of the 95% confidence range around the predicted choice threshold, figure 1). This led to intermediate rates of premature cannibalism (mean of 32%) that

were not linked to total courtship duration. In comparison, during competitive contexts when rivals were simultaneously introduced, courtship was accelerated (Stoltz *et al.* 2008, 2009). Males made first contact with females after about 30 min, with the first copulation typically occurring after 93 min, but this courtship was interspersed with bouts of competition. This is at the low end of our courtship threshold model (range 83–125 min; figure 1) and leads to the highest reported rate of premature cannibalism (mean of 44%; Stoltz *et al.* 2008, 2009). Variation in courtship among males is tightly linked to variation in cannibalism in this case.

It is unlikely that female redback spiders use sample-based mating decisions to determine the success of their first mate. If females had a sample-based decision rule, we would have expected them to discriminate against brief courting, intruding or smaller males in this experiment (as intruders and smaller males reduce courtship in the presence of larger rivals; Stoltz *et al.* 2008; this study). In contrast, we provide evidence that females do not discriminate against brief-courting males, as long as at least one male courts prior to the instigation of competition (compare this study with Stoltz *et al.* 2008, 2009). Moreover, females were never observed to cannibalize smaller intruding males that mated first, even though they provided extremely brief courtship prior to copulation (approx. 20 min; figure 3). Our results suggest that female receptivity increases after residents court, which in turn reduces the likelihood of premature cannibalism after the first copulation, regardless of which male copulates (but see Harari *et al.* in press). Females thus do not or cannot identify the source of stimulatory courtship. How this affects female fitness is unclear (see also Smith & Reichard 2005; Reichard *et al.* 2007).

Despite general predictions that sample-based rules will yield higher fitness returns when search costs are minimal for the choosy individual (Janetos 1980; Real 1990), many features of spider mating systems suggest sample-based decisions may decrease female fitness if males arrive sequentially in the wild. First, some female spiders apparently remain unmated in nature (Arnqvist & Henriksson 1997; Andrade & Kasumovic 2005), an outcome that may be more likely if females reject early-arriving males. Second, sampling males would require the sustained presence of males on the web. This may be costly because cohabiting males may be kleptoparasites of prey caught by females (Watson 1993) and may engage in conspicuous courtship, which can reduce foraging success (Craig 1986, 1988; Herberstein *et al.* 2002), increase the risk of predation (Herberstein *et al.* 2002) and result in damage to portions of the web (Watson 1986; Elgar 1991; Anava & Lubin 1993). Consistent with this, there is indirect evidence that redback females minimize the attraction of subsequent males after an initial copulation by turning off sex pheromone production (Stoltz *et al.* 2007), although they may commence production again later in the reproductive season (Perampaladas *et al.* 2008).

In addition to allowing us to probe female choice mechanisms in a biologically relevant way, this study allowed examination of how residency status, male size and courtship duration may interact to affect male success. This is interesting because a large male advantage in competition was documented elsewhere (Stoltz *et al.*

2008, 2009), but this apparently arises only when rival males encounter a female simultaneously. It seems more likely that one male will arrive prior to rivals in nature (male cohabitants range from 0 to 8 per web; Andrade 2003; M. C. B. Andrade 1983, personal observation) and thus will have a window of uninterrupted courtship, as simulated here. If these residents manage to mate prior to the arrival of intruders, premature cannibalism will be low and relative mating success high (e.g. Kasumovic & Andrade 2009). Regardless of the relative size of the resident, however, an intruder will have a significant opportunity for success under this scenario if he arrives before the resident mates. Thus, rather than selection for a particular phenotype, female choice rules may favour flexibility in male behaviour as a function of context (e.g. Kasumovic & Andrade 2009).

In this study, we show that females use threshold based decisions and the context of competition determines whether or not the threshold value is reached. Very few examples of choice via thresholds exist in the literature. This may be because this decision rule is rare, but it may also be because thresholds are plastic, or female tactics shift under different situations. Thus, there may be advantages to examining dynamics of female choice criteria in species such as redback spiders, where mating interactions strongly reflect the decision rules of physically dominant females (owing to female-biased size dimorphism). Here, the use of this system has revealed an unexpected, major effect of a choice threshold on the success of male mating tactics.

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