

GENERAL ARTICLE

The Fascinating Mating Swarms of Dance Flies (Diptera: Empididae: Empidinae)

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Abstract

Dance flies (Diptera: Empididae: Empidinae: *Hilara*, *Empis* and *Rhamphomyia*) exhibit some of the most striking reversals of conventional sex roles among insects. Their mating systems are characterized by swarm-based courtship, obligatory nuptial gifts and frequent female ornamentation. Empirical, ecological and phylogenetic studies demonstrate that female-specific ornaments function as sexual signals in male mate choice and have evolved repeatedly under conditions of female-biased operational sex ratios. While ornamentation enhances mating success, it incurs survival costs, highlighting trade-offs between sexual and natural selection. Male counter-strategies, including deceptive nuptial gifts, further reveal intense sexual conflict. Together, these dynamics make Empidinae an exceptional model for studying sexual selection and mating system evolution.

Keywords: Dance flies, Empidinae, female ornamentation, nuptial gifts, sexual selection

Introduction

The dance flies (sometimes called balloon flies or dagger flies) from the subfamily Empidinae (Diptera: Empididae) is divided into three genera, *Hilara*, *Empis* and *Rhamphomyia* consisting of approximately 1,450 described species worldwide. Empidinae are known for their unusual mating behaviour where individuals aggregate in mating swarms with the exception of a few species and where the males approach the females from below. The male presents the female with a nuptial gift, often in the form of prey, sometimes wrapped in silk. In many Empidinae species, adult females rely almost entirely on nuptial gifts as their primary source of protein. Males actively hunt

prey items to present during courtship and this foraging behavior is thought to expose them to greater mortality risk compared with the relatively sedentary females. Approximately, 28 per cent of species within the genera *Rhamphomyia* and *Empis*, females display conspicuous secondary sexual traits. These female-specific ornaments include inflatable abdomens, pinnate (feather-like) scales on the legs and enlarged or darkened wings. Such traits believed to be a signalling mechanism to attract mates, either for their gametes or to obtain more prey from males to provide for ovarian maturation since mating behaviour is repeated by both sexes (Myllyaho, 2022).



Figure 1. (Left) Balloon fly (*Hilara* sp.) showing typical slender body and elongated legs (Source: <https://savemountdiablo.org/blog/7-new-species-of-dance-flies-discovered-in-the-diablo-range/>) and (Right) Dagger fly (*Empis* sp.), a predatory empidid with elongated proboscis and agile flight typical of dance flies (Source: [https://commons.wikimedia.org/w/index\).arch=dagger+flies&title=Special%3AMediaSearch&type=image](https://commons.wikimedia.org/w/index).arch=dagger+flies&title=Special%3AMediaSearch&type=image)).

Female ornaments as signals in male mate choice

Empirical research has provided strong support for the role of these ornaments as signals used by males during mate choice. Funk and Tallamy (2000) confirmed the male preference for enlarged abdomen females by using plastic models of varying sizes (Figure 2 & 3). Given choice for four sizes, male approached the largest of the model more significantly. Also, a simple regression of female's abdominal area against egg length in lekking sites of *Rhamphomyia sociabilis* (Williston) revealed a highly significant relationship. They also studied the exaggerated sexual traits of *R. longicauda* Loew, which provided misleading sexual signals to males. Females had bizarre abdominal extensions that might deceive males indicating the incorrect size and particularly, the maturity status of their eggs.

While elaborate ornaments can improve mating success, they also impose fitness costs. Gwynne and Bussière (2002) demonstrated that ornamented females of *R. longicauda* experienced

higher rates of predation, particularly from web-building spiders. The increased body size, altered flight dynamics and conspicuous appearance of ornamented females likely make them more vulnerable to capture by the predators and make females less capable of escaping from webs. These findings illustrate the classic evolutionary trade-off between sexual and natural selection, sexual selection favours exaggerated traits, while natural selection - penalises traits that reduce survival.

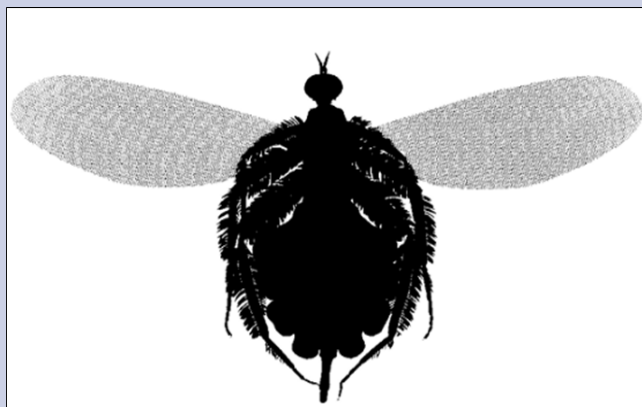


Figure 2. Black and white composite print used as an artificial model of an inflated *R. longicauda* female for quantifying the effect of female size on male preference (Source: Funk and Tallamy, 2000).

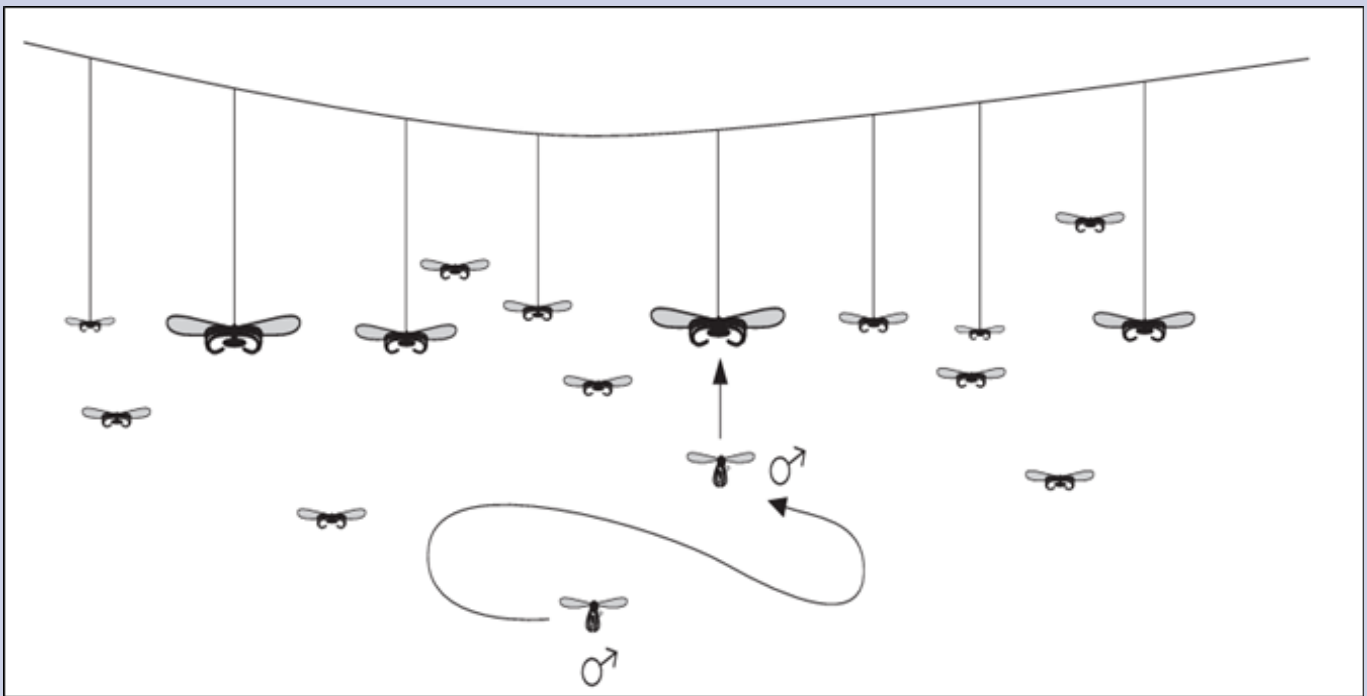


Figure 3. The pattern in which various-sized models of inflated *R. longicauda* females were suspended from monofilament line among actual lekking females to quantify the effect of female size on male preference (Source: Funk and Tallamy, 2000).

Phylogenetic origins of female ornamentation

The evolutionary origins of female ornamentation in dance flies have been explored using molecular phylogenetic approaches. Murray *et al.* (2020) analysed *cad* gene sequences across 22 Empidinae species and demonstrated that female-specific ornaments evolved multiple times independently from unornamented ancestors. Their results revealed a strong association between mating system structure and ornament evolution; species with strongly female-biased operational sex ratios in mating swarms exhibited more pronounced female ornamentation. This pattern supports the idea that intense competition among females for access to males drives the evolution of exaggerated female traits.

Reproductive Dependence on Nuptial Gifts

The degree to which females depend on nuptial gifts varies considerably among dance fly species. Hunter and Bussière (2019) showed that in

ornamented species, egg development was strictly dependent on successful mating and the receipt of nuptial gifts. Unmated females in these species failed to develop mature eggs, underscoring the central role of male-provided resources

in female reproduction. In contrast, unornamented species exhibited weaker (facultative) dependence on mating for egg development, suggesting that reliance on nuptial gifts has evolved in tandem with female ornamentation and sex role reversal.

Male Strategies and Sexual Conflict

Males are active participants in the sexual selection process, as selection acts on their ability to obtain, produce and present nuptial gifts, thereby influencing both male behaviour and morphological traits associated with prey capture and mating success (Murray *et al.*, 2022). LeBas *et al.* (2004) showed that in *R. sulcata*, smaller males carrying smaller gifts achieved higher mating success than larger males with more substantial

offerings. This counterintuitive result suggests that constraints related to flight performance and manoeuvrability can outweigh the benefits of large gifts, favouring efficiency over extravagance.

In addition, males in some Empidinae species have evolved deceptive strategies of their own. Rather than providing nutritious prey, some males present inanimate or low-quality items such as empty prey husks, plant seeds or silk-wrapped debris. Others exaggerate the apparent size of gifts using silk balloons or enlarged tarsal segments that mimic prey items. These forms of male deception, documented by Daugeron *et al.* (2011), further illustrate the ongoing sexual conflict over reproductive investment, with each sex evolving strategies to maximise its own fitness.

Conclusion

Taken together, these studies reveal a highly dynamic mating system in which males and females are locked in a continual evolutionary arms race. Nuptial gifts, female ornamentation, male choice and deceptive signalling all interact to shape reproductive outcomes. Rather than following a fixed pattern, the direction and intensity of sexual selection in dance flies can shift depending on ecological conditions, population structure and the relative costs and benefits of reproduction for each sex.

Because of their remarkable diversity of mating strategies and their frequent departures from conventional sex roles, Empidinae dance flies have emerged as valuable model organisms for studying the evolution of mating systems, sexual selection and sexual conflict. However, progress in this field has been constrained by practical challenges. Dance flies often fail to exhibit natural behaviours under laboratory conditions

and their mating swarms are fast-moving, short-lived and difficult to observe in the field. Despite these obstacles, continued research on dance flies promises to yield important insights into how complex reproductive behaviours evolve and persist. Ultimately, the courtship behaviour of dance flies serves as a powerful reminder that the rules of reproduction are far from universal. By reversing traditional sex roles and embracing both honesty and deception in sexual signalling, these small insects challenge long-held assumptions about mating systems and underscore the creative force of evolution in shaping life's diversity.

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