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Accepted for publication in *Proceedings of the Royal Society B: Biological Sciences*, published by the Royal Society. The definitive published version is available at: https://doi.org/10.1098/rspb.2018.1525

Sexual selection on multiple female ornaments in dance flies

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Abstract

Sex-specific ornaments typically occur in males, but they can also develop in females. While there are several models concerning the evolution of male-specific ornaments, it is not clear how, or under what circumstances, those models apply to female-specific ornament evolution. Here, we present a manipulative field experiment that explores the theoretical 'trait space' of multiple female-specific ornaments to study how these unusual traits evolved. We measured the attractiveness of two female-specific ornaments (pinnate leg scales and inflatable abdominal sacs) in the dance fly *Rhamphomyia longicauda* in a wild mating swarm. We found significant directional preferences for larger ornaments of both types, however, variation in one of the ornaments (abdominal sacs) was almost three times more effective at improving attractiveness. The abdominal ornament was consistently effective in increasing attractiveness to males regardless of leg ornament expression, while leg ornament size was only effective if abdominal ornaments were very small. These results are consistent with predictions from a sexual conflict model of ornament expression in supporting the probable role of deception in the evolution of female-specific ornaments among dance flies. Sexual conflict can be an important force in generating elaborate sex-specific ornaments in females as well as males.

Key Words

multiple ornaments, sexual conflict, sexual selection, female ornamentation, dance fly, honest signaling

Introduction

Sexually selected ornaments are among the most fantastic and bizarre traits found in nature. While extravagant ornaments undoubtedly can improve an individual's reproductive success [1], they might also trade off with other important life history traits. Benefits from increased reproductive success must, therefore, outweigh any costs in order for an ornament to persist. The trade-off between sexual displays and other characters may be particularly important in explaining the rarity of female ornaments [2, 3]. Compared to males, female reproductive fitness is typically more resource limited [4], so investing in costly sexual traits might decrease fecundity in females more often than it constrains reproductive success in males [5].

Given their potential costs, the persistence of female ornaments in a few rare taxa is puzzling [6-9] and remains understudied. The problem is probably resolved in some taxa because what appear to be ornaments have evolved for reasons other than for improving sexual attraction [9-13]; in such cases the costs of investing in elaborate traits are outweighed by advantages in other aspects of life history. For example, female ornaments might evolve primarily for the purposes of intrasexual competition for resources rather than for access to mates [6, 7, 13, 14].

If, however, female ornaments arise through adaptive mate choice (e.g., via male choice for honest signals of fecundity) mediated by sexual competition, the resource investment required to express ornaments must be compensated by the subsequent payoff of winning contests for mates. One clear scenario in which this is true is if resources used to construct ornaments are not limiting for offspring production [5]; in that case spending resources on ornaments need not compromise a female's reproductive effort. However, such a scenario underlines a further problem for female ornament evolution via male choice: the ornaments must not only compensate for their expression costs, but also honestly provide information to males about female reproductive value [7, 15, 16].

A further, and potentially more serious, constraint on the signal value of ornaments could occur if females store sperm from multiple partners. In such cases, the expected benefit of ornamentation to females (in terms of heightened attractiveness) is frequently associated with a cost to their mates; males should generally prefer relatively unattractive but monandrous females over attractive ones that present higher risks or intensities of sperm competition [5, 8, 17, 18]. In other words, the heightened attractiveness of adorned females dilutes the share of eggs to which any individual male has access, which should undermine the usefulness of any attractive trait for signaling reproductive value. However, the cost to a male of mating with an attractive female would be reduced if males were able to identify females in which the conditions of sperm competition are most favourable. In many insects, the last male to mate before oviposition often has a distinct paternity advantage, and males could conceivably identify females that are ready to oviposit by preferring mates with large abdomens that indicate late stages of vitellogenesis [8, 19].

Sexual ornaments might therefore provide males with cues of female value, including egg number and egg development stage (i.e., egg size) that are difficult to perceive externally. Previous studies of female-specific ornaments [15, 20-22] have assessed the value of female ornaments as honest indicators of fecundity or egg maturity providing mixed support both across and within species. Ornaments are often positively correlated with female egg numbers or size, but the degree to which the signal improves male abilities to discern female reproduction (e.g., relative to the situation in an unadorned ancestor) is not clear. For pipefish, temporary female ornaments served to honestly signal female mating success and fecundity [20]. In a study of dance flies [8], abdomen size predicted 23% of variation in egg size in *Rhamphomyia longicauda*, a species with multiple ornaments, but the unadorned female abdomens of a closely related species (*R. sociabilis*) predicted much more (72%) of the variation in egg size [8]. The authors argued that female ornaments were deceptive traits rather than honest signals, which served to improve female access to food gifts provided by males during copulation, even though the males themselves gained relatively little information from the ornaments [8]. Further, the relatively small amount of egg size variation predicted by abdomen size in *R. longicauda* [8] could be indicative of a cost associated with producing ornaments in some females that are forced to trade off egg quality (in this case, egg size) in order to attract mates, as predicted by Fitzpatrick *et al* in [5]. In another study of *R. longicauda* [22], abdominal ornament size predicted only 6% of variation in fecundity, but 49% of variation in egg size; however, ornaments on the legs had no significant relationship with either egg number or size. In *R. tarsata* (a congener of

R. longicauda and a species that displays only leg ornamentation), leg ornament expression predicted female fecundity better than other morphological traits, but did not significantly predict egg size [15]. In fact, LeBas et al [15] argue that positioning of legs during courtship displays may actually impair male assessments of egg size. A clear constraint on the signal value of any insect exoskeleton trait (including the ornaments of dance flies) is that such characters are fixed in size at eclosion, and cannot therefore track the development of ovaries that occurs during an adult's lifespan. While such characters might conceivably indicate overall size, and therefore larval resource acquisition, it is hard to imagine how they might improve male detection of female ovarian condition. Clearly, the role of female ornaments as signals of female reproductive fecundity or ovarian maturity is, at best, unclear.

Dance flies from the subfamily Empidinae (Diptera: Empididae) display considerable interspecific variation in mating system. Roughly a third of the species from the group feature female ornaments, including species with some of the most extravagant female-specific ornaments yet described [8, 15, 23]. Empidine ornaments can take several forms, including darkened, patterned or enlarged wings, feathery "pinnate" leg scales and, more rarely, inflatable abdominal (pleural) sacs [23, 24]. Males of many species provide direct benefits to females by offering a prey item as a nuptial gift during copulation. In most species, females are not known to hunt as adults, and seem to rely on protein from male-provisioned gifts to supplement their nutritional reserves [25]. As is typical for insects, female dance flies can store sperm from many males, and eggs are only fertilized immediately prior to oviposition. Although the precise mechanics of sperm precedence are not yet known with certainty, two lines of evidence suggest that last male sperm precedence is operating. First, the spermathecae are broadly spherical and sclerotized (our own observations), which means that they cannot expand in volume indefinitely, but rather facilitate displacement of one ejaculate by another through flushing. Second, the mean proportion of paternity assigned to the most successful genotype is not sensitive to total mate number, as predicted if the last mate displaces rival ejaculates [26].

Females of the long-tailed dance fly, *R. longicauda*, possess two extravagant ornaments: pinnate scales over the length of all femora and tibia, and abdominal pleural sacs that are inflated just prior to swarming. Relatively few empidine dance fly species have abdominal ornaments, whereas pinnate leg scales are reasonably common throughout the group (see [23, 24, 27]). Both ornaments appear to exaggerate a female's apparent size and to improve female attractiveness [8] in the highly competitive context of *R. longicauda* mating swarms (which are usually heavily female-biased; [8, 22, 28]).

Previous work using plastic models of females within the mating swarm showed that *R. longicauda* males are more attracted to larger females, consistent with directional selection on ornament size [8]. However, Wheeler et al. [16] found that females with intermediate levels of ornamentation were more likely to mate than either extreme. This inconsistency of selection across episodes remains unexplained. One possibility is that patterns of selection are inconsistent across populations of dance flies, while another is that the initial attraction during male approaches is only part of what determines eventual mate choice. In order to clarify these possibilities, we experimentally manipulated the relative size of both leg and abdominal ornaments using plastic models similar to those employed by Funk and Tallamy [8] and quantified both the independent effect of each trait on attractiveness, and the combined effects of both.

Methods

Study system

In Northeastern North America, courtship swarms of *R. longicauda* form annually along riverbanks and occur from the end of May until the beginning of July [25, 29]. Swarms are crepuscular, form beneath gaps in the forest canopy, and are typically strongly female-biased [8, 23, 30]. Before they enter the swarm, female *R. longicauda* swallow air to inflate abdominal sacs that exaggerate their body size. Within the swarm, females fly parallel to the ground and position their pinnate-scaled legs laterally around their inflated abdomen, which further exaggerates their size when they are viewed from below.

Female silhouette creation

We independently manipulated both female ornaments and mating swarm position in order to disentangle the partial effects of selection for attractiveness on each of the ornamental modules (abdomens and leg scales). There is strong natural covariance between both ornament types in wild female flies (because females who accumulate more resources as larvae are likely to invest heavily in both ornaments; [31], which makes separating the effects of selection on each ornament in real specimens difficult [16]. Our artificial silhouettes break apart the natural covariance, and display combinations of ornaments that do not exist in nature. This manipulation improves both our ability to visualize the whole fitness landscape, as well as our statistical power for measuring partial selection on each character; it also allows us to measure the combined effects of variation in both ornaments (i.e., to determine if the signals are complementary or otherwise).

We created 25 artificial female silhouettes (Figure. 1) using a template provided by David Funk (Figure. 3 in [8]). We manipulated the abdomen size independently of leg scales such that we had five different abdomen widths: mean +/-2SD, mean +/-SD, and population mean (estimates of population means and standard deviations come from Wheeler [16]). Although we initially attempted to similarly restrict our models' pinnate scales to the range of natural variation, we could not precisely and consistently control the apparent size of the legs across models, which made such fine scale variation impractical. Consequently for leg scales we used a larger range of sizes including legs similar to males (the ancestral condition) and legs twice as large as the largest found in nature: mean +/-10.8SD, mean +/-5.4SD, and population mean.

We printed the artificial silhouettes on plastic transparencies and attached each of them to a 30cm length of fishing line. To simulate the positioning of female dance flies in the mating swarm, we fastened fishing weights above the models to keep the silhouettes parallel with the ground. We placed a stake on either side of the swarm site (1.5m apart) with a piece of fishing line stretched between them 1m above the ground. For each sampling interval (e.g., each swarming event), we then chose five silhouettes at random (without replacement) from the panel of 25 and spaced them 15cm apart across the centre of the line such that the flanking silhouettes were approximately 37cm from a stake. This design ensured that our artificial silhouettes were usually greatly outnumbered by wild females; natural swarms vary in size over time and space, but during peak swarming can feature hundreds of flies packed rather densely into the swam space (with gaps of a few cm between adjacent flies). Our initial trial date includes observations for only two silhouettes, rather than five. Three silhouettes, and their associated male approach data, were discarded when they were found (after the trial) to have errors associated with their printing. As a consequence, ten days of observations yielded data for 47 silhouettes being approached by males.

Experimental set up

We carried out male mate choice trials from June 13-22, 2012 at the study site (used for previous studies of this species [16, 30, 32]), located near Glen Williams, Ontario, Canada on an island in the Credit River (43$_{o}$41’11”N, 79$_{o}$55’34”W). A trial consisted of a single swarming event at dawn (roughly 4:45am) lasting approximately one hour. We set up female silhouettes the evening before a trial began (at least eight hours in advance) so that they were already *in situ* when the swarm started. Each trial began when a male first approached one of the female models, by which time wild females had always already joined the simulated swarm, and outnumbered the artificial flies. We recorded data by directly scoring male approaches to silhouettes within the swarm. We used one observer who was blind to the phenotypes of the female silhouettes being scored. Following methods described in [8], an approach to a model was recorded when a male fly carrying a nuptial gift hovered approximately less than 5cm beneath a female silhouette for more then 3 seconds. We did not record rejections (i.e. males that did not pause beneath silhouettes). Swarm position, ornament sizes and number of male approaches were tallied for each silhouette on each date. We concluded a trial when five minutes passed without observing a male approach (typically between 5:45 and 6am). All raw data are available as electronic supplementary material (ESM1).

Statistical Analyses

We computed all analyses using R statistical software [33]. To investigate the relationship between female silhouette morphology and male attraction, we fit all models with the number of approaches by courting males as the response variable and ornament expression levels and the swarm position of silhouettes (distance from the centre of the swarm; position within the swarm is thought to affect attractiveness [32]) as predictor variables. We scaled morphological predictors in phenotypic standard deviations to facilitate comparisons between traits. Because our standardized coefficients are not strictly equivalent to selection gradients, (attraction is only the first stage of mating success), they cannot be straightforwardly translated into fitness [16].

The nature of selection varies as a function of swarm composition, which can differ substantially from day to day [22]. Therefore we built generalized linear mixed models with Poisson error and log-link (because attraction is measured in male approaches and is a count variable), including "date" as a random effect (to represent the potentially distinct composition of each swarm), and using the lme4 package in R [34]. Pinnate leg scale size, abdomen inflation and position within swarm were fit as fixed effects. We included each predictor variable as well as its square and cross-products in order to assess curvilinear and correlational effects of morphology on attractiveness [35]. We did not fit a three-way interaction for these data because we wanted to mainly focus on correlational selection. We illustrate the partial effects of each ornamental trait by plotting the fit effects after setting the other covariates to their mean value.

One of the ways in which the two ornaments might conceivably combine to affect attractiveness is if males simply perceive the overall actual size of legs and abdomens together, irrespective of whether the ornament is located on the abdomen or legs. To test this hypothesis, we performed a separate analysis in which we regressed male approaches on the total area (mm^2) contributed by each ornament type to the silhouette area (instead of the standardized trait size). If males are primarily concerned with the total size of ornaments, we expect to see similar improvements in attractiveness for an additional unit of female silhouette area, regardless of whether that increase in area comes from leg scales or abdominal inflation. By contrast, if the abdominal ornament represents a recent evolutionary innovation brought about by increasing levels of male resistance to deceptive leg pinnation, we predict that abdominal ornaments should be more effective at improving attractiveness than leg ornaments, whether these ornaments are computed in terms of absolute area or phenotypic standard deviations. All code is available as electronic supplementary material (ESM2).

Results

We recorded a total of 1479 male approaches over the course of ten mating swarms. We cannot be sure of exactly how many males this represents, but given the large number of receptive females, this number is unlikely to represent many repeated approaches by the same male. Consistent with Funk and Tallamy [8], and our own predictions, males preferentially approached female silhouettes displaying larger ornaments (leg scale pinnation B = 1.35 ± SE 0.379; z = 3.57; $P < 0.0001$; abdomen size B = 3.72 ± 0.438; z = 8.50; $P < 0.0001$; Table 1). Males were also more likely to approach and court a female silhouette if it was positioned near the centre, rather than the periphery, of the swarm (swarm position B = -2.94 ± 0.216; z = -13.6; $P < 0.0001$; Table 1, Figure 2).

Figure 3 illustrates the partial effects of abdomen and leg scale size on numbers of male approaches. We have superimposed the raw data to assist with visualization, but note that much of the variation in attractiveness is explained by orthogonal dimensions of the silhouette phenotype that are accounted for in the estimation of the partial effects. We also note that although the effects illustrated in Figure 3 appear curvilinear, this is due to the back-transformation from loglinear phenotypic space; on the log scale there was no evidence of significant quadratic selection on either of the ornaments (leg scale pinnation B = -0.278 ± 0.252; z = 1.11; P = 0.269; abdomen size B = -0.0731 ± 0.433; z = -0.169; P = 0.866; Table 1). Instead, we found straightforward directional selection for both ornamental traits: males are more likely to approach female silhouettes with larger pinnate leg scales and larger abdomens. Although the variation in silhouette pinnate leg scales was larger than variation in abdominal ornamentation, (+/- 10.8SD compared with +/- 2SD, respectively), male dance flies responded much more strongly to variation in abdomens than in pinnate leg scales (Figure 3).

We also found a significant negative coefficient associated with the term describing an interaction between abdominal and leg ornamentation (B = -0.0136 ± 0.0031; z = -4.36; P < 0.0001; Table 1). Figure 4 helps to illustrate this nonlinear correlational effect: the convex curvature near the apex shows that the two ornaments combine in a less than additive way. Furthermore, while abdominal ornaments are always important for attracting mates, pinnate leg scales are only important if a female's abdomen is small.

In order to compare the effects of both ornaments on attractiveness as a function of overall signal area (rather than in terms of phenotypic variation), we performed the same analysis as that described in Table 1 except using the area (in mm^2) of each ornament as a predictor. Table 2 illustrates that abdominal area still has a stronger effect on attractiveness than leg scales; a given unit of silhouette area is nearly twice as effective at improving attractiveness if it contributes to the abdomen ($B = 11.29 \pm 1.86$; $z = 6.07$; $P < 0.0001$) rather than the leg ($B = 6.98 \pm 1.59$; $z = 4.38$; $P < 0.0001$).

Discussion

We measured male attraction to two female-specific ornaments in *R. longicauda* and show that males are attracted to both ornaments, but that variation in inflatable abdominal sacs has a stronger effect on attractiveness than variation in pinnate leg scales. Furthermore, rather than combining additively, as predicted for multiple ornaments that reinforce an honest signal of quality [36, 37], we found that large leg ornaments are only favoured when abdominal ornaments are small. This difference in selection is sustained whether we regress attractiveness on units of ornament area or phenotypic standard deviations, which suggests that the two ornaments are not simply acting together to reinforce a single signal of overall size. Below we discuss the implications of our study for understanding the nature of sexual selection on female dance flies.

The effect of mating swarm position on female attractiveness

Our results show that a female silhouette is more likely to attract courting males if it is displayed closer to the centre of the lek-like mating swarm (Figure 2). This finding is consistent with previous work on a male-lekking insect species, *Ceratitis capitata*, which found that male lek position was an important indicator of attractiveness [38]. Further, many studies investigating diverse taxa with lek mating systems have shown that centrally positioned males are the most attractive [39-41]. In many male leks, intra- as well as intersexual selection for a central position is described, however, in *R. longicauda* mating swarms, while we have compelling evidence for intersexual selection on swarm position (Figure 2), there is no evidence that females physically engage with one another [22, 32]. Previous work on *R. longicauda* swarm position [32] showed that female flies at the bottom of the swarm (where males enter) were larger than females higher up in the swarm. Our study suggests that the swarm may also be structured horizontally; with centrally located females possessing an advantage due to their proximity to the entry point for swarming males. Additionally or alternatively, being close to the periphery of the swarm might make individuals more vulnerable to predation. *Tetragnatha* spiders build webs around the periphery of *R. longicauda* mating swarms and dance flies are frequently preyed upon [42]. It is likely that being in the centre of the swarm means that both sexes are safer from spider predation, which could confer an advantage to centrally positioned silhouettes in the absence of any intraspecific competition for position.

How did multiple female ornaments evolve in dance flies?

Several hypotheses could explain how multiple female-specific ornaments arise in *R. longicauda*, including nonadaptive mate choice models (involving Fisherian processes, e.g., via sensory biases), adaptive models (e.g., honest signaling of direct or indirect benefits), and sexually antagonistic coevolution via sexual conflict.

Nonadaptive models [43, 44] could conceivably have contributed to the origin of female ornaments in dance flies, because larger objects are easier to perceive from a distance. Although these models may well have been crucial for the initial evolution or ornaments, however, the extravagance of pinnate leg scales and inflatable abdomens (and the presumably large costs that accompany their expression, (see[30, 45])) suggests that they are probably maintained by other mechanisms.

Adaptive models based on direct benefits are frequently invoked in systems featuring male choice, because variation among females in fecundity or sperm competition intensity is expected to be most important for choosing males [19, 46]. In dance flies, if ornaments can communicate the remaining time required for vitellogenesis, then males might favour females primarily because their chosen mates would be less likely to mate again prior to oviposition (assuming a last male paternity advantage in sperm competition; [8, 46-48]). Under this "honest signaling" hypothesis, female ornaments evolve in spite of their costs because they clarify or exaggerate an aspect of female phenotype that is difficult for males to discern from the unadorned female's phenotype [21].

Many previous studies investigating female ornamentation have concluded that ornaments serve to honestly signal female fecundity or egg maturity [15, 20-22]. In one sample from our study site, *R. longicauda* abdominal ornaments predicted 49% of the variation in egg size, but did not covary with fecundity; furthermore, leg ornaments did not predict egg size or number [22]. If female ornaments are generally serving to honestly signal mate quality to males, then we would expect that all ornamental traits should have evolved to correlate with some measure of female quality and that many would continue to do so. While it is possible that the two ornaments in *R. longicauda* evolved for different purposes [37], (e.g. maybe pinnate leg scales are important in intrasexual competition, while abdominal ornaments are important for intersexual competition) this explanation seems unlikely. First, there is no evidence of physical competition between swarming females [32] and second, in other dance fly species leg scales are known to be involved in intersexual selection [15]. In addition, the fact that dance fly ornaments are fixed in size at eclosion (and therefore cannot accurately reflect differences in ovarian development as vitellogenesis progresses) undercuts the potential for ornaments to be honest signals of female quality related to egg maturity. Finally, if exaggerated ornaments were strong signals, it is unclear why there would be such a striking divergence in selection between patterns of attraction to large ornaments (Figure 3; [8]) and copulation with individuals displaying moderate ornaments [22] in this species.

Our experimental design allowed us to assess how the ornaments combined to improve attractiveness. Both the combined effect of ornaments in standardized phenotypic space (Table 1, Figure 4) and our analysis of ornament area (Table 2) suggest that males are not simply attending to the overall size of a silhouette. This finding suggests that the multiple female-specific ornaments displayed by *R. longicauda* are not providing complementary information that additively contributes to male perceptions of mate quality [37].

An alternative to adaptive mate choice is that sexual conflict [49] helps to maintain ornament expression in this species (7). In fact, an arms race resulting from sexual conflict might explain the presence of two extravagant female ornaments in *R. longicauda* without requiring adaptive male choice: female ornaments are favoured because they improve female access to male-provisioned nuptial gifts, while males try to resist seduction by deceptive females by more closely inspecting mates prior to passing over prey. Cyclic bouts of sexually antagonistic coevolution [50] (in which females develop deceptive ornaments, and males evolve to resist them) would result in the development of a series of ornamental traits, of which some are only marginally effective thanks to selection for resistance by the opposite sex. As we found for pinnate scales, weaker selection is expected for more ancestral forms of ornamentation (pinnate leg scales are a prevalent form of ornamentation that is presumably relatively ancient among dance flies, although further phylogenetic study is needed [51]) compared to more recently derived ornaments (possibly including inflatable abdominal sacs). Moreover, pinnate leg scales are only effective at increasing attractiveness when the abdominal ornament is small; when abdominal sacs are large there is no discernible effect of pinnate leg scales (Figure 4).

Our results indicate that abdomens currently have a bigger influence on male impressions of female attractiveness than legs do. Perhaps there is an advantage for males that attend more closely to the details of a female's phenotype. We predict that inspections prior to pair formation (such as are observed in *R. longicauda*) should be especially prolonged in taxa featuring female ornaments that might otherwise disguise a female's ovarian condition. Similarly, any trait (such as visual acuity) that allows males to better distinguish between potentially deceptive ornaments and cues of actual fecundity should be favoured, and increase selection for novel ornaments that circumvent male resistance. The inflatable abdomens found in *R. longicauda* (and which may have evolved independently in a few other dance flies) may be more effective disguises because the degree to which they exaggerate fecundity may be difficult to detect by male sensory systems (i.e., it is probably harder to distinguish egg-filled from air-filled abdomens than it is to separately assess ovarian condition and pinnate leg ornament expression). It may also be easier to differentiate a deceptive fecundity signal that evolves on the legs compared to the abdomen simply because abdomen size is more closely associated with fecundity [19]. Interestingly, it is unknown whether *R. longicauda* females display variation in the amount they inflate their abdomens. While their maximum inflation size is fixed during the moult to adulthood, it is possible that the amount females inflate their abdominal sacs could vary with changes in environmental conditions, through space or time; it is possible that variable inflation could provide a mechanism by which egg development and ornament were temporally related.

We note that episodes of selection beyond initial attraction are undoubtedly important for determining mating success in dance flies. Following male approach, a female might undergo further assessment by her mate, resulting in discrimination against (overinvesting) females displaying the largest ornaments that are a greater cost to fecundity [5, 21]. In fact, Wheeler et al [16] showed that *R. longicauda* females displaying the largest ornaments are less likely than intermediately ornamented females to mate. An alternative explanation for the intermediate female advantage predicted by Chenoweth [21] and observed by Wheeler [16] is that females displaying the largest ornaments are actually too cumbersome (e.g. awkward for males to carry females with large, inflated abdomens) or heavy (e.g. larger pinnate scales) for some males to carry while flying united. Further study investigating the biomechanics of aerial copulation as well as quantifying the total load a male carries (female and nuptial gift) and traits related to a male's own load-lifting ability (e.g. wing load, aspect ratio) is required to fully assess the role of constraints in the evolution of female ornaments [52].

Although our findings are compellingly consistent with a partial role of sexual conflict, it is important to recognize that the alternative models of ornament evolution need not be exclusive, and that patterns from one species may not reflect the evolutionary trajectories for its entire subfamily. We need more work comparing selection on ornaments in other dance fly species, including taxa with different numbers of ornaments and levels of ornament expression. Such work will need to be creative to overcome the currently limited capacity for experimental work on these systems.

Tables

Table 1. Parameter estimates for a generalized linear mixed effects model describing how standardized ornamentation and swarm position traits affect female attractiveness. Variance component: 0.768.

	trait	estimate	standard error	z value	p value
linear	swarm position	-2.94	0.216	-13.6	<0.0001
	leg scale pinnation	1.35	0.379	3.57	<0.0001
	abdomen size	3.72	0.438	8.50	<0.0001
quadratic	swarm position	-1.02	0.187	-5.43	<0.0001
	leg scale pinnation	-0.278	0.252	-1.11	0.269
	abdomen size	-0.0731	0.433	-0.169	0.866
interaction	swarm position * leg scale	0.0078	0.0067	1.16	0.246
	swarm position * abdomen	-0.0196	0.0294	-0.667	0.505
	leg scale * abdomen	-0.0136	0.0031	-4.36	<0.0001

Table 2. Parameter estimates for a generalized linear mixed effects model describing how area (mm^2) of ornamentation and swarm position affect female attractiveness. Variance component: 0.782.

	trait	estimate	standard error	z value	p value
linear	swarm position	-4.39	2.44	-1.8	0.0725
	leg scale pinnation	6.98	1.59	4.38	<0.0001
	abdomen size	11.29	1.86	6.07	<0.0001
quadratic	swarm position	-1.00	0.188	-5.32	<0.0001
	leg scale pinnation	-0.273	0.235	1.161	0.246
	abdomen size	-0.0894	0.43	-0.208	0.835
interaction	swarm position * leg scale	0.114	0.118	0.966	0.339
	swarm position * abdomen	-0.0284	0.069	-0.412	0.68
	leg scale * abdomen size	-0.532	0.119	-4.47	<0.0001

Figure captions

Figure 1. Silhouettes of 25 plastic models of females created to display to males within the mating swarm. Silhouettes vary in the amount of two female-specific ornaments on display. Abdomen ornament sizes are population mean, mean ± 1.5 SD and mean ± 2.5 SD. Leg scale ornament sizes are population mean, mean ± 5.4 SD and mean ± 10.8 SD.

Figure 2. The partial quadratic effect of female swarm position on male visitation from a linear mixed effects model. Swarm position was measured as the distance from the centre of the mating swarm in increments of 15cm. The shaded area represents the standard error around the measure, values for the mode are reported in Table 1.

Figure 3. The partial effect of manipulated female ornamentation (abdomen width and pinnate leg scale length) on male courtship attempts overlaid on the raw data. Abdomen size was partitioned from the population's natural size variation ranging from two standard above and below the mean population size (-2 to 2 on the x-axis). The leg scale length was manipulated such that males were presented with ornament sizes from outside the natural population range (no scales (mean male leg size), 0.5×, 1.5× and 2× mean female scale length).

Figure 4. The mate attraction landscape incorporating linear and correlational attraction on abdominal ornaments and pinnate leg scales in *R. longicauda* females, as visualized using a nonparametric thin plate spline. Values on contour lines indicate the predicted number of male visitors for the trait space that each line occupies.

Data accessibility

All data and code used in this manuscript are available as supplementary materials

Competing interests

We have no competing interests.

Authors' contributions

RM and LB conceived the experiment; RM, JW, DG carried out the field experiment; RM and LB carried out the statistical analysis; all authors contributed to the writing of the manuscript. All authors gave final approval for publication.

Acknowledgements and Funding

We would like to thank E. J. Herridge, T.M. Houslay, R. W. Ness, T. J. Little, P. Lee, K. Vahed and three anonymous for their discussions and/or helpful comments on this manuscript. Funding was provided by the University of Stirling (Horizon Scholarship to RM) and NSERC (Discovery Grant to DG and PGS-D to RM).

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