Quick guide: peacock flies

C. Ruth Archer & David J. Hosken

Centre for Ecology and Conservation, University of Exeter, Penryn, Cornwall, TR10 9FE, UK

Email: c.archer@exeter.ac.uk

In most animals, only one sex displays to charm potential mates, and in the vast majority of cases, it is males that sexually signal to attract females. Peacock flies may be an exception to this general pattern as both males and females perform extravagant displays. Why do they do this?

What are peacock flies?

Peacock flies (*Callopistromyia annulipes*) are members of the large and varied group of picture-winged flies (the Ulidiidae) that includes their two-species genus. They are small (ca. 4mm long) and rather pretty, but it is their behaviour, first described over 100 years ago, that makes them so striking for such a small animal. Many videos of dancing peacock flies can be found on-line. In them, mottled flies perform a stuttering sort of dance, with wings held vertically to form striking patch-worked, iridescent-fans, which are moved in an arrhythmic jerking motion, while flies periodically runs to and fro. It is this behaviour that gives the flies their common name, as the way the wings are brought together, as well as their coloured patterns, strongly evoke the more familiar peacock's tail (Figure 1). Normally, these sorts of display are performed by males trying to attract a female mate: this is what male peacocks do for example. In peacock flies however, it seems that both males and females engage in these dances. So why are both sexes signalling? One idea is that in peacock flies are a species in which there is mutual mate choice.

What is mutual mate choice?

Mutual mate-choice occurs when both males and females are choosy of their potential mates. This is unusual, as typically it is males that compete for females, and females choose among males. That is, males tend to be more competitive and females more choosy. This general pattern has its roots in anisogamy – the difference in gamete size that defines the sexes. Males produce many small sperm, females relatively few larger eggs, and the law of supply and demand means females can afford to be more choosy, while males must compete for access to the limited supply of eggs. However, this rule is not absolute. In some species, notably pipe-fish, there is complete sex-role reversal and males choose from competing females, while in other species both sexes are choosy (mutual mate choice). This mutual choice manifests itself as both females and males courting and accepting or rejecting potential sexual partners, and given the wide-spread occurrence of female mate-choice, understanding heightened male choosiness seems to be the key to explaining it.

Why are some males choosy?

Given that eggs are in short supply, why are males in some species so choosy? For male mate-choice to occur, there must be variation in female quality to give males something to choose amongst and the variation present must be large enough to make choice worthwhile. These pre-requisites are probably met in many species, as for example larger females are often more fecund and hence should be favoured partners. Perhaps more importantly, males are more likely to be picky when their costs of reproduction are high. This is because when reproduction is costly, caution should be taken not to waste difficult to replace reproductive effort. Reproductive costs are often greatest in species where males provide parental care and, not surprisingly, in these groups males are often the choosy sex, or at least display some mate choice. Humans being a case in point. But even when males do not provide any care for offspring, the costs of mating can still be high. For example, intense courtship can reduce male lifespan and making large ejaculates can be hugely expensive. This is true of some insects where a single ejaculate can represent more than 10% of a males' body-mass. If mating is costly for males, then there may be strong selection for them to preferentially mate with high quality females to ensure they are not wasting costly investment.

Then why aren't all males choosy?

Although being choosy has clear benefits, there are also costs to choosiness. For example, if picking mates requires time that could otherwise spend mating, then males may improve their fitness by mating with larger numbers of low-quality females instead of searching for high quality partners. Similarly, if males encounter females sequentially or at very low rates, then the cost of passing up any mating opportunity is high and males should be less discriminate about their mates. Furthermore, it may not always be obvious which females are of high quality, because females may actively conceal quality to avoid male harassment, in which case male choosiness could be difficult to sustain. All this means that we should probably only anticipate mutual mate choice in species where there is variation in female and male quality, the costs of mating are high and the benefits of being choosy are even higher. The relative magnitude of costs and benefits can also vary temporally and spatially. This is exemplified by an Australian bushcricket where males transfer a nutrient rich nuptial gift at mating. Here, females, but not males, are choosy when food is plentiful, but when food is scarce males become choosy and females competitive. This is because when food is rare, males cannot easily make nuptial gifts, but females are hungry and so compete for this now limited resource.

If both sexes are choosy, what are the benefits of choice?

The benefits of being choosey have mostly been investigated from a female perspective. Females often choose mates that offer direct, non-heritable benefits of mating (e.g. parasite free males, nuptial gifts, large territory) or indirect genetic benefits that improve the viability and/or attractiveness of offspring.

Males may also pick females on the basis of heritable female quality. This may be particularly true in monogamous species, where males cannot simply increase offspring number by

mating with more females, and so try to improve their fitness by mating with high quality females, thereby siring high-quality young. This is the case in male barn owls (*Tyto alba*), who prefer females with more black spots on their plumage: a heritable trait that signals superior immune function. Males may also pick mates on the basis of how well they are likely to provision offspring. This appears to be the case in the blue-footed booby where males prefer females with more vibrant foot pigmentation, which indicates that females are in good condition and hence good at catching food.

In more promiscuous species, a male's fitness may be more dependent on *how many* offspring he can sire than on the quality of offspring, and so in at least some species, males appear to prefer highly fecund females. If fecundity is heritably this may also provide indirect genetic benefits via daughter quality, but males often pick females that are fecund because of their age or state (i.e. virgin vs. non-virgin). In these cases, choosing fecund females provides a direct benefit (more offspring) to male mate-choice. Male red-legged salamanders, *Plethodon shermani* use this kind of cue when differentiating between mates, and so perform a longer courtship "foot dance" for more gravid females. Clearly, males make their mating decisions on a broad range of cues and the sex-specific strategies for picking mates may align (e.g. both sexes prefer high genetic quality in their mates) or not (e.g. female choice for male quality, but male preference for age or state).

Does mutual mate choice explain why some females are showy too?

In some species both sexes have exaggerated sexual ornaments, showy colours or conspicuous behaviours (e.g. song). In females, these traits may evolve as a correlated response to selection on males because the same gene(s) are expressed in both sexes. However, many females are not ornamented and female transitions from ornamented to non-ornamented states show that sexes can clearly evolve independently, at least after some evolution of genetic architecture (i.e. so that each sex can express the shared genome in a sex-specific manner). In these cases, the lack of ornamentation may reflect naturally selected costs of female displays. However, sexual selection can also be important in the evolution of female ornamentation. For example, in the African cichlid fish *Pelvicachromis taeniatus,* female ornamentation reveals important information about female quality to mates (e.g. readiness to spawn, female quality, offspring fitness) and is under strong sexual-selection by male choice, and by natural selection through female-female resource competition too.

What are the wider evolutionary consequences of mutual mate choice?

Mutual mate choice is probably under appreciated, but can facilitate sympatric speciation and help to maintain species barriers after population divergence has occurred. Mutual mate choice may also affect the mean fitness of a population. It can increase population level fitness if, for example, males better provision preferred females and so increase the contribution of these females to the next generation. Alternatively, mutual mate choice may decrease mean population fitness if male harassment harms high-quality, more preferred females and so reduces their reproductive output relative to that of low quality females.

Does mutual mate choice apply to peacock flies?

While the peacock flies display has been implicated in mutual mate choice, how likely is this to be the case? Many of the criteria for mutual mate choice are probably met in peacock flies. Female fecundity often varies in insects as a function of size and, if males dance to attract females, then the costs of male mating may be high. That said, and assuming female dance is energetically expensive, it is rather surprising to find a male insect picking females on the basis of an energetically demanding female display. Most male insects pick mates on the basis of traits that signal female fecundity (e.g. size, mating status, age) and while the elaborate peacock-fly dance and colouring seem likely to reveal information on female quality, it probably reduces female fecundity. However, some male insects do prefer mates that are likely to produce high quality offspring rather than lots of them. For example, male cockroaches *Blattella germanica* prefer to court unrelated females. Given that peacock flies have even been reported to display towards a stray entomologists finger, might the primary function of this dance in females be related to competition over territories?

In short, we don't know, but the fact that dances occur in places that are not likely to be ideal resource patches (like car windscreens), a sexual role seems likely. To improve our understanding of male mate-choice, female competition and mutual mate choice, more research into these somewhat ignored "non-traditional" behaviours is needed, and peacock flies seem a good place to start.

Where can I find out more?

Baldauf, S,A., Bakker, T.C.M., Kullmann, H., and Thünken, T. (2011). Female nuptial coloration and its adaptive significance in a mutual mate choice system. Behav. Ecol. *22*, 478–85.

Kokko, H., and Johnstone, R.A. (2002). Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. Phil. Trans. R. Soc. Lond. B *357*, 319–330.

Edward, D.A., and Chapman, T. (2011). The evolution and significance of male mate choice. Trends Ecol. Evol. *26*, 647–54.

Roulin, A., Jungi, T.W., Pfister, H., and Dijkstra, C. (2000). Female barn owls (*Tyto alba*) advertise good genes. Proc. R. Soc. Lond. B *267*, 937–41.

Torres, R., and Velando, A. (2005). Male preference for female foot colour in the socially monogamous blue-footed booby, *Sula nebouxii*. Anim. Behav. *69*, 59–65.

Eddy, S.L., Wilburn, D.B., Chouinard, A.J., Doty, K.A., Kiemnec-Tyburczy, K.M., and Houck, L.D. (2016). Male terrestrial salamanders demonstrate sequential mate choice based on female gravidity and size. Anim. Behav. *113*, 23–29.

Bonduriansky, R. (2001). The evolution of male mate choice in insects: a synthesis of ideas and evidence. Biol. Rev. *76,* 305–339.

Almeida, C.R., and de Abreu, F.V. (2003). Dynamical instabilities lead to sympatric speciation. Evol. Ecol. Res. *5*, 739–757.

West, R.J,, and Kodric-Brown, A. (2015). Mate choice by both sexes maintains reproductive isolation in a species flock of pupfish (*Cyprinodon* spp) in the Bahamas. Ethology *121*, 793–800.

Hosken, D.J., Alonzo, S., and Wedell, N. (2016). Why aren't signals of female quality more common? Anim. Behav. *114*, 199-201.

Lihoreau, M., Zimmer, C., and Rivault, C. (2008). Mutual mate choice: when it pays both sexes to avoid inbreeding. PLoS One *3*, e3365.

Simmons, L.W., and Bailey, W.J. (1990). Resource influenced sex roles of zaprochiline tettigoniids (Orthoptera: Tettigonidae). Evolution *44*, 1853-1868.

Figure Legend.

Figure 1. A peacock fly. Note the position of the wings, which are held this way during displays (image courtesy of Katja Schulz).