Contrasting sexual selection on males and females in a role-reversed swarming dance fly, Rhamphomyia longicauda Loew (Diptera: Empididae)

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Introduction

Even though male sexual ornaments are well documented in many species (Jennions & Petrie, 1997), their adaptive significance for males and signalling value for females remains a subject for considerable debate (Houle & Kondrashov, 2002; Kokko et al., 2003). Although there is significant interest in showing that sexually selected male ornaments indicate heritable genetic quality, the evidence that such indirect benefits can outweigh the direct costs of choosing or of mating with males is equivocal (Cameron et al., 2003; Kokko et al., 2003). Several recent reviews have underscored the need for more empirical work on the ultimate causes of choice and consequent dimorphisms that arise through sexual selection (Chapman et al., 2003; Kokko et al., 2003; Pizzari & Snook, 2003).

One particularly promising avenue of research concerns investigations of the relatively rare systems featuring elaborate ornaments in females (Kokko & Johnstone, 2002), in part because the balance of direct and indirect benefits available through mate choice is significantly different for males compared with that of females (Bonduriansky, 2001). Whereas in many species males provide very little direct investment in offspring production, the minimum investment by females is still substantial: the size and quality of the eggs themselves. This level of investment in offspring may be enough to constrain the evolution of elaborate female ornaments in most species, because females that invest in ornaments at the expense of offspring lose direct fitness, and males should prefer to mate with females that invest in offspring rather than ornaments (Fitzpatrick et al., 1995; Berglund et al., 1997).

Given the potential trade-off between offspring and ornaments, why are females of some species elaborately ornamented? One possibility is that ornamentation has evolved because such a trade-off is resolved through the investment of different kinds of resources in ornaments as opposed to offspring (Fitzpatrick et al., 1995). An alternative view (Chenoweth & Blows, 2005; Chenoweth et al., 2006) is that a resource trade-off between ornamentation and offspring does not prevent the evolution of female ornaments in some species for which direct assessment of females is difficult, e.g. in mating swarms.
If ornaments have arisen as a signal of fecundity to males, Chenoweth et al. (2006) predict stabilizing selection on ornament expression, such that males mate females with intermediate investment in ornaments over those that invest so heavily in ornaments that they incur a fecundity cost. Finally, female ornaments that impair fecundity could also evolve in spite of male interests if they are favoured by nonsexual selection (Heinsohn et al., 2005; LeBas, 2006). In these cases, the signalling value of the ornament in other contexts would presumably offset fecundity costs, and male choice for ornamentation could arise as an adaptation to reap the benefits of these signals, or maladaptively if the males are caught in a sensory trap that causes them to favour ornamented females in spite of their reduced fecundity (Heinsohn et al., 2005; LeBas, 2006).

Whether or not they involve conspicuous ornamentation, the evolution of sexual dimorphisms requires that selection on morphology is different across the sexes (Lande, 1980). Few studies have attempted to measure selection on the same traits across the sexes in any species (Chenoweth & Blows, 2005), much less in species showing sex role reversal (but see Kraaijeveld et al., 2007 for a review of empirical studies examining the causes of ornamentation in both males and females of a species). Dance flies (Diptera: Empididae) are well suited for this research (LeBas et al., 2003). Within the subfamily Empidinae, in particular, there is considerable variation in both mating system and the level of female ornamentation of wings, legs and abdomens (Downes, 1970; Svensson & Petersson, 1987; Cumming, 1994; Svensson, 1997). Cumming (1994) has estimated that 28% of almost 600 identified species within the related Empidinae genera Empis and Rhamphomyia show some form of female ornamentation, including wing colouration (Svensson, 1997), exaggerated wing size (Svensson & Petersson, 1987), pinnate scales on female tibiae (LeBas et al., 2003) and in some cases elaborate eversible pleural sacs on the abdomen (Funk & Tallamy, 2000). Female ornamentation appears to have resulted from sexual selection in the context of female competition for ‘nuptial gifts’ of prey (Cumming, 1994); mating is thought to be the only occasion for female emplidines to acquire dietary protein as adults (Downes, 1970; Cumming, 1994).

Mating opportunities for females of the long-tailed dance fly, Rhamphomyia longicauda are particularly limited as the swarms where matings originate convene for less than an hour just after dawn and just before dusk. Swarms consist predominantly of females flying up to two metres above the ground in gaps in the tree canopy along rivers (Newkirk, 1970). Sexually competitive females in these swarms possess large pleural sacs, enlarged wings and pinnate tibial scales; mating behaviour appears to be sex role-reversed (Funk & Tallamy, 2000). Females within the swarms compete for access to the male nuptial gifts provided during mating. The sexually dimorphic abdomens, wings and legs of this species probably exaggerate female size to males that ascend from below, presumably to assess the fecundity of females above them silhouetted against the light in canopy gaps. Funk & Tallamy (2000) demonstrated that choosy males favoured larger silhouette models in the swarm, and argued that the female traits disguised female fecundity to some degree, and thus may represent deceptive signalling.

In this study, we set out to compare sexual selection on phenotypic traits shared by male and female R. longicauda in the wild. We used multivariate selection analysis to determine whether mating success was associated with different suites of phenotypic traits in males and females, to test the prediction that contrasting patterns of sexual selection have driven the evolution of sexual dimorphism in these traits. We also tested for patterns of assortative mating by examining whether the phenotypes of mated individuals were related to those of their mating partners or to the nuptial gift provided by the male to the female during mating. Finally, given that males of other species sometimes compete within all-male swarms for optimal mate-obtaining swarm positions (e.g. in a bibionid fly, Thornhill, 1980), we tested whether female dance fly morphology was associated with lower positions in mating swarms, which might be advantageous because this is the part of the swarm from which prey-carrying males enter.

Methods

Biology of Rhamphomyia longicauda

The prey-hunting, swarming and mating behaviour of R. longicauda is described in more detail by Funk & Tallamy (2000) and Newkirk (1970). Rhamphomyia longicauda swarms form annually under gaps in the canopy along the Grand and Credit rivers in southern Ontario in late June and early July. Swarms tend to be heavily female biased (Funk & Tallamy, 2000; Gwynne et al., 2007), sometimes with hundreds of females competing for access to a few males. Before swarm formation, males hunt for nuptial gifts in surrounding areas, whereas females inflate their pleural sacs whilst alighting on vegetation. Fully inflated females hover within swarms and appear to compete for space with rivals. Mating occurs on the wing when the male transfers the prey to the female and assumes a position above the female; the pair then mate during a nuptial flight while flying in stereotypical circular or ‘figure 8’ patterns near the swarm.

Sample collection

Samples were collected during swarming seasons (late June to early July) in 1998 and 2000. For individual analyses, samples were collected within a single season or seasons were combined after finding no significant
between-season effect. The collection site is located on the banks of the Credit River, near Glen Williams (Halton Co., ON, Canada; 43°41′11″N, 79°55′34″W), and is the same site that we used in other studies of this species (Gwynne & Bussière, 2002; Gwynne et al., 2007).

One special problem with analysing selection on 
R. longicauda is that solitary males and mating pairs will immediately drop any carried prey when their flight is disturbed by, for example, a collecting net. In addition, mating animals quickly separate when disturbed, making the assignation of mating partners and their associated nuptial gift difficult in net sweeps, especially because 
R. longicauda populations can be very dense near mating swarms. We have found the most reliable way to collect mating pairs and their associated nuptial gift is by hand – the slow and stereotyped pattern of nuptial flights allows experienced collectors to snare a mating male and female and its nuptial gift in the palm of a hand, to be transferred to a collecting vial.

Unfortunately, the inflated abdomens of females are very often damaged in the process of collecting by hand, and it is possible that the likelihood of damage to the pleural sacs correlates with the extent of inflation. As a result, we were unable to directly assess the strength of selection on pleural sac size for these samples. We were able to measure pleural sac area for solitary females. To keep these inflated females from deflating within collection vials before measurement of the pleural sac size, we placed the samples directly into dry ice pellets in the field, and transferred the samples to a −70 °C freezer until measurements could be taken.

To estimate selection on male and female 
R. longicauda, we compared the morphology of mated animals (N = 80 females and 76 males; some males were accidentally damaged and could not be included in the analysis) to solitary animals from the surrounding vegetation and from the swarm itself (N = 181 females and 33 males) that were collected on the same days as mated individuals. The relatively small sample for unmated males reflects their scarcity at the swarm site. This cross-sectional sample is a conservative representation of animals that failed to mate, as some of these flies would have been successful in acquiring mates in the past or could have been successful in the future. Because the solitary males bearing nuptial gifts that were collected in this way dropped their prey upon capture, we could not assign individual prey to males, and thus could not analyse selection on males based on prey morphology. However, as almost all males that bear any gift at all are likely to mate (swarming females vastly outnumber males with prey), the fraction of mating selection on males that is related to prey quality is likely to be small. We estimated standardized gradients of linear and nonlinear selection on these morphological traits separately in males and females (Lande & Arnold 1983) and statistically compared the multivariate response surfaces.

Assortative mating

Reproductive success is defined not only by the probability or frequency of mating success, but also by the quality of mating partners (Parker, 1983). For example, if all males with prey acquire mates, but the most fecund females associate only with males having particular phenotypes, mating success is an incomplete measure of reproductive success. To complement our analysis of selection based on mating success, we analysed the correlations in morphology between mated individuals and their associated nuptial gift in an attempt to determine how male and female morphology covaried within mating pairs.

Swarm stratification

We predicted that the most competitive females might occupy positions lower in the courtship swarm, closer to the point at which males enter bearing nuptial gifts. To determine whether female morphology correlated with swarming position, we compared the morphology of females captured from net sweeps taken high in the swarm (approximately 1 m above the ground vegetation) with those from low sweeps (approximately 0.3 m above the ground vegetation).

Morphological measurements

We measured phenotypic traits using a microscope fitted with a digital video camera connected to a Power Macintosh, and using NIH image (version 1.61; National Institutes of Health, Bethesda, Maryland, USA), a digital imaging program, to compute the following five morphometric measurements: left and right wing length, left and right hind tibia length, thorax length, and the abdominal area (as an estimate of pleural sac extension). For a subset of unpaired inflated females, we also counted the developing eggs within the abdomen and measured the length of live eggs from each female. For prey captured with mating pairs, we identified the prey to the family level whenever this was possible, and measured the length and width of the prey as an index of its visual appearance (in case females used this to assess male quality).

Statistical analyses

Area measurements (for pleural sac size and prey size) were square-root transformed before analysis so that all traits were measured in the same units. All relevant distributions were first checked for significant deviations from normality using Lilliefors tests. None of the distributions deviated significantly from normality (all Lilliefors P > 0.1); therefore, we used parametric tests for all analyses. Unless otherwise noted, all statistical analyses were computed using SPSS software (Anonymous, 2005).
Before selection analyses, we converted mating success to relative fitness by dividing by mean fitness for each sex (as recommended by Lande & Arnold 1983). We used standard regression-based selection analyses (Lande & Arnold 1983) to estimate the vector of linear selection gradients, $\beta$, and the matrix of nonlinear selection gradients, $\gamma$. The fraction of mating females within a swarm can change dramatically over the season and because we do not have estimates of this fraction for each sampled swarm, we could not correct our estimates of linear selection using the correction of Blanckenhorn et al. (1999).

Commercial statistics packages including SPSS give estimates of quadratic selection that are equal to half the quadratic selection gradient (Stinchcombe et al., 2005), and we present the corrected (i.e. doubled) gradient estimates. The nonlinear gradients provide a conservative estimate of stabilizing and disruptive selection on multivariate phenotypes, and we therefore also used canonical rotation of the nonlinear response surface to determine whether there was any significant nonlinear dimension to major axes of selection (Phillips & Arnold, 1989; Blows & Brooks, 2003). As this analysis did not reveal any patterns that were meaningfully different from the uncorrected analysis, we present only the methodologically simpler analysis of $\gamma$ below. To visualize selection on traits in multivariate space, we plotted nonparametric thin-plate splines (as suggested by Blows & Brooks, 2003) using the ‘fields’ package in R statistical software (http://www.r-project.org/). These splines plot changes in the predicted fitness surface across variation in two phenotypic traits without making assumptions about the statistical distributions or relationships between different traits. We used the partial $F$-test approach suggested by Chenoweth & Blows (2005) to test the significance of differences in the selection operating on males and females.

To analyse the effect of female morphology on swarm position, we performed a multiple logistic regression of operating on males and females. As the results of the $\chi^2$-test did not depend on the model selection protocol we used, we present the omnibus model below.

## Results

### Phenotypic covariances between morphological traits in female and male flies

Measures of female size were strongly and positively correlated (Table 1). In our sample, mean wing length and mean hind tibia length (which were themselves highly correlated) were roughly equivalent in their correlation with pleural sac area. Both egg length and egg number significantly predicted abdominal area, in magnitudes similar to those reported by Funk & Tallamy (2000), but, as in their study, the amount of variation in abdominal size explained by egg length or egg size in *R. longicauda* was low (Pearson’s $r$ for $\sqrt{\text{abdomen area}}$ and fecundity $= 0.495$; for $\sqrt{\text{abdomen area}}$ and egg size $= 0.334$; see Table 1). Male morphology was analyzed in a similar way, and as for females all measures were positively correlated (see Table 2).

### Sexual dimorphism and selection analyses

Wing length, hind tibia length and thorax length all exhibited significant levels of sexual dimorphism (equal variances not assumed; wing length $t = 9.423$, tibia length $t = 15.362$, pronotum length $t = 3.585$, 368 d.f., all $P < 0.001$; see Table 3 for trait means).

We found significant linear sexual selection on two of the three female morphological traits measured. There was significant selection for longer wings and shorter tibiae (see Table 4). We found no evidence of significant nonlinear selection (Table 4). The selection on female wing and tibia lengths is visualized in a thin-plate spline in Fig. 1. For males, the only significant selection was negative linear selection on mean wing length.

### Table 1 Pearson correlation matrix for female characters in samples ($N = 107$) taken over a 1-week period in 2000.

<table>
<thead>
<tr>
<th>Character</th>
<th>Wing length</th>
<th>Tibia length</th>
<th>Thorax length</th>
<th>Fecundity</th>
<th>Egg length</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pleural sac area</td>
<td>0.550</td>
<td>0.543</td>
<td>0.466</td>
<td>0.495</td>
<td>0.334</td>
</tr>
<tr>
<td>Mean wing length</td>
<td>0.941</td>
<td>0.919</td>
<td>0.643</td>
<td>0.502</td>
<td>0.488</td>
</tr>
<tr>
<td>Mean tibia length</td>
<td>0.910</td>
<td>0.640</td>
<td>0.488</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thorax length</td>
<td>0.618</td>
<td>0.519</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fecundity</td>
<td>0.572</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

All correlations are significant ($P < 0.001$) using two-tailed tests.

### Table 2 Pearson correlation matrix for male characters in samples ($N = 98$) taken over a 1-week period in 2000.

<table>
<thead>
<tr>
<th>Character</th>
<th>Mean tibia length</th>
<th>Thorax length</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean wing length</td>
<td>0.772</td>
<td>0.740</td>
</tr>
<tr>
<td>Mean tibia length</td>
<td>0.808</td>
<td></td>
</tr>
</tbody>
</table>

All correlations are significant ($P < 0.001$) using two-tailed tests.
As for females, there was no significant nonlinear selection (Table 5). We illustrate the selection on male wing and tibia length in Fig. 2.

The opposing patterns of linear selection on males and females (Figs 1 and 2) are significantly different (comparison of response surfaces using partial F-test, $F_{3,220} = 5.77$, $P < 0.001$), and this was due to differences in selection on both wing and tibia length ($sex \times \beta_{wing}$: $F_{1,220} = 16.13$, $P < 0.001$; $sex \times \beta_{tibia}$: $F_{1,220} = 7.86$, $P = 0.006$). There were no significant differences in nonlinear selection on males and females (partial $F_{6,208} = 0.376$, $P = 0.893$).

**Selection on female phenotype via male or nuptial gift quality**

There were no significant correlations between female phenotype and the characters of mates or nuptial gifts ($N = 56$; all $r < 0.171$; all $P > 0.2$; see supporting Table S1), meaning that larger females did not consistently mate larger males or males with larger nuptial gifts. Moreover, the (family level) taxon of prey (see supporting Table S2) was not associated with the size of female attracted by the prey item ($F_{7,76} = 1.006$, $P = 0.434$).

**Body size and swarm position**

A logistic regression of female traits on swarm position was highly significant, indicating that female phenotype does predict swarm position (see Table 6). We had predicted that the same traits that conferred a mating advantage would be associated with relatively lower positions in the swarm, as these females would be closer to males entering the swarm from below. The only univariate factor that predicted swarm position was tibia length, but, in contrast to the pattern for mating success,
Table 6 Summary of univariate components for a multiple logistic regression of female morphology on swarm position (negative coefficients indicate that larger individuals are found lower in the swarm).

<table>
<thead>
<tr>
<th>Source</th>
<th>β</th>
<th>SE</th>
<th>Wald</th>
<th>d.f.</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean wing length</td>
<td>0.229</td>
<td>1.682</td>
<td>0.018</td>
<td>1</td>
<td>0.892</td>
</tr>
<tr>
<td>Mean tibia length</td>
<td>-8.947</td>
<td>3.591</td>
<td>6.209</td>
<td>1</td>
<td>0.013</td>
</tr>
<tr>
<td>Thorax length</td>
<td>5.008</td>
<td>4.666</td>
<td>1.152</td>
<td>1</td>
<td>0.283</td>
</tr>
<tr>
<td>vPleural sac area</td>
<td>-0.335</td>
<td>0.746</td>
<td>0.202</td>
<td>1</td>
<td>0.653</td>
</tr>
<tr>
<td>Constant</td>
<td>16.929</td>
<td>4.923</td>
<td>11.823</td>
<td>1</td>
<td>0.001</td>
</tr>
</tbody>
</table>

The omnibus model is statistically significant (N = 96 females; χ² = 23.05, 4 d.f., P < 0.001).

in this case larger tibiae were associated with the presumed advantage of lower swarm position (see Table 6).

Discussion

Contrasting sexual selection in males and females

*Rhamphomyia longicauda* shows a reversal in the mating roles and a striking sexual dimorphism in traits. We document sex-dependent differences in the direction of selection for mating success on two of three traits shared by flies of both sexes: wing length and tibia length. These differences in selection are consistent with the observed direction of sexual dimorphism in wings, but not with observations of dimorphism in tibia lengths. In spite of this equivocal support for the role of sexual selection in driving sexual dimorphism, our data remain one of very few demonstrations of contrasting sexual selection for phenotypes (see also Chenoweth & Blows, 2005).

Our finding that sexual selection for mating success favours longer wings in females could be explained by male preference for longer wings (e.g. if wings exaggerate size, improve the quality of a swarming performance or direct display to males) or the effects on one or more unmeasured correlates of wing size. In a number of role-reversed species of *Rhamphomyia* and *Empis* dance flies, the female traits that have been shown to be under the strongest sexual selection are those that exaggerate body size such as legs with tibial scales (Funk & Tallamy, 2000; LeBas et al., 2003) and inflated abdomens that are displayed during swarming flight (Cumming, 1994; Funk & Tallamy, 2000). The larger wings (relative to males) noted in females of several *Rhamphomyia* species (Svensson, 1997; and this study) and *Empis borealis* (Svensson & Petersson, 1987) may arise due to correlational selection for larger wings and ornaments that exaggerate body size. Unfortunately, we could not assess this possibility because one of the traits most likely to act as ornaments, pleural sacs, could not be measured in mating females. The precise pathways driving selection for longer wings provide an interesting avenue for direct future study.

In contrast to females, we found selection for shorter wings in males as a consequence of mate competition. The association between opposing directions of selection on wing size in males and females and the larger wings of female *R. longicauda* suggests that sexual selection within mating swarms could play a role in the sexual dimorphism in this trait. An alternative explanation is that dimorphism results from sexual differences in flight due to the loss of aerial hunting by females (Svensson, 1997). However, even if this is true, sexual dimorphism might still be a consequence of sexual selection, because the loss of female predation in empidines is presumably linked to a shift towards acquiring protein from male courtship-feeding behaviour (Downes, 1970; Cumming, 1994).

Nevertheless, alternative explanations for sexual dimorphism will require more explicit testing before any firm conclusions can be drawn on its ultimate causes in this species. The most important potential confounding factor is selection on fecundity, which could cause dimorphism in the absence of differences in sexual selection for mating success. Evaluating the relative importance of selection on mating success and fecundity in these dance flies is made difficult by several factors: (1) our method of capturing mated females often damages female abdomens and the eggs they contain, making a fair assessment of phenotypic covariance between fecundity and other traits difficult among mated females; (2) mating success is potentially influenced by fecundity (because more fecund females are likely to be more attractive to mates; Funk & Tallamy, 2000), but fecundity is in turn probably influenced by mating success thanks to the nutrients obtained from nuptial gifts; (3) we lack any information on the effect of nuptial feeding on fecundity, and so cannot estimate the potential for assortative mating (for which there was no evidence in our study) to moderate or increase selection on morphology in females; and (4) there are no data on relationships between phenotype and mating rates or reproductive success for either males or females that could suggest how mating influences lifetime reproductive fitness. Estimating integrated selection on male and female morphology over successive episodes of mating and oviposition (Conner, 1996) is therefore difficult to achieve in the absence of a capacity for experimental manipulation in the system. Finally, it is clear that intersexual genetic correlations may play a role in the phenotypic expression of shared traits, such that the observed distribution of phenotypes within a sex are likely to be influenced by selection on the same trait in the opposite sex (Rice, 2001; Kraaijeveld et al., 2007).

Such alternatives notwithstanding, contrasting sexual selection for mating success in males and females may help explain sexual dimorphism in legs and wings in this species and other sex role-reversed empidids. In both *Rhamphomyia marginata* and *E. borealis*, Svensson et al. report sexual dimorphism in the length of the first femur,
a trait that is longer in males which they argue has evolved in the context of male hunting efficiency (Svensson & Petersson, 1987; Svensson, 1997). By contrast, in Rhamphomyia sulcata, a species with all-male swarms (i.e. no role-reversal), LeBas et al. (2004) report that sexual selection favours males with smaller hind tibiae that carry small gifts. They argue that small males claspers small gifts may have greater flight manoeuvrability during swarming and pairing. Similarly, there is a mating advantage for large male Empis snoddyi with small gifts, where the silken ‘balloons’ provided by males are nutritionally worthless but appear to function in mate attraction (Sadowski et al., 1999). Sadowski et al. also speculated that selection for small gifts arose because of an advantage associated with increased mobility when carrying small courtship gifts.

For R. longicauda, flying performance almost certainly plays a large role in male mating ability, because the capture of prey and assessment of mating partners takes place while flying, and pair formation and copulation also occur on the wing. Males do not carry females during the copulatory flight in other studied empidines, including Rhamphomyia tarsata (LeBas & Hockham, 2005), R. sulcata (LeBas et al., 2004), R. marginata (Svensson, 1997) and E. borealis (Svensson & Petersson, 1987). Therefore, R. longicauda may have a very different suite of selection pressures on leg structure (the dorsally mounted male grasps the prey-feeding female, Funk & Tallamy, 2000) and wing shapes for males and females than in most other empidines. The extent to which wing shape and tibia length influence flight performances in both sexes from the time of prey capture through copulation would be an intriguing avenue for future research. For example, the vastly broader wings of female E. borealis relative to males have been suggested to be an adaptation to the very long swarming period of females each day (Svensson, 1997).

Our estimates of linear selection are probably underestimates for females because we have almost certainly over-represented the mating females in our sample of flies for selection analysis, where mated females accounted for 80 of 261 females (Blanckenhorn et al., 2007). Although it is difficult to estimate the degree to which mated females are over-represented in our sample, in another study (Gwynne et al., 2007) we estimated that females account for 88% of swarming animals, and this suggests that a large fraction of females in a given evening do not successfully find a mate.

Chenoweth et al. (2006) argue that sexually selected female traits may experience stabilizing (i.e. quadratic) selection, whereby, on the one hand, these traits are required to signal fecundity (if direct fecundity assessment by males is difficult within mating swarms) and, on the other hand, males are reluctant to mate with females that over-invest in ornamentation at the expense of fecundity. LeBas et al.’s (2003) results with R. tarsata are not consistent with stabilizing selection on ornamentation: they did find nonlinear selection on females, but it was in the form of quadratic escalating selection for large trait values rather than selection for intermediately ornamented females. We found no evidence for nonlinear selection of any kind on female size, but our data do not strongly refute the prediction of Chenoweth et al. (2006) that female ornaments should be under stabilizing selection for two reasons. First, because we did not analyse selection on the full suite of traits likely to be under sexual selection (e.g. pleural sacs), we cannot reject the possibility of stabilizing selection on some of these traits. Second, there was no evidence in our study that relative investment in female ornaments was associated with a strong fecundity cost. Ornament size was positively correlated with fecundity (Table 1), and residual ornament size (corrected for wing length as an index of female size) did not covary negatively with either fecundity or egg size (for fecundity, Pearson’s $r = 0.169$, $P = 0.082$; for egg length, $r = 0.069$, $P = 0.479$; $N = 107$). If anything, there was a trend towards a positive phenotypic relationship between investment in ornaments and fecundity. Our results tentatively suggest that the quadratic relationship predicted by Chenoweth et al. (2006) may not be a ubiquitous outcome of sexual selection on females.

Selection via mate quality

We found no evidence for assortative mating between males and females, and no association between the size of prey and the size of either males or females within a mating pair. Acquiring prey may involve sufficient stochasticity to obscure any hunting advantage related to size, and female choice on the basis of prey may take place after copulation if the duration of sperm transfer is related to prey quality (LeBas & Hockham, 2005).

Spatial distributions of females

We found support for our prediction that the swarm is stratified according to female size, with the largest females occupying lower positions in the swarm, where prey-laden males first enter. Although the significance of swarm stratification for selection in the context of mate competition is unclear, we note that any selective advantage of a lower swarm position is not completely consistent with the pattern of sexual selection for mating success, in which females with longer wings and shorter tibiae had an advantage. In our analysis, larger rather than smaller tibiae were significantly associated with lower swarm positions, and wing length did not contribute significantly to the swarm position. If flying low in the swarm is advantageous, one possible explanation is that stratification within the swarm is an aspect of female competition in an analogous way to positional advantages for males in another swarming fly (with conventional all-male swarms, Thornhill, 1980) and a male-lekking.
mammal (Appolonio et al., 1989). If this is true, it is unsurprising that the precise characters under selection are not identical, as the ideal phenotypes in the context of intersexual and intrasexual selection can often differ (Moore & Moore, 1999). In the role-reversed E. borealis and R. marginata dance flies, there appears to be no positional advantage to females in the swarm (Svensson, 1997) perhaps because prey-laden males do not enter from predictable locations. The information for these two species also appears to rule out the hypothesis that the lower swarm positions of large female R. longicauda is due to some physical constraint such as heavy females tending to end up lower in the swarm.

Although there is no obvious direct (physical) female–female competition in R. longicauda and other dance flies (Svensson, 1997), the possibility exists that indirect female competition plays a role in swarm positioning and mating success. This suggests an intriguing additional role for female ornaments: that they signal quality not only to choosy males, but also to rival females. Heinsohn et al. (2005) have recently shown that ornamentation in female Eclectus roratus parrots has probably evolved in the context of intrasexual resource competition. Perhaps some of the phenotypic traits of female R. longicauda help mediate spatial competition within the swarm, reducing the energetic and mating opportunity costs of contests for space between rival females. This intriguing hypothesis deserves more explicit testing in R. longicauda, and will enable a more integrative assessment of the total fitness consequences of morphology for selection in both sexes of dance flies.

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References

Contrasting sexual selection in dance flies


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Supporting information

Additional supporting information may be found in the online version of this article:

**Table S1** Pearson correlation matrix for male, female and nuptial gift traits within captured mating pairs (N = 56). All P > 0.2 before Bonferroni correction.

**Table S2** Taxonomic families of prey (and estimates of their dimensions) collected as nuptial gifts for copulating *Rhamphomyia longicauda* pairs.

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