FEMALE MATING SWARMS INCREASE PREDATION RISK IN A ‘ROLE-REVERSED’ DANCE FLY (DIPTERA: EMPIDIDAE: RHAMPHOMYIA LONGICAUDA LOEW)

by

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Summary

Mate acquiring activities often expose males to increased risks of predation. In species where females are more competitive than males (i.e. a reversal in the conventional mating roles), the mate-acquiring biology of females is expected to increase their exposure to predators. Our observational study of a role-reversed dance fly, Rhamphomyia longicauda Loew (Empididae), supports this prediction. Within predominantly female swarms, R. longicauda display structures in flight that are assessed by males. Structural and behavioural components of the display should increase the risk of predation on females. We found more females than males captured in spider webs. This bias in predation was not due to a female-bias in population sex-ratios of the dance fly and the nature of web predation appears to rule out the hypothesis that spiders actively favour females as prey.

Introduction

Costs of sexual competition, typically suffered by males, are expected to include increased risks of predation (Sakaluk, 1990; Magnhagen, 1991; Kotialho, 2001). Although the available evidence is consistent with this prediction (Elgar & Wedell, 1996), a full test is difficult because it would...

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require an investigation of all sources of predation associated with mating. Typical supportive evidence relates the mate-acquiring biology of males with increased risk from one type of predator. Causes of male mortality include not only sex-specific traits, such as signals (Burk, 1982; Zuk & Kolluru, 1998; Mougeot & Bretagnolle, 2000) and secondary sexual characters (Koga et al., 2001) that attract predators, but also mate-searching or competitive movements that lead to encounters between males and natural enemies (e.g. Thornhill, 1975; Gwynne, 1987).

Accordingly, in systems in which females are more competitive than males, i.e. where the conventional mating roles are reversed, the acquisition of mates by females is expected to expose females to a greater risk of predation (Gwynne & Dodson, 1983; Elgar & Wedell, 1996). No study of role-reversed vertebrates has assessed predation risk directly, although, for a pipefish *Syngnathus typhle*, Fuller & Berglund (1996) examined sexual differences in response to variation in perceived risk of predation. For insects, Gwynne & Dodson (1983) studied predation on the sexes of a role-reversed katydid *Anabrus simplex* (Orthoptera: Tettigoniidae) and, consistent with predictions, found that more females than males were captured by a sphecid wasp. The wasps hunt at the same time that female katydids make perilous movements while seeking out males able to supply nutritious spermatophore meals. However, an alternative explanation for sex-biased predation is that wasps actively selected larger female katydids in areas where these prey were very common (Gwynne & Dodson, 1983).

Some species in two genera of empidine dance flies (Diptera: Empididae) with nuptial meals also show reversals in the conventional mating roles. Empidine females of most species obtain their food exclusively from prey provided by males. Prey is transferred in flight to the female within mating swarms. In most species, competitive swarming is by males (Cumming, 1994) but some *Empis* and *Rhamphomyia* species have all-female swarms that appear to be competitive assemblages, possibly resulting from male-captured prey being in short supply (Svensson & Petersson, 1987, 1988; Cumming, 1994; Svensson, 1997; Funk & Tallamy, 2000). In *R. longicauda*, Loew females compete in swarms beneath gaps in the tree canopy for about an hour around sunset. Males preferentially approach large females within swarms (Funk & Tallamy, 2000) and sexual selection on females has apparently produced striking sex-specific structures that exaggerate body size: before entering a swarm, a female inflates a pair of abdominal sacs and,
while in flight, fringed legs held at the periphery of the inflated abdomen further enhance size (Newkirk, 1970; Funk & Tallamy, 2000).

In this paper we examine spider predation on *R. longicauda* and support the hypothesis that displaying by females is associated with a risk of predation. In contrast to empidine species with male swarms, females in species with female swarms are expected to suffer predation as a consequence of their behavioral or structural adaptations for displaying. At our study sites the webs of several spider species were found close to areas where both sexes of *R. longicauda* congregate during the day and where hundreds of female flies displayed each evening. The nature of web capture probably rules out the possibility of direct predator preferences for prey that are likely in other systems (e.g. Gwynne & Dodson, 1983).

**Methods**

We studied the flies and spiders along the banks of the Credit River, near Glen Williams (Halton Co, Ontario, Canada) for the entire swarming season of the flies: from June 13 to July 14, 2001. We focused on six female swarms each of which was located beneath gaps in the woodland canopy along the banks of the river. As small sample sizes were collected for each site, data were pooled for analysis. Sites had a ground cover of water hemlock (*Cicuta* sp.), at 20-30 cm in height, and higher clumps of mainly ostrich fern, *Matteuccia struthiopteris*. In these sites during the day both sexes of the fly perched on the plants or made short flights and, at sunset, the predominantly female swarms were active approx. 20 to 150 cm above the vegetation. Within an hour after the end of swarming activity (occurring at dusk — approx. 9:30 pm), we collected prey from the webs of araneid, tetragnathid and theridiid spiders within approx. 2-3 m from each area of fly activity, some of which bordered the river. Some dance flies were actually noted to fly into webs while we observed swarms. *R. longicauda* was easy to identify among spider prey and sexual differences (particularly the distinct pinnate scales on the legs of females) allowed identification of the sex of *R. longicauda* even after it had been killed and wrapped in silk. To rule out the hypothesis that sex biased predation was due to a female-biased adult sex ratio, which has been reported to occur at the end of the swarming season in *Empis borealis* (Svensson & Petersson, 1987; Svensson et al., 1989), we censused flies throughout the season by walking transects through areas of fly activity during the day and again in early evening (approx. 8:30 pm), the latter timed to occur just before swarming began.

**Results**

Twenty-one *R. longicauda* prey collected from 11 spider webs containing dance fly prey (six tetragnathids, four araneids and one theridiid) showed,
as predicted, significantly more females ($N = 18$) than males ($N = 3$) ($\chi^2$ (with Yates correction, which results in a conservative test when $N < 30) = 9.3, p < 0.005$). The female bias (14:2) remained significant when only dead prey were used (four females and one male escaped from webs) ($\chi^2 = 7.56, p < 0.01$).

The female bias in prey was not a consequence of a greater abundance of females: on the first day we observed flies (June 13) our census revealed no sex bias (44 females and 42 males: $\chi^2 = 0.12, p > 0.5$). And for samples throughout the remainder of the *R. longicauda* swarming period, six daytime censuses also showed no sex bias (133:121, 48:53, 26:25, 41:44, 48:50, 54:45: Wilcoxon $z$ on differences in proportions of the sexes = 1.1, $p = 0.25$). However, there was a temporary female bias in each early evening sample (44:2, 30:11, 25:8, 63:8, 27:10, Wilcoxon $z = 2.03, p = 0.042$). This was expected, however, because in early evening males move away from the swarming areas to hunt before returning with prey to the evening swarm (where occasionally there was a brief male bias in swarms early in the swarming period: Bussière, unpubl. obs.).

**Discussion**

A number of observational studies have linked the mate acquiring activities of males to a male-bias in predation (see Introduction). Our study is the first to associate female sexual competition with increased predation risk for a species showing a reversal in the conventional mating roles: in *R. longicauda*, more females than males are killed by spiders in locations where both sexes are active during the day and where females compete and display at sunset. It is unlikely that foraging females are ensnared because all the prey eaten by empidine females comes from nuptial gifts (Cumming, 1994). The female bias in spider predation *per se* was not reflected in a sex-ratio bias toward males in the local population toward the end of the season. This is either because the decline in female numbers was too small to be detectable in our sex ratio samples or because there are other sources of predation on males. Our focus on web building spiders in the vicinity of fly activity included webs (particularly those of tetragnathids) in riverside vegetation which males would have flown near when moving from day-time areas to hunting areas along the river. However, our study did not include
other sources of predation. Consequently, as in studies of male animals, without observing all pre-mating predation (see Introduction) we cannot directly address the hypothesis of a sex difference in risk from all sources of predation arising from pre mating activities (Gwynne & Dodson, 1983; Elgar & Wedell, 1996).

Our findings do, however, suggest a cost to female *R. longicauda* of structural and/or behavioural components in an elaborate display that is known to influence mating decisions by choosy males (Funk & Tallamy, 2000). The female bias in predation could be due to risky behavior *per se* or to secondary sexual structures (see Koga *et al.*, 2001). Risky behavior by female *R. longicauda* might involve flying close to vegetation near the swarm where we observed many of the spider webs. Alternatively, the bias in predation may come from the structural modifications carried by a swarming female which includes inflated abdominal pouches, which increase her overall body size, as well as the impediment of possessing legs fringed with pinnate scales (Cumming, 1994). These traits, not expressed in males, may either make it more likely that flying females are caught in the first place or more difficult for females to extricate themselves from webs before being immobilized by the spider.

References


