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Cross-modality effects of prey odour during the intraspecific interactions of a mosquito-specialist predator

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Abstract

One of the predictions from evolutionary game theory is that individuals will increase their willingness (i.e., become primed) to escalate aggression when they detect the presence of a limiting resource. Here we test this prediction in the context of prey odour priming escalation decisions during vision-based encounters by *Evarcha culicivora*. This East African jumping spider (Salticidae) feeds indirectly on vertebrate blood by actively choosing blood-carrying female mosquitoes as preferred prey. Unlike many salticid species, it also expresses pronounced mutual mate choice. As predicted, we show here that, in the presence of odour from their preferred prey, both sexes of *E. culicivora* escalate during vision-based same-sex encounters. This is further evidence that the odour of blood-carrying mosquitoes is salient to this salticid. For both sexes of *E. culicivora*, this particular prey may be a resource that matters in the context of intrasexual selection.

Keywords

aggression; game theory; perception; predation; priming; olfaction; Salticidae

Introduction

One of the predictions from evolutionary game theory is that same-sex conspecific individuals will escalate their expression of aggression with each other when they detect the presence of a limiting resource (Maynard Smith & Harper 2003). One way animals escalate is by becoming willing to get closer to a rival's weapons (e.g., mouthparts), while another way is by becoming willing to persist longer when interacting with rivals (Bradbury & Vehrencamp 2011). Experiments that corroborate this prediction are also of interest in the context of animal cognition because they may reveal particular resources that are salient to the escalating individual (Shettleworth 2010). We have been especially interested in using jumping spiders (Salticidae) for considering these cognitive implications.

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A frequently acknowledged trend among animals (Bateman 1948; Trivers 1972; Andersson 1994), including salticids (Jackson & Pollard 1997), is that one sex, usually the female, tends to express mate-choice behaviour more strongly, whereas the other sex, usually the male, tends to be more active in courtship and tends to be less discriminating. However, envisaging sex roles as being qualitatively different is overly simplistic (see Altmann 1997) and recent research (Gowaty et al. 2012; Tang-Martinez 2012) suggests that pronounced mutual mate choice and active courtship by both sexes may be more common than formerly appreciated.

There may also be widespread differences between males and females in the importance of access to food as a limiting resource. For example, eggs are often costly for females to produce, and it may be common among animals (e.g., Vézina & Williams 2005), including spiders (Jackson & Pollard 1997; Heiling & Herberstein 1999), for females to feed voraciously as a step toward egg production. Females in turn may be more inclined than males to escalate in same-sex interactions when preferred food is detected (see: Adamo & Hoy 1995; Nilsen et al. 2004). One of the most well documented examples of this male-female difference comes from experiments on *Drosophila melanogaster*. For this insect, male-male contests appear to be related primarily to competition for access to potential mates and female-female contests appear to be related primarily to competition for access to yeast, a food resource known to be especially important for the females of this species (Spieth 1974; Dow & von Schilcher 1975).

We have been particularly interested in using salticid spiders for determining whether prey odour and mate odour lower an individual's threshold for making escalation decisions during vision-based intraspecific interactions (i.e., whether odour primes the individual's vision-based decisions). Salticids are especially suitable subjects for this research because they have eyes that support vision based on exceptional spatial acuity (Harland et al. 2012; Land & Nilsson 2012), and they also have well-developed capacity for chemoreception (Uhl 2013). It is also known that, of the more than 5,000 described species in the family Salticidae, some express remarkably specific preferences for particular types of prey (Nelson & Jackson 2011).

From earlier studies (Cross et al. 2007a; Cross & Jackson 2009), we know that mate odour influences escalation decisions during the male-male interactions of four salticid species (*Evarcha culicivora*, *Portia fimbriata*, *Portia africana* and *Jacksonoides queenslandicus*). More specifically, we identified three distinct ranks, or intensity levels, in these four species, and we found that the level reached before an interaction ended tended to be higher in the presence, rather than in the absence, of the odour from potential mates. Only the males of *P. fimbriata*, *P. africana* and *J. queenslandicus* escalated conflict when they were presented with the odour from potential mates, consistent with the trend for salticid males to perform courtship more actively and for females to engage more actively in expressing mate-choice behaviour. However, the females as well as the males of *E. culicivora*, a species for which mutual mate-choice is pronounced (Cross et al. 2007b, 2008), escalated conflict when the odour of potential mates was present (Cross & Jackson 2009).

For one of these four salticid species, *P. fimbriata*, we know that prey odour also influences decisions made during interactions between same-sex conspecific individuals (Cross & Jackson 2011). All species from the genus *Portia* appear to be araneophagic, where ‘araneophagy’ refers to active preference for spiders as prey. In Queensland (Australia), *Jacksonoides queenslandicus* is an especially abundant salticid (Jackson 1988a) on which *P. fimbriata* preys (Jackson & Blest 1982). The earlier research (Cross & Jackson 2011) showed that *P. fimbriata* females escalate to a higher level of aggressive behaviour when in the presence than in the absence of the odour of *J. queenslandicus*, but there was no significant effect of *J. queenslandicus* odour on *P. fimbriata* males. Moreover, these effects were remarkably specific. The odour of *Tauala lepidus*, a salticid that is closely related to *J. queenslandicus* and present in same habitat (Jackson 1988b), did not significantly influence the escalation decisions of *P. fimbriata* males or females. These findings, in conjunction with the findings from the earlier experiments using mate odour (Cross & Jackson 2009), suggest that access to mates is more important for *P. fimbriata* males and that access to a particular prey species is more important for *P. fimbriata* females.

Determining how prey odour affects *E. culicivora*’s escalation decisions is of interest because, besides expressing unusually pronounced mutual mate choice (Cross et al. 2007b, 2008), *E. culicivora* has an unusual predatory strategy. This salticid feeds indirectly on vertebrate blood by actively choosing blood-carrying female mosquitoes as preferred prey (Jackson et al. 2005) and there is a remarkable entanglement of this species’ mating and predatory strategies. Both sexes of *E. culicivora* express a preference for potential mates that have recently had indirect blood meals (Cross et al. 2009). There is no evidence of an olfaction-based preference for same-sex conspecifics or for opposite-sex heterospecifics on this diet (Cross & Jackson 2013), suggesting that blood has an important role in the context of intersexual selection for *E. culicivora*. On this basis, we predict that, in the presence of odour from blood-carrying mosquitoes, both sexes of *E. culicivora* will escalate during vision-based same-sex encounters.

As in the earlier research on *P. fimbriata*, we investigate whether prey odour influences the level of aggression reached in same-sex interactions of *E. culicivora*. However, we also consider whether *E. culicivora* individuals become willing to interact for longer in the presence than in the absence of preferred-prey odour.

Methods

Our experimental subjects came from laboratory cultures (F2 generation) started from *E. culicivora* collected in western Kenya (for field-site details, see Cross et al. 2008). For standardisation, all test spiders matured in the lab 2–3 weeks before used, none had mated and all were of standard size (body length 5 mm, accurate to the nearest 0.5 mm). When spiders dispersed from their egg sacs, we housed them in one per cage and kept each individual isolated from other salticids. We conducted our experiments between 0800h and 1300h (laboratory photoperiod 12L:12D, lights on at 0700 hours), and we based our experiments on test spiders encountering their own mirror images. Salticids readily respond to their own mirror images in much the same way as they respond to living same-sex conspecific rivals (Homann 1928; Forster 1982; Lim & Li 2006; Cross et al. 2007a; Cross &

Jackson 2009), and this was important because it meant we could ascertain the test spider's decisions to escalate or desist without the decisions of a living, responsive rival introducing confounding variables (see Briffa & Sneddon 2007).

We staged encounters in a transparent Perspex box (test arena; Fig. 1) with a removable glass top. One of the arena's ends was a mirror (length 110 mm, height 20 mm). There were two holes (diameter 10 mm) in each of the longer sides of the arena, one being 15 mm from the mirror end and the other being 15 mm from the opposite end of the arena. A silicone tube (diameter 10 mm) was placed in each of the four holes, one end of the tube being flush with the inner surface of the arena wall and the other end extending away from the arena. The opening of the tube into the arena was covered with nylon netting which blocked entry by the test spider.

There was an airflow system, the function of which was to permeate the entire arena with odour (i.e., our goal was to test for olfactory priming of the test spider's response to its own mirror image). We put the odour sources in two glass chambers ('stimulus chambers') situated behind the arena. Using silicone tubing (diameter 10 mm), we connected the stimulus chambers to the arena and, using flowmeters, we pumped air into the arena through the two holes nearer the mirror. The other two holes in the arena were for outflow. We adjusted airflow to 800 ml/min (Matheson FM-1000 flowmeter), and there was no evidence that this airflow setting impaired locomotion or had any adverse effects on the salticid in the arena. A barrier hid the odour source from the test spider's view.

For ensuring that the arena was permeated with prey odour, we connected the stimulus chambers and started airflow 60 min before we introduced a test spider into the arena. A hole (diameter 10 mm), situated in the floor of the arena and centred between the two outflow holes, was used for introducing the test spider ('introduction hole'). In experimental trials, each of the two stimulus chambers contained 10 blood-carrying female mosquitoes (*Anopheles gambiae* s.s., body length 4.5 mm; fed on human blood 4–5 h before used). Although we did not record the duration of feeding by mosquitoes, they all fed long enough for their abdomens to become red and swollen. Moreover, presenting the spider with 10 mosquitoes per stimulus chamber made it unlikely that we might have used, by chance, only mosquitoes with an odour that was insufficient for the spider to detect (see Jackson et al. 2005). For control trials, we put 10 individual non-biting midges (*Nilodorum brevivucca*, Chironomidae; body length 4.5 mm) into each of the two stimulus chambers. Our rationale for using *N. brevivucca* in control trials was that, in earlier olfactometer experiments (Jackson et al. 2005), there was no evidence of *E. culicivora* responding to female mosquitoes that had not fed on blood, to male mosquitoes or to midges (i.e., they responded only to blood-carrying female mosquitoes). No spider had any experience with either blood-carrying female mosquitoes or midges before being used in experiments (i.e., the spiders we used were only reared on females of *An. gambiae* that had not fed on blood). The mosquitoes came from laboratory cultures but we collected the midges from the field immediately before testing began. No insects were used more than once as odour sources. For standardising hunger level, we subjected each spider to a 7-day pre-trial fast.

Before testing began, the spider was transferred from its maintenance cage to a 50-mm long glass tube (diameter 10 mm, stopper in each end of the tube) where it was kept for 15–20 min, after which the stopper in the introduction hole and one of the stoppers in the glass tube were removed and the open end of the tube was fit into the introduction hole. If the test spider had not spontaneously walked out of the tube and into the arena 5 min later, then the other stopper was removed and, using a soft brush, the spider was lightly prodded, whereupon it promptly moved into the arena. We aborted testing if the test spider entered the arena by running, instead of walking, out of the tube and also if, after walking into the arena, 60 min elapsed without the test spider displaying at the mirror. Adopting these rules resulted in fewer than 5% of the trials in any experiment being aborted.

The test spider's entry into the arena defined the beginning of a trial. In successful trials, the spider displayed and we recorded the level of aggression ('rank'; see below) reached in the interaction with the mirror and also the time elapsing between the first display and the end of the interaction (interaction duration). We ended trials when test spiders retreated from the mirror and did not return or display again for 30 s. For any spider that interacted with its mirror image for as long as 30 min, we terminated the trial, recorded the highest rank reached (see below) and recorded 30 min as interaction duration. We tested each individual spider twice (one experimental trial and one control trial), with a mirror being present in the arena during both trials. For each test spider, the two trials were on successive days and we decided at random whether the control or the experimental trial came first. No spider was used in more than one test pair.

Levels of aggression

As in earlier studies (Cross et al. 2007a; Cross & Jackson 2009, 2011), we recognised three levels of aggression ('ranks'). We based these ranks on discrete categories of behaviour and the rank we recorded was the highest reached before the test spider retreated and failed to return. 'Rank' can be envisaged as being the level of risk the spider was willing to accept in a given contest, with rank 1 being the lowest and rank 3 being the highest. Below we provide a general characterisation of the three ranks (for details, see Cross et al. 2008).

Rank 1 (posturing from a distance): while facing the mirror, the spider adopted distinctive positioning of forelegs, chelicerae and abdomen, sometimes accompanied by a distinctive walking pattern.

Rank 2 (propulsive displays): the spider ran, lunged or leapt toward the mirror, but with little or no contact being made.

Rank 3 (face-to-face contact): the spider pushed against the mirror, with the front of its cephalothorax touching the mirror and with its forelegs usually extending out to the side and touching the mirror.

Data analysis

We calculated a rank score for each test spider, where the rank attained in the control trial was subtracted from the rank attained in the experimental trial (i.e., a positive score indicated that the test spider escalated to a higher rank in the experimental trial, whereas a

negative number indicated that the test spider escalated to a higher rank in the control trial). We also calculated a duration score (the test spider's interaction duration in the control trial subtracted from its interaction duration in the experimental trial). As each individual test spider was tested twice, the relevant data were the distribution of scores, not the separate distributions of rank for experimental and control tests. Distribution of scores did not meet the prerequisites for parametric data analysis and, accordingly, we used Wilcoxon matched-pairs tests for data analysis (null hypothesis: score = 0). Using Mann-Whitney *U*-tests, we also compared the scores for different groups of test spiders (null hypothesis: scores for one group of test spiders matched scores for another group of test spiders). Bonferroni adjustments were applied whenever there was repeated analysis of the same data (adjusted alpha, 0.017). For details about statistical procedures, see Howell (2002).

Results

Effect of prey odour on *E. culicivora*'s escalation decisions

For both sexes, rank scores in the presence of preferred-prey odour were not significantly different from rank scores in the absence of this odour (females, $Z = 1.294$, $p = 0.196$; males, $Z = 0.686$, $p = 0.493$; Fig. 2). However, for both sexes, duration scores were significantly higher in the presence than in the absence of preferred-prey odour (females, $Z = 2.912$, $p = 0.004$; males, $Z = 2.854$, $p = 0.004$; Fig. 3). Rank and duration scores for females were not significantly different from rank and duration scores for males (rank, $Z = 0.101$, $p = 0.920$; duration, $Z = 0.678$, $p = 0.498$).

Comparisons with earlier data on *Portia fimbriata*

In our earlier research using *P. fimbriata*, the only data we considered came from ranking the test spider's behaviour (e.g., Cross & Jackson 2011), but the methods we used in the earlier study were the same as those used in the present study. As we wanted to compare the duration scores for *E. culicivora* with the duration scores for *P. fimbriata*, we went back to our raw data from testing *P. fimbriata* and extracted, for the first time, data on interaction duration. We found that duration scores for females, but not for males, of *P. fimbriata* were significantly higher in the presence than in the absence of odour from the prey spider *J. queenslandicus* (females, $Z = 3.764$, $p < 0.001$; males, $Z = 1.045$, $p = 0.296$; Fig. 4). We also found that duration scores for *P. fimbriata* females were significantly higher than duration scores for *P. fimbriata* males ($Z = 3.800$, $p < 0.001$).

Although we adopted a paired-testing design for our experiments, it is also of interest to compare the distribution of ranks in the presence of a particular prey's odour with the distribution of ranks in the absence of this odour (Fig. 5). Ranks were significantly higher for *P. fimbriata* females than for *E. culicivora* females in experimental trials ($Z = 3.142$, $p = 0.002$) but not in control trials ($Z = 1.682$, $p = 0.093$). The ranks for *P. fimbriata* males were not significantly different from the ranks for *E. culicivora* males in experimental ($Z = 0.129$, $p = 0.897$) or control trials ($Z = 1.033$, $p = 0.302$).

Duration was significantly longer for *P. fimbriata* females than for *E. culicivora* females in experimental trials ($Z = 4.066$, $p < 0.001$) and in control trials ($Z = 4.456$, $p < 0.001$). Duration

for *P. fimbriata* males was not significantly different from duration for *E. culicivora* males in experimental ($Z = 2.331$, $p = 0.020$) or control trials ($Z = 1.487$, $p = 0.137$) (Fig. 6).

Discussion

We know from an earlier study (Cross & Jackson 2011) that, for *P. fimbriata* females, rank scores during intrasexual encounters are higher in the presence than in the absence of the odour of a specific prey type, namely *J. queenslandicus*. However, for both sexes of *E. culicivora* in the present study, we found no evidence that the presence or absence of preferred-prey odour was a variable that affected the rank scores. Had we gone no further, it would have been tempting to conclude that preferred-prey odour simply has no effect on *E. culicivora*'s behaviour during intrasexual encounters. However, we did go further by also considering duration scores and we found, for both sexes of *E. culicivora*, that interaction duration was significantly longer in the presence than in the absence of preferred-prey odour. On the basis of duration scores, but not on the basis of rank scores, we have evidence that prey odour influences *E. culicivora*'s response to mirror images. This is an interesting reminder that non-significant outcomes from statistical analyses are not simply evidence that a null hypothesis is true.

Moreover, when we went back to our raw data for *P. fimbriata* (Cross & Jackson 2011) and considered interaction duration for the first time, we found that duration scores were significantly higher for females in the presence of odour from *J. queenslandicus*. For *E. culicivora* and *P. fimbriata*, duration scores appear to be sufficiently sensitive for revealing how prey odour influences a spider's response to its mirror image. However, rank scores appear to be sufficiently sensitive in our experiments for only *P. fimbriata*. This suggests that these two salticid species may rely on different decision-making criteria, with *P. fimbriata* relying more strongly than *E. culicivora* on the specific behavioural category (rank) a rival is willing to adopt. The underlying reasons for this difference between *P. fimbriata* and *E. culicivora* have not been investigated.

For females of *P. fimbriata* (Cross & Jackson 2011) and for both sexes of *E. culicivora* (this study), we now have evidence that the odour of a particular type of prey is salient during same-sex interactions (*J. queenslandicus* for *P. fimbriata* and blood-carrying mosquitoes for *E. culicivora*). Moreover, in both studies, test spiders had no prior experience with the prey used as odour sources. This implies that females of *P. fimbriata* and both sexes of *E. culicivora* are innately prepared to use the odour of a particular prey type as an escalation cue during vision-based encounters with same-sex rivals. Unlike *P. fimbriata*, *E. culicivora* is a species that expresses pronounced mutual mate-choice behaviour and we corroborated our prediction that both sexes of *E. culicivora* are innately predisposed to escalate in the presence of odour from a specific prey type.

Earlier research on pisaurid and lycosid spiders (Kreiter & Wise 2001; Wilder & Rypstra 2008) has shown that female fecundity increases when feeding increases and we might propose that this is a widespread trend in spiders. Yet we found no evidence to suggest that access to preferred prey was any more important for *E. culicivora* females than it was for males as an escalation cue during encounters with potential rivals. These findings are further

evidence that, for *E. culicivora*, blood-carrying mosquitoes are a particular prey type that has relevance beyond simply being a source of nutrition. Earlier research (Cross et al. 2009) showed that both sexes of *E. culicivora* express an olfaction-based preference for potential mates that have recently fed on a blood-carrying mosquito (i.e., for this salticid, a preference for blood-carrying mosquitoes as prey appears to be driven in part by intersexual selection). Here we have shown that, for both sexes, access to blood-carrying mosquitoes may also be a resource that matters in the context of intrasexual selection.

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Fig. 1.

Testing arena (140 mm long $\times$ 110 mm wide $\times$ 20 mm high; not drawn to scale) made from transparent Perspex. Glass lid not shown. Thick arrows indicate direction of airflow into arena through silicone tubes. Each of two stimulus chambers (length 115 mm, inner diameter 25 mm) held, for *Evarcha culicivora*, 10 prey items (*Anopheles gambiae* s.s. females or *Nilodorum brevibucca* females). In the earlier study (Cross & Jackson 2011), each stimulus chamber held, for *Portia fimbriata*, one prey item (*Jacksonoides queenslandicus* female or *Tauala lepidus* female). Barrier (opaque plastic) prevented test spiders from seeing the prey items used as odour sources. Test spider entered arena through introduction hole. Mirror was one end piece of arena. All end pieces of arena held in place with plastic clamps.

Fig. 2. Rank scores attained for females (N = 45) and for males (N = 45) of *Evarcha culicivora*. Score: rank attained while exposed to odour of blood-carrying *Anopheles gambiae* s.s. females minus rank attained while exposed to odour of *Nilodorum brevibucca* females.

Fig. 3. Duration scores attained by females ($N = 45$) and by males ($N = 45$) of *Evarcha culicivora*. Score: interaction duration while exposed to odour of blood-carrying females of *Anopheles gambiae* s.s. minus interaction duration while exposed to odour of *Nilodorum brevibucca* females.

Fig. 4. Duration scores attained by females (N = 30) and by males (N = 30) of *Portia fimbriata*. Score: interaction duration while exposed to odour of *Jacksonoides queenslandicus* females minus interaction duration while exposed to odour of *Tauala lepidus* females.

Fig. 5.
Ranks attained when spiders were exposed to odour of preferred prey (Experimental trials) and odour of non-preferred prey (Control trials).

Fig. 6.
Interaction durations when spiders were exposed to odour of preferred prey (Experimental trials) and odour of non-preferred prey (Control trials).