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

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Abstract

Sex-specific ornamentation is widely known among male animals, but even among sex-role reversed species, ornamented females are rare. Although several hypotheses for this pattern exist, too few systems featuring female ornaments have been studied in detail to adequately test them. Empidine dance flies are exceptional in that many species show female ornamentation of wings, abdomens, or legs. Here we compare sexual selection in males and females of the long-tailed dance fly, *Rhamphomyia longicauda* Loew (Diptera: Empididae), a sex-role reversed fly in which swarming females aggregate in competition for the nuptial gifts provided by males during mating. Females in this species possess several secondary sex characters, including eversible abdominal sacs, enlarged wings, and decorated tibiae that may all function in mate attraction during swarming. Males preferentially approach large females in the swarm, but the strength and shape of selection on females and the degree to which selection is sex-specific are unknown. We estimated linear and nonlinear sexual selection on structures expressed in both male and female flies, and found contrasting patterns of sexual selection on wing length and tibia length in males and females. In females, long wings and short tibiae were associated with mating success, whereas selection on males was significantly different: males with short wings and long tibiae were most likely to mate (although tibia length was a marginally non-significant predictor of male mating success). We found no evidence for assortative or disassortative mating. Although the largest females occupied positions within the swarm closest to the entry point for choosy males, in contrast to selection for mating success these females tended to have larger tibiae than rivals. We discuss our findings in the context of the mating biology of *R. longicauda* compared

to other empidine dance flies, and its relevance to the evolution of sexual dimorphism in general.

Introduction

Even though male sexual ornaments are well documented in many species (Jennions & Petrie, 1997), their adaptive significance for males and signaling value for females remains the subject of considerable debate (Houle & Kondrashov, 2002, Kokko et al., 2003). While 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 not strong (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 (Kokko et al., 2003, Chapman 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 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 ornaments in many 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). Empirical

studies in systems featuring ornamented females might resolve whether ornaments

have evolved in spite of this constraint 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), via stabilizing selection on ornament expression (in species

in which female ornaments are necessary to signal fecundity to males, e.g., because

direct assessment of fecundity by males is difficult, Chenoweth et al., 2006), or

because ornaments are favoured by non-sexual selection (Heinsohn et al., 2005,

LeBas, 2006).

Whether or not they involve conspicuous ornamentation, the evolution of

sexual dimorphisms require 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 systems 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 (Cumming, 1994, Downes, 1970, Svennson, 1997,

Svensson & Petersson, 1987). Cumming (1994) has estimated that 28% of almost 600

identified species within the related Empidine genera *Empis* and *Rhamphomyia* show

some form of female ornamentation, including wing colouration (Svennson, 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 empidines to acquire dietary protein as adults (Cumming, 1994, Downes, 1970).

Females of the long-tailed dance fly, *Rhamphomyia longicauda*, possess large pleural sacs, enlarged wings, and pinnate tibial scales, and show sex-role reversed behaviour within mating swarms (Funk & Tallamy, 2000). Swarms consisting predominantly of female flies convene just after dawn and just before dusk up to a metre above the ground in gaps in the tree canopy along rivers (Newkirk, 1970). Females within the swarms appear to 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 and 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 signaling.

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, in order 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 sometimes compete within all-males swarms for optimal mate-obtaining swarm positions (e.g., in a bibionid fly, Thornhill, 1980), we tested whether female

morphology was associated with lower positions in mating swarms, where prey-carrying males enter.

Methods

Biology of R. longicauda

 The prey-hunting, swarming and mating behaviour of *R. longicauda* is described in more detail in Funk & Tallamy (2000) and Newkirk (1970). *R. 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, while females inflate their pleural sacs while alighted on vegetation. Fully inflated females hover within courtship 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-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, Ontario, Canada: 43°41'11''N, 79°55'34''W), and is the same site that we have used in other studies of this species (Gwynne & Bussière, 2002, Gwynne et al., 2007).

 One special problem with analyzing 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, since 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 analyze selection on males based on prey morphology. However, since almost all males who 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.

In addition to computing standard linear and nonlinear selection on morphological traits Lande & Arnold 1983, we also conducted a canonical rotation of the correlation matrix for morphological traits (Phillips & Arnold, 1989, Blows & Brooks, 2003). Since this analysis did not reveal any patterns that were not exhibited in the unrotated multivariate space, we do not present these results here.

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 analyzed 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 (approx. 1 m. above the ground vegetation) to those from low sweeps (approx 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), a digital imaging program, to compute the following five morphometric measurements: left and right wing length, left and right hind tibia length, thorax length, the abdominal area (as an estimate of pleural sac extension). For a subset of inflated females, we also counted the developing eggs within the abdomen and measured the length of five 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 (as recommended by Lande & Arnold 1983). We used standard regression-based selection analyses (Lande & Arnold 1983) for estimate the vector of linear selection gradients, $\boldsymbol{\beta}$, and the matrix of non-linear selection gradients, $\boldsymbol{\gamma}$. In order to visualize selection on traits in multivariate space, we plotted non-parametric thin-plate splines using the "fields" package in R statistical software (http://www.r-project.org/). We used the partial F-test approach suggested by

Chenoweth and Blows (2005) to test the significance of differences in the selection operating on males and females.

To analyze the effect of female morphology on swarm position, we performed a multiple logistic regression of female phenotypic traits on the relative position of a female in a swarm (high versus low). As the results of the analysis did not depend on the model selection protocol 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 (see supplementary Table s1a). 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 Funk & Tallamy's study, the amount of variation in abdominal size explained by egg length in *R. longicauda* was low. Male morphology was analyzed in a similar way, and as for females all measures were positively correlated (see supplementary Table s1b).

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 df, all *P* < 0.001; see supplementary table s2 for trait means).

We found significant linear selection for mating success on two of the three female morphological traits measured. There was significant selection for longer wing length and shorter tibia length (see Table 1). We found no evidence of significant non-linear selection (Table 1). The selection on wing and tibia lengths is visualized in

a thin-plate spline in Figure 1. For males, the only significant selection was negative linear selection on mean wing length (see Table 2). As for females, there was no significant non-linear selection (Table 2). We illustrate the selection on male wing and tibia length in Figure 2.

The opposing patterns of linear selection on males and females (Figure 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 non-linear 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 supplementary Table s3), meaning that larger females did not consistently mate larger males or males with larger nuptial gifts. Moreover, the (family level) taxon of prey (see supplementary Table s4) 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 3). 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, in this case larger tibiae were associated with the presumed advantage of lower swarm position (see Table 3).

Discussion
Contrasting sexual selection in males and females

R. 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 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 (longer wings and shorter tibiae in females). This evidence therefore supports the idea that divergent sexual selection is responsible for sexual dimorphism in these traits, and remains one of very few demonstrations of such an effect (Chenoweth & Blows 2005).

Our finding that sexual selection favours longer wings in females could be due to male preference for longer wings (e.g., if females exaggerate size or 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 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 (Funk & Tallamy, 2000, Cumming, 1994). The larger wings (relative to males) noted in females of several *Rhamphomyia* species (Svennson, 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. 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 plays 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 predation by females (Svennson, 1997). However, even if this is true, sexual dimorphism is probably still 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).

Contrasting sexual selection in males and females may also explain sexual dimorphism in legs and wings in other sex-role reversed empidids. In both *R. marginata* and *E. borealis*, Svennson and colleagues 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 (Svennson, 1997, Svensson & Petersson, 1987). In contrast, in *R. 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 clasping small gifts may have greater flight maneuverability during swarming and pairing. Similarly, there is a mating advantage for large male *Empis snoddyi* with small gifts, where the "balloons" provided by males are nutritionally worthless but appear to function in mate attraction (Sadowski et al., 1999). Sadowski and colleagues 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 in particular pair-formation and copulation also occur on the wing. Males do not carry females during the copulatory flight in other studied empidines, including *R. tarsata* (LeBas & Hockham, 2005), *R. sulcata* (LeBas et al., 2004), *R. marginata* (Svennson, 1997), and *Empis borealis* (Svensson & Petersson, 1987). Therefore, *R. longicauda* may have a very different suite of selection pressures than in most other empidines on leg structure (the dorsally mounted male grasps the prey-feeding female, Funk & Tallamy, 2000) and wing shapes for males and females. 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 (Svennson, 1997).

Our estimates of linear selection are probably underestimates for females because we have almost certainly overrepresented the mating females in our sample of flies for selection analysis, where mated females accounted for 80 out of 261 females (Blanckenhorn et al., 1999). Although it is difficult to estimate the degree to which mated females are overrepresented 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 and colleagues (2006) argue that sexually selected female traits may experience stabilizing selection, whereby on one hand these traits are required to signal fecundity (Chenoweth et al., suggest that direct fecundity assessment by males

may be difficult within mating swarms) and on the other males are reluctant to mate with females who 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 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 arguments of Chenoweth and colleagues for two reasons. First, because we did not analyze 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 (supplementary Table s1a), 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. We note that this stratification 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. One possible explanation is that stratification within the swarm is an aspect of female competition for advantageous positions 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 contrast to *R. longicauda*, for the role-reversed *E. borealis* and *R. marginata* dance flies there appear to be no positional advantage to females in the swarm (Svennson, 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 (Svennson, 1997), the possibility exists that indirect female competition plays a role in 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 likely 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*.

Acknowledgments

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Table 1. The vector of standardized linear selection gradients on females ($\boldsymbol{\beta}$)
and the matrix of standardized non-linear selection gradients ($\boldsymbol{\gamma}$).

	B	Wing length	Tibia length	Thorax length
Mean wing length	0.403**	-0.029		
Mean tibia length	-0.297*	0.213	-0.059	
Thorax length	-0.092	0.026	-0.310	0.192

* $P < 0.05$, ** $P < 0.01$

Table 2. The vector of standardized linear selection gradients on males (β) and the matrix of standardized non-linear selection gradients (γ).

	β	Wing length	Tibia length	Thorax length
Mean wing length	-0.242*	0.015		
Mean tibia length	0.188	-0.171	0.212	
Thorax length	-0.009	0.172	-0.307	0.123

* $P < 0.05$

Table 3. 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). The omnibus model is statistically significant (N = 96 females; χ^2 = 23.05, 4 df, P < 0.001).

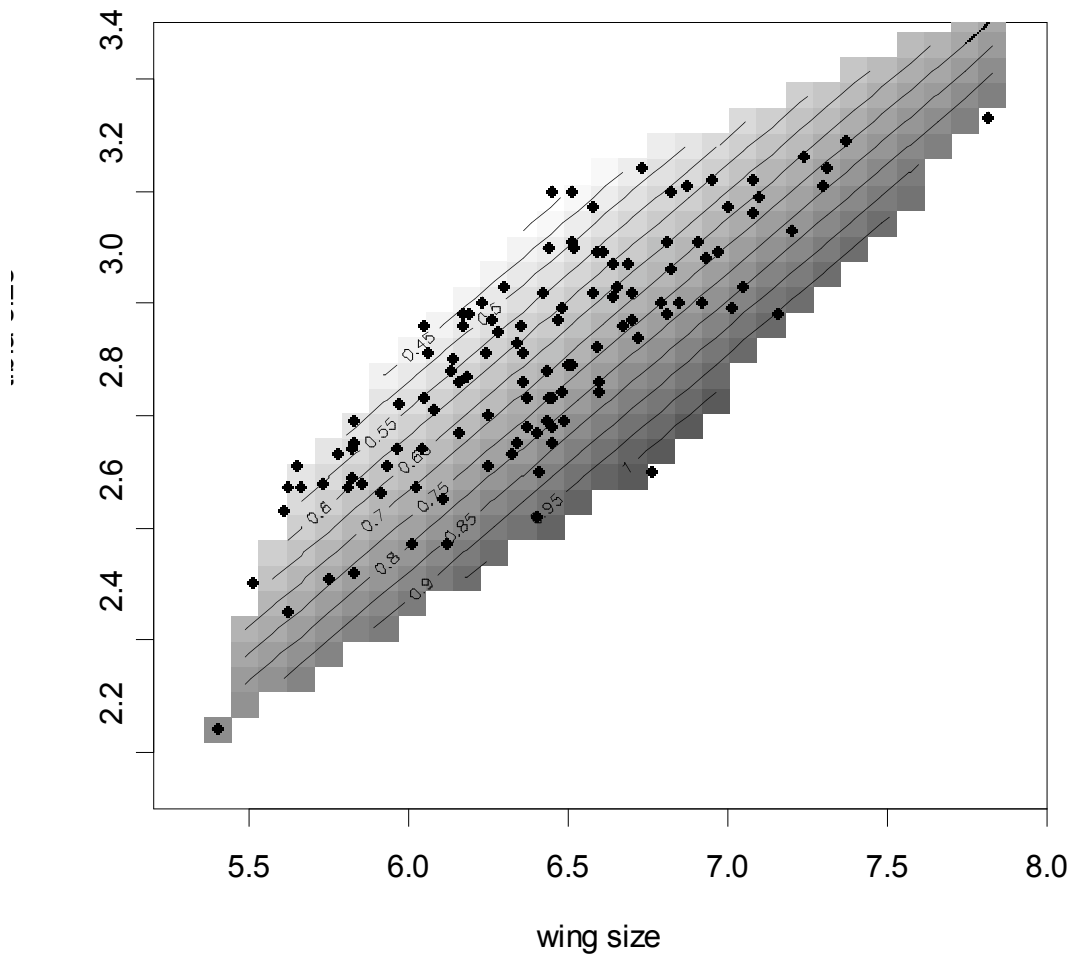| Source	β	S.E.	Wald	df	P
Mean wing length	0.229	1.682	0.018	1	0.892
Mean tibia length	-8.947	3.591	6.209	1	0.013
Thorax length	5.008	4.666	1.152	1	0.283
√ Pleural sac area	-0.335	0.746	0.202	1	0.653
Constant	16.929	4.923	11.823	1	0.001

Figure 1. Selection on female wing and tibia size, the two major axes of selection.

The surface is a thin-plate spline, and original data points supporting the surface are
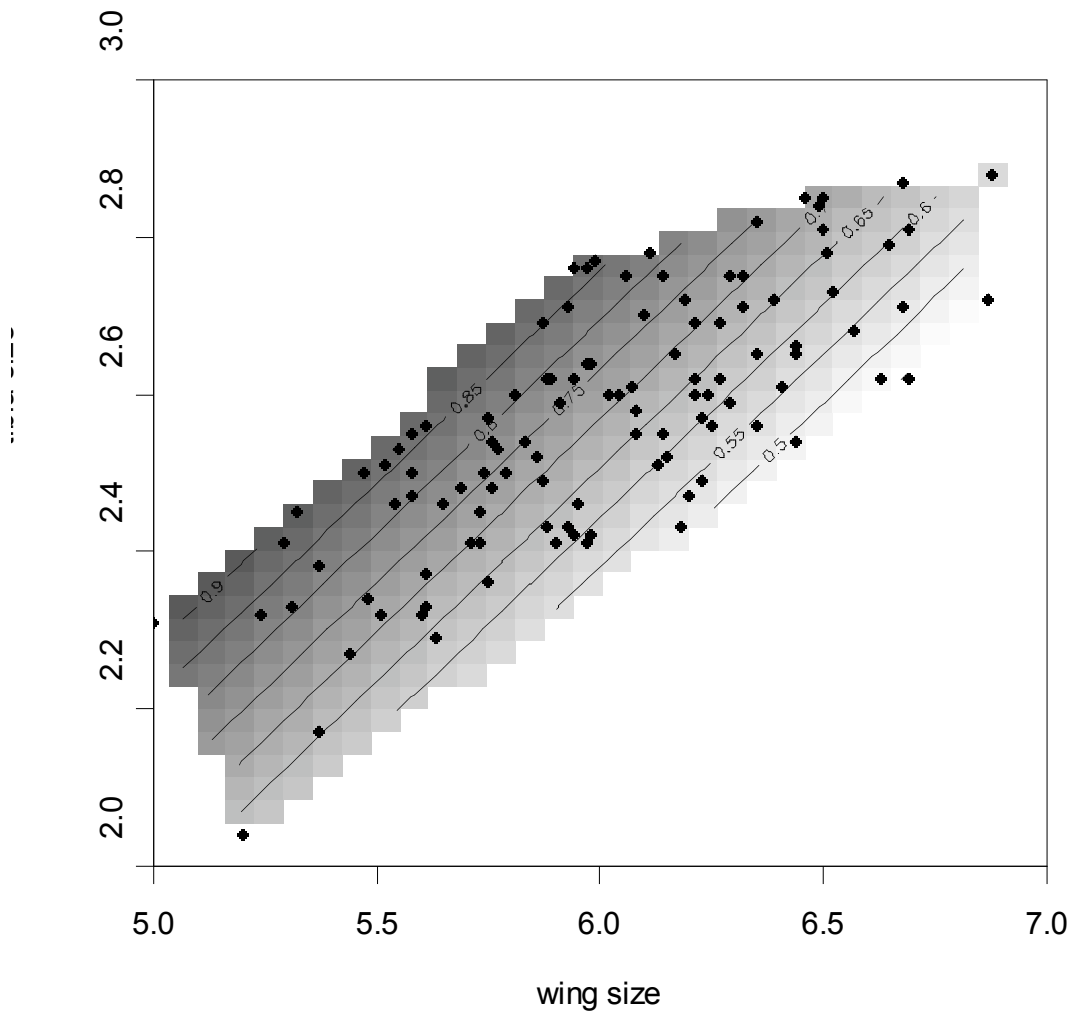
plotted.

Figure 2: Selection on male wing and tibia size. The surface is a thin-plate spline, and original data points supporting the surface are plotted.

Online supplementary material

Table s1a. Pearson correlation matrix for female characters in samples (N = 107) taken over a one-week period in 2000. All correlations are significant (p < 0.001) using two-tailed tests.

Character	Wing length	Tibia length	Thorax length	Fecundity	Egg length
√Pleural sac area	0.550	0.543	0.466	0.495	0.334
Mean wing length		0.941	0.919	0.643	0.502
Mean tibia length			0.910	0.640	0.488
Thorax length				0.618	0.519
Fecundity					0.572

Table s1b. Pearson correlation matrix for male characters in samples (N = 98) taken over a one-week period in 2000. All correlations are significant (p < 0.001) using two-tailed tests.

Character	Mean tibia length	Thorax length
Mean wing length	0.772	0.740
Mean tibia length		0.808

Table s2. Mean (± SE) morphological trait values for males and females included in our selection analysis.

Trait value (mm)	Females		Males	
	Paired (N=80)	Solitary (N=181)	Paired (N=76)	Solitary (N=33)
Mean wing length	6.47 ± 0.06	6.45 ± 0.04	5.96 ± 0.05	6.09 ± 0.07
Mean hind tibia length	2.90 ± 0.02	2.86 ± 0.02	2.57 ± 0.02	2.57 ± 0.03
Mean thorax length	1.57 ± 0.01	1.56 ± 0.01	1.51 ± 0.01	1.53 ± 0.02

Table s3. Pearson correlation matrix for male, female and nuptial gift traits within captured mating pairs (N = 56). All P > 0.2 before Bonferroni correction.

	Female wing length	Female tibia length	Female thorax length
Male wing length	0.034	-0.078	0.040
Male tibia length	-0.008	-0.013	0.009
Male thorax length	-0.061	-0.105	-0.026
Prey mass	0.013	0.069	0.054
√ Prey size (length X width)	-0.158	-0.164	-0.171

Table s4. Taxonomic families of prey (and estimates of their dimensions) collected as nuptial gifts for copulating *R. longicauda* pairs.

Nuptial gift prey family	N	Mean ± SE √(prey area)
Caenidae	6	2.15 ± 0.12
Chironomidae	32	2.11 ± 0.07
Culicidae	1	2.75
Dixidae	1	1.55
Philopotamidae	8	2.03 ± 0.12
Tipulidae	15	2.33 ± 0.14