Courtship rituals of dance flies: Mating swarms and female ornamentation

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Dance flies (balloon flies or dagger flies), known for their captivating mating dance, display some of the most fascinating and unusual courtship behaviors in the insect world. These are predatory dipterans of the family Empididae, whose subfamily Empidinae is divided into three genera *viz., Hilara, Empis* and *Rhamphomyia* with approximately 1,450 species worldwide. Sex role reversal in relation to the usual male and female reproductive behaviour is an important evolutionary behaviour among these dance flies. Males typically provide the female with a nuptial gift at the time of mating and many species form lek-like mating swarms in approximately 28% of the species in the genera *Rhamphomyia* and *Empis*, females have some sort of secondary sexual characteristics/ornaments. These ornaments include inflatable abdomen, pinnate (feathery) leg scales and enlarged or darkened wings (Fig. A). The female ornaments are believed to be a signalling mechanism to attract male mates, either for their gametes or to obtain more prey/nuptial gifts from males to provide for ovarian maturation (Myllyaho, 2022).

Mating behaviour

The Empidinae dance flies display a number of interesting mating traits; males typically provide the female with a nuptial gift at the time of mating, and many species form lek-like mating swarms. The elaborate mating behaviour can be broken down to three distinct stages in adults *i.e.* hunting, swarming, and mating. Mating swarms in the dance flies can vary substantially by species in terms of density, sex ratio and timing. Many species form mating swarms at a 'swarm marker' (puddles, rocks, or distinctive vegetation, or open patches of sky) and return to the same site annually with specific individuals revisiting the swarm for the duration of the mating season.

The preference of female by male could depend on the size of the female or its position in a swarm and several other factors. The effect of female size on male mate choice was experimented by Funk and Tallamy (2000), using two-dimensional models of inflated females. Accurate models were designed by photographing parts of inflated females that had been snap-frozen in flight as they swarmed. The various female parts (wings, legs, head, thorax and abdomen) were combined in the darkroom into black and white composite prints that represented an intact female in flight. Printing was done at several magnifications including life size (*i.e.* actual size of average field-collected females), 0.75X, 1.5X and 2.0X. Then the images from the film were cut and trimmed as closely as possible. Activities were recorded on videotape. Two models of each of the four sizes were used with positions re-randomized each night and the data were collected. It was found that males either accepted or rejected each model as a potential mate after flying beneath it. When given a choice between models of four sizes, males approached the largest model (twice life size) significantly more often than the other sizes (P=0.0002). Several hypotheses were explained for this preference

1. Large females may be more capable of laying larger egg clutches or clutches comprised of larger eggs.
2. Females with the largest inflatable sacs may be preferred because they bear 'good attractiveness' genes and will thus produce

'sexy' daughters.

3. Inflated abdomens may compromise survivorship through lost manoeuvrability and thus convey 'good viability' genes *via* the handicap principle.
4. Females with larger abdomens may be further along in the gonotrophic cycle (process of ovarian development and egg laying) and thus be closer to oviposition than females with smaller abdomens.

Exaggerated sexual traits of ***Rhamphomyia longicauda***

Loew were also studied, which revealed that female provide misleading sexual signals to males. Thus, the act of deception does operate in dance flies. Females had bizarre abdominal extensions that might deceive males indicating the incorrect size and particularly, the maturity status of their eggs.

Female swarm position also becomes important to attract the incoming male which was experimentally explained. A total of 1479 male approaches over the course of 10 mating swarms were recorded. Males were more likely to approach and court a female silhouette if it was positioned near the centre, rather than the periphery of the swarm (Murray *et al.,* 2018). Thus, the swarm is stratified according to female size, with the largest females occupying lower positions in the swarm. Indirect female competition plays a role in swarm positioning and mating success. Additional role for female ornaments: that they signal quality not only to choosy males, but also to rival females (Bussiere et al., 2008).

Beautifully flawed!

Everything comes with a cost so does the ornamentation in females of dance flies. Scientifically speaking it's the handicap principle and dance flies are not an exception! The flies and spiders along the banks of the Credit River, for the entire swarming season of the flies, were studied. The number of flies caught in the spider webs was counted. Twenty-one *R. longicauda* prey collected from 11 spider webs containing dance fly prey showed as predicted, significantly more females than males. The reason for female bias in predation according to researchers could be due to secondary sexual structures. Two possibilities for this increased predation were considered. One is that females make swarms near the spider webs or the bias in predation may come from the structural modifications carried by a swarming female which includes mated abdominal pouches, which increase her overall body size, as well as the impediment of possessing legs fringed with pinnate scales. These traits, which are 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 (Gwynne and Bussiere, 2002).

Conclusion

The remarkable courtship behaviour of Empidinae dance flies has stimulated a renewal of interest in using them as models in studying the evolution of mating systems. However, the progress in studying mating systems in dance flies has been hampered by the fact that dance flies do not behave as expected in lab environments and by the speed of natural swarms.

References

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Fig. A. Female-specific ornamentation in *Rhamphomyia longicauda* (Murray *et al.* 2022)

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