

molecular corset also highlights its role in shaping tissues, and raises the possibility that the polarised arrangement of ECM fibrils will be important in other morphogenetic processes.

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Sexual Selection: Do Flies Lie with Asymmetric Legs?

A newly described species of empidid or ‘dance fly’ shows a bizarre polymorphism in their forelegs, which presumably serve as a mating lure. This trait may have evolved by frequency-dependent deceptive male signalling.

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Empidid flies are well-known for the extraordinary variation in their mating systems. To increase their chances of securing a mating, the males of most species donate prey items, captured flies of other species, as nuptial gifts to females [1]. However, empidid flies show a remarkable extent of apparently deceptive sexual signals in both sexes [2,3]. The nuptial gift often leads to reversed sex-roles, such that females compete for the attention of choosy males [4]. This role reversal can be reflected in sexually selected body parts. The females of some species, for instance, possess flattened scales on their legs which, when held against the body, increase the apparent girth of the female’s abdomen — males show a preference for rotund females [5]. In *Rhamphomyia longicauda*, females take this trick a step further by inflating their abdomen using specialised abdominal sacs [2,6]. Male empidids, however, can be especially devious: in some species, males present the female with a real nuptial gift, an edible insect, while the males of other species present their mates with dried insect remains or inedible items wrapped in silk. In some species, the males take this deceit further and entice females

using an entirely empty balloon of silk [7,8]. Even in species which offer genuine prey gifts, males sometimes cheat by using an inedible ball of willow fluff as a substitute gift, such as in *Empis opaca* [9]. Female *Rhamphomyia sulcata* can be experimentally induced to mate with males whose nuptial gift has been replaced by a cotton ball [10].

Now, a recently discovered species of empidid fly from the slopes of Mount Fuji, *Empis jaschhoforum*, provides an extraordinary addition to the list of apparently deceptive traits in empidid flies [11]. The new species shows remarkable and previously undescribed variation in a male sexual ornament, with some males being unornamented while others can sport ornaments on either or both forelegs [11]. How this extraordinary variation is maintained by evolution in this species is currently not understood, but one intriguing possibility is that it could reflect antagonistic frequency-dependent evolution between males and females in a sexual system driven by cheating.

When collecting exemplars of the new species, Daugeron *et al.* [11] found that some males of *E. jaschhoforum* possess greatly enlarged tarsi (‘foot’ segments) on the first pair of legs, fringed with long hairs, which probably mimic a prey gift. Other species of

empidids are also known to have clubbed feet which resemble males holding prey items. However, what is remarkable about the new species is that the possession of enlarged foreleg tarsi was found to vary greatly between individual males: in one of 33 males sampled, both tarsi were enlarged; in 14, only one, either right or left, was enlarged, while the remaining 18 males showed no modification at all (Figure 1).

How could such an unusually high level of polymorphism and asymmetry be maintained? The authors ruled out the possibility that the asymmetrical males were gynandromorphs (mosaic animals containing male and female parts of the body), as no males possessed other female characters. Partial feminisation due to infection by parasitic nematodes was also thought unlikely. Moreover, differences in body size between males did not appear to account for the extent of expression of the secondary sexual traits, as occurs in some species [12] — males with modified legs were no larger than those with un-modified legs. Daugeron *et al.* [11] thus suggest that a type of disruptive selection could favour both males with the enlarged tarsi, which may be better at attracting females from a distance, and males with unmodified legs, who may be subject to less drag and be able to impress females at close range with better aerobic skills [8]. Alternatively, if the tarsi do mimic males carrying genuine nuptial gifts, frequency-dependent selection might act. In general, mimicking strategies work better when the mimics occur at a lower frequency than the model they are mimicking, as in classic Batesian model–mimic systems,



Figure 1. Variation in the forelegs of male *Empis jaschhoforum*.

A male fly in which both forelegs are modified. The insert shows the forelegs of a male with only one foreleg modified; this is the most common morph. Photos by A. Stark and C. Daugeron.

where there would be frequency dependent selection between mimicking and non-mimicking males.

However, we need a further explanation of why there should be such variable antisymmetry in leg modification. If the swollen legs mimic prey items, having only one exaggerated leg might be most convincing (males usually carry only one nuptial gift). The species is probably sex-role reversed or at least shows mutual mate choice, because females have hairy legs, as in other empidids with male mate-choice [2]. But how does such adaptive antisymmetry arise mechanistically? Could the developmental mechanism involved lead to arbitrary sidedness, or has variable antisymmetry itself evolved as part of the frequency-dependent variation in the polymorphism? Many animals seem to have evolved consistent asymmetry without much trouble — most gryllid crickets, for example, have consistently asymmetrical wings due to their method of stridulation [13] — so the arbitrary asymmetry seen here remains intriguing. Another case of variable antisymmetry is seen in fiddler crabs, where either the left or right claw is greatly enlarged and used as a visual signal to attract females [14]. The reasons for why this asymmetry is apparently random are obscure. As the claw is used in male–male competition as well as a visual signal, the equal frequencies of left and right-handed

enlargement may provide a nice biological analogy of a resolution of the frequency-dependent advantage thought to accrue to left-handed boxers. There is another case of asymmetry as a frequency-dependent polymorphism; the famous examples of side-mouthed predatory fish, which attack prey from either the left or right side and show morphological ‘handedness’ of their mouths [15]. Prey alertness provides frequency-dependent selection maintaining the frequencies around 50%. Frequency-dependent selection involving more than two morphs is very rare, but other examples do exist, including game playing side-blotched lizards [16] and isopods with alternative male mating morphs, such as a female-mimicking sneaker morph [17].

There are many aspects of the biology of *E. jaschhoforum* which remain to be discovered. Samples were collected using Malaise traps so the behaviour of live specimens sadly could not be observed. Do males with un-modified forelegs carry genuine nuptial gifts instead? Exactly how do males use their modified fore-tarsi during swarming, courtship and copulation? How do the frequencies of the morphs vary between years? Do males or females form mating swarms? (The possession of pinnate leg scales in the females of this species suggests that females may swarm [2,7].) Do females prefer males with only one swelling? Daugeron *et al.* [11] suggest this new species has the potential to provide a novel model

system for the study of the evolution of secondary sexual traits and body asymmetry. It is certainly a further addition to the bizarre world of mating strategy variation in empidid flies.

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