

# Nonlinear and correlational sexual selection on 'honest' female ornamentation

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Female ornamentation has long been overlooked because of the greater prevalence of elaborate displays in males. However, the circumstances under which females would benefit from honestly signalling their quality are limited. Females are not expected to invest in ornamentation unless the fitness benefits of the ornament exceed those derived from investing the resources directly into offspring. It has been proposed that when females gain direct benefits from mating, females may instead be selected for ornamentation that deceives males about their reproductive state. In the empidid dance flies, males frequently provide nuptial gifts and it is usually only the female that is ornamented. Female traits in empidids, such as abdominal sacs and enlarged pinnate leg scales, have been proposed to 'deceive' males into matings by disguising egg maturity. We quantified sexual selection in the dance fly *Rhamphomyia tarsata* and found escalating, quadratic selection on pinnate scales and that pinnate scales honestly reflect female fecundity. Mated females had a larger total number and more mature eggs than unmated females, highlighting a potential benefit rather than a cost of male mate choice. We also show correlational selection on female pinnate scales and fecundity. Correlational selection, equivalent investment patterns or increased nutrition from nuptial gifts may all maintain honesty in female ornamentation.

**Keywords:** female ornamentation; correlational selection; sexual selection; honest signalling; *Rhamphomyia*; dance flies

## 1. INTRODUCTION

Lower investment into offspring and higher variance in male reproductive success usually leads to sexually selected ornamentation in males rather than females (Bateman 1948; Trivers 1972; Parker & Simmons 1996). Male ornamentation is frequently an honest indication of male quality, and cheating on costly ornamentation has been shown to be difficult (Zahavi 1975; Grafen 1990). The extent and signalling role of female ornamentation has received considerable recent interest (Amundsen 2000b; Roulin *et al.* 2000; Amundsen & Forsgren 2001; Domb & Pagel 2001, 2002; Houde 2001; Zinner *et al.* 2002). However, although male choice of larger females is common, demonstrations of male choice for female ornaments are rare (Amundsen 2000a; Bonduriansky 2001).

Females can invest directly into offspring for which they have guaranteed maternity. Whereas multiple matings by females can enhance their reproductive success (Tregenza & Wedell 1998; Arnqvist & Nilsson 2000) it is not typically to the same extent as in males (Bateman 1948). Assuming some cost to honest ornamentation, the benefits to females of investing in ornaments must outweigh those of directly investing these resources in offspring. Potentially, females may benefit from ornamentation when it increases their chance of obtaining resources held by males or of mating with higher-quality males (Amundsen 2000a). Males may benefit from discriminating among females when males invest heavily in reproduction, have low search costs or female quality varies widely (Parker 1983; Johnstone *et al.* 1996; Kokko & Johnstone 2002). Whether female ornamentation will be

honest is not clear (Fitzpatrick *et al.* 1995; Berglund *et al.* 1997). Females that invest in ornamentation may be less able to invest in offspring than females of equivalent resources who only invest in offspring (Fitzpatrick *et al.* 1995; Berglund *et al.* 1997). Further, when males discriminate between non-virgin females or those not temporally close to fertilization, females that benefit from multiple matings may actually be under selection to deceive males about mating status and egg maturity (Funk & Tallamy 2000; Bonduriansky 2001).

Dance flies (Empididae) have attracted much interest due to the diverse array of nuptial gifts that the males of this group transfer to females during mating (Kessel 1955; Thornhill & Alcock 1983; Vahed 1998; Sadowski *et al.* 1999). Males present females with gifts that vary across species from genuine nutritious prey gifts, to stones or silk balloons (Cumming 1994). In dance flies it is frequently the female that is ornamented rather than the male (Cumming 1994). The ornamentation can take the form of abdominal sacs, enlarged leg pinnate scales or larger or darkened wings. Abdominal sacs are eversible sacs on the pleural membrane of the abdomen, which may be inflated before the female entering a lek (Cumming 1994; Funk & Tallamy 2000). Enlarged pinnate scales are cuticular extensions, usually located on the hind legs, which are often wrapped around the female's abdomen during lekking (Cumming 1994). An aerodynamic role for these female traits has not been excluded (Svensson & Petersson 1987). However, the absence of these traits in lekking males and the lack of aerodynamic function for some of the traits (e.g. silvery wings) suggest another role for these traits in females (Cumming 1994).

In the dance fly *Empis borealis*, males discriminate between females and prefer to mate with females that are younger and larger (Svensson & Petersson 1987, 1988,

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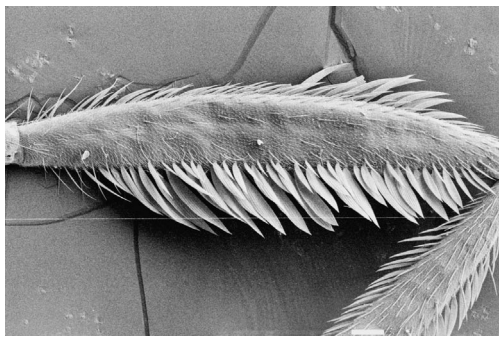


Figure 1. Scanning electron micrograph of the pinnate scales on the hind femur of female *R. tarsata*. Scale bar, 0.1 mm.

1994; Svensson *et al.* 1989). A recent study of the dance fly *R. longicauda* showed that the female abdominal sacs disguise the state of egg maturation compared with a species that lacked this trait (Funk & Tallamy 2000; Hockham & Ritchie 2000). Males were also found to prefer models of females that were larger in overall body size in experimental trials (Funk & Tallamy 2000). Many female empidids have lost the ability to hunt (Cumming 1994) and it was proposed that females use these novel traits to deceive males into mating to obtain a nutritious nuptial gift (Funk & Tallamy 2000). However, no study of empidids has partitioned correlates of female mating success and hence it is unknown whether female ornamentation predicts mating success independent of body size.

The selective pressures and potential sexual conflicts that led to the evolution of these female traits are unknown, but once present, males do not have the option of choosing females that lack the ornament. Of current selective importance is whether males who choose females on the basis of the ornament bear a cost or obtain a benefit as a result of that choice. Males of the dance fly *Rhamphomyia tarsata* provide a nutritious nuptial gift, and lek in mixed sex swarms. Female *R. tarsata* have enlarged pinnate scales on the hind leg (figure 1), which are wrapped around the abdomen during lekking. Males and females approach one another within the lek and only a subset of these interactions result in pairings. Previous studies have demonstrated that male dance flies can discriminate between females within swarms (Svensson *et al.* 1989) and show male choice (Funk & Tallamy 2000). Male eyes in empidids have enlarged facets that would allow visual assessment of females during these interactions. Females have not been observed to interact with one another within a lek and there is no evidence of female scramble competition in empidids. Male mate choice rather than female competition is thus likely to be the major component of sexual selection in this species. We used selection analysis to uncouple the targets of sexual selection in a field population of *R. tarsata*. We classified mating females as chosen by males and unmated females in the lek as rejected. We also investigated the relationships between female leg pinnate scales and fecundity to determine whether pinnate scales were currently deceptive or honest.

## 2. MATERIAL AND METHODS

This study was conducted in June and July 2001 on farmland in eastern Fife, Scotland.

### (a) Sample collection

*Rhamphomyia tarsata* (Meigen 1822, identified from Collin 1961) form leks *ca.* 3–4 m off the ground and next to stands of vegetation. Pairs form in the lek, but always mate on the vegetation during which the female consumes the male's nuptial gift. Pairs have been observed to split during the descent flight to the vegetation. To quantify selection, random samples were taken from the lek by sweep netting and mating pairs collected off the vegetation. Females from the lek were the non-selected sample and females in mating pairs were the selected (mated) sample. All flies were collected from the one swarm. We collected 121 mating pairs off the vegetation, and 106 males and 57 females from the lek. We have interpreted the sexual selection obtained from these samples as primarily the consequence of male choice for the reasons outlined in the introduction. We acknowledge, however, that this interpretation is based on our opinion of the most parsimonious explanation for our findings and that we have not conclusively excluded all other possibilities. Flies were immediately fixed and preserved in Bouin's solution to maintain abdomen shape. As both males and females enter the lek to mate, the operational sex ratio (OSR) at the lek was estimated as the proportion of males to females in random sweeps of the lek.

### (b) Trait measurement

We examined selection on female traits that were likely to be assessed by males: female body size (hind tibia length), weight, area of the abdomen and pinnate scale length and area. All traits were measured by using a dissecting microscope with a digital camera attached and Scion IMAGE Analysis software. Pinnate length was measured as the length of the longest scale, and pinnate area as the total area of all the pinnate scales on the inside of one femur (figure 1). Abdomen area was the total area of the abdomen measured ventrally. Female fecundity was quantified as total egg number and egg maturity quantified as average egg size. All of the egg measurements were taken from dissected females rather than laid clutches. Egg size was the area of the egg determined by the perimeter of the egg in plan view and was averaged over three randomly selected eggs. Male body size (tibia length) and weight were also measured to determine if there was sexual selection acting on both sexes. Nuptial gift size is likely to be an important variable for female choice; however, as this study concentrated on female ornamentation we did not measure this variable for unmated males in the lek. We did, however, measure the size of the prey within the mating pairs. Prey tibia length, wing length and total prey area (excluding wings) were measured with Scion IMAGE. The first principal component (PC1) of these variables was used to summarize prey size (81% of variance explained; component loadings: tibia length = 0.89, prey area = 0.88, wing length = 0.94).

### (c) Statistical analysis

Selection analyses (differentials, linear and quadratic gradients) were performed using standard multiple regression techniques (Lande & Arnold 1983; Arnold & Wade 1984; Brodie *et al.* 1995), with standardized traits and relative fitness (mating success). Correlational selection is the partial regression coefficient of cross-product terms and is indicative of a change in the covariance between two traits (Brodie *et al.* 1995). Separate regression analyses were used to estimate the linear and quadratic coefficients because of the lack of multivariate normality (Lande & Arnold 1983). Coefficients were taken from multiple regression and significance from logistic regression (Fairbairn &

Table 1. Selection differentials and multiple regression selection analysis of female morphology in *Rhamphomyia tarsata*. (Multivariate linear selection gradients ( $\beta$ ) and multivariate nonlinear (quadratic) selection gradients ( $\gamma$ ) with standard errors (s.e.m.). Gradients are estimated from multiple regression, significance testing from logistic multiple regression (Fairbairn & Preziosi 1996). All traits are standardized.  $n = 172$ .)

	differential	$\beta \pm \text{s.e.m.}$	$\gamma \pm \text{s.e.m.}$
tibia length	$0.107 \pm 0.052^*$	$-0.162 \pm 0.093$	$-0.254 \pm 0.122$
weight	$0.188 \pm 0.050^{***}$	$0.386 \pm 0.117^{**}$	$-0.780 \pm 0.210$
abdomen area	$0.119 \pm 0.052^*$	$-0.125 \pm 0.093$	$0.157 \pm 0.137$
pinnate area	$0.131 \pm 0.051^*$	$0.117 \pm 0.083$	$0.470 \pm 0.096^{**}$
pinnate length	$0.064 \pm 0.052$	$-0.081 \pm 0.068$	$0.029 \pm 0.072$

\*  $p < 0.05$ , \*\* $p = 0.01$ , \*\*\* $p = 0.001$ .

Preziosi 1996). The form of the fitness surface was examined with non-parametric univariate (Schluter 1988) and multivariate (Schluter & Nychka 1994) cubic spline analyses. Cubic splines were performed on unstandardized traits. Significance tests and standard errors in cubic spline analyses are based on bootstrapping (Schluter & Nychka 1994).

### 3. RESULTS

#### (a) Selection analysis

Selection differentials encompass direct and indirect selection (Arnold & Wade 1984) and in *R. tarsata* show significant directional selection on all traits except pinnate length (table 1). Multivariate selection analysis (Lande & Arnold 1983) revealed this total selection was due to linear selection on weight and quadratic selection on pinnate area (table 1). Quadratic selection gradients estimate the curvature of the selection function. Positive gradients can be indicative of disruptive selection and negative gradients of stabilizing selection (Brodie *et al.* 1995). An examination of the fitness surface of a non-parametric univariate cubic spline (Schluter 1988; figure 2a) indicates that directional selection persists on pinnate scales after controlling for body size. Examination of the fitness surface of a multivariate cubic spline (Schluter & Nychka 1994) including weight and pinnate area (figure 2b,c) revealed the quadratic function did not represent disruptive selection. Instead the quadratic term was indicative of low selection over most of the pinnate size distribution, with rapidly increasing selection on pinnate size in the positive tail of the distribution.

We found significant positive correlational selection between pinnate length and weight ( $\gamma_{ij} = 0.340 \pm 0.149$ ,  $p = 0.03$ ), tibia length and weight ( $\gamma_{ij} = 0.639 \pm 0.245$ ,  $p = 0.04$ ), and near significant but negative correlational selection between pinnate scale area and tibia length ( $\gamma_{ij} = -0.257 \pm 0.154$ ,  $p = 0.058$ ). Female weight is largely due to egg number ( $r = 0.64$ , d.f. = 176,  $p < 0.001$ ) and egg size/maturity ( $r = 0.51$ , d.f. = 176,  $p < 0.001$ ). A separate correlational analysis including only tibia, pinnate length and egg number confirmed that the correlational selection on weight and pinnate length generated correlational selection on pinnate length and egg number ( $\gamma_{ij} = 0.180 \pm 0.079$ ,  $p = 0.028$ ). The strong positive directional selection on weight and the lack of selection on pinnate scale length suggests the nature of the correlational selection is a peak of fitness for females with both long pinnate scales and high weight. In particular,

the correlational selection suggests that females with large pinnate scales are not selected unless they are also heavy. The indication of negative correlational selection between pinnate area and tibia length is antagonistic to the strong phenotypic correlation between these traits ( $r = 0.71$ , d.f. = 176,  $p < 0.001$ ) and suggests selection is acting to uncouple these traits.

#### (b) Egg maturity

Egg size varied from 0.004 to 0.159 mm<sup>2</sup> (mean =  $0.049 \pm 0.003$ ) indicating that females enter the lek with eggs at all stages of maturity (figure 3). An examination of the distribution of egg sizes shows a skewed distribution and suggests that females with mature eggs may be less frequent in the lek. This skewed distribution is not a consequence of female body size variation as there is no relationship between female body size and egg size (see below).

Female ornaments in empids have been considered to exaggerate and disguise the state of egg maturity (Funk & Tallamy 2000). Egg size is indicative of egg maturity and in *R. tarsata*, abdomen size and female weight correlate with egg size in a partial correlation controlling for date of collection and the number of eggs (abdomen,  $r = 0.25$ , d.f. = 168,  $p = 0.001$ ; weight,  $r = 0.29$ , d.f. = 168,  $p < 0.001$ ). Fixed morphological traits are not expected to covary with a temporal trait such as egg maturity, and indeed neither tibia length ( $r = 0.08$ , d.f. = 168,  $p = 0.27$ ), pinnate scale area ( $r = 0.01$ , d.f. = 168,  $p = 0.98$ ) nor pinnate length ( $r = 0.03$ , d.f. = 168,  $p = 0.71$ ) show a relationship with egg size. The positioning of the pinnate scales around the abdomen, however, may prevent male assessment of abdomen size and hence egg maturity.

#### (c) Female fecundity

Partial correlations controlling for date and egg size show that both pinnate length ( $r = 0.34$ , d.f. = 168,  $p < 0.001$ ) and pinnate area ( $r = 0.35$ , d.f. = 168,  $p < 0.001$ ) correlate with egg number, though as tibia also correlates with egg number ( $r = 0.42$ , d.f. = 168,  $p < 0.001$ ), the pinnate relationships may be a correlated effect of body size. In a multivariate analysis including date and egg size as controls and tibia length, weight, abdomen ventral and pinnate length or area, it was only pinnate length ( $t_{(6,165)} = 1.98$ ,  $\beta = 1.281 \pm 0.648$ ,  $p = 0.05$ ) and weight ( $t_{(6,165)} = 2.47$ ,  $\beta = 3.383 \pm 0.168$ ,  $p = 0.014$ ) that predicted female egg number, whereas tibia length did not ( $t_{(6,165)} = 0.84$ ,  $\beta = 0.836 \pm 0.992$ ,  $p = 0.40$ ). Hence, it

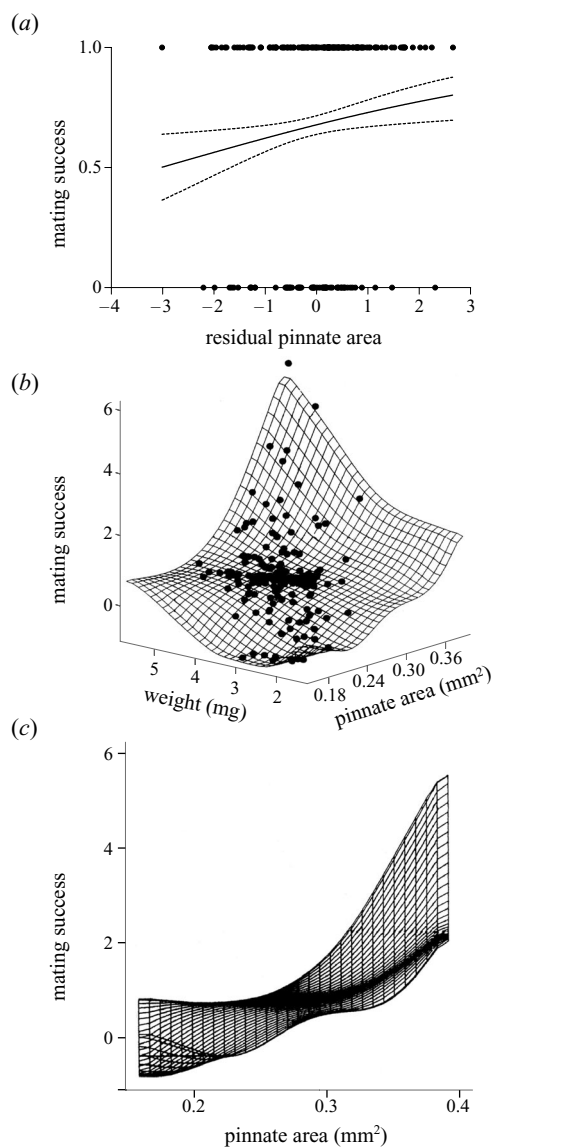


Figure 2. Cubic spline derived fitness surfaces for female traits. (a) Univariate cubic spline (Schluter 1988) representing the non-parametric fitness surface of female mating success on residual pinnate scale area (residuals from regression on tibia length). Dotted lines represent  $\pm 1$  s.e.m. of the fitness prediction (Schluter 1988). Standard errors were derived from 1000 bootstrap replications. (b) Multivariate cubic spline (Schluter & Nychka 1994) fitness surface for female weight and pinnate area. Pinnate area coefficient =  $0.99 \pm 0.038$ ,  $p < 0.003$ ; weight coefficient =  $0.01 \pm 0.126$ ,  $p = 0.27$ . The significance for the overall projection is  $p = 0.12$ . Significance tests for projection pursuit regression (derived from bootstrap replication) have not been tested and hence should be treated as a guide only (Schluter & Nychka 1994). Smoothing parameter,  $\ln(\lambda) = -10.3$ , number of projections = 1 and number of parameters = 5.17. (c) Cross section of the multivariate fitness surface for the pinnate scale axis. The quadratic nature of the surface is evident in the escalating selection on pinnate scales at the positive end of the distribution.

is only female weight and pinnate scales that reliably indicate female fecundity. Regressions of standardized pinnate length and standardized egg number on female body size (tibia length) revealed an extraordinary equivalence of allometry of ornaments and eggs (figure 4).

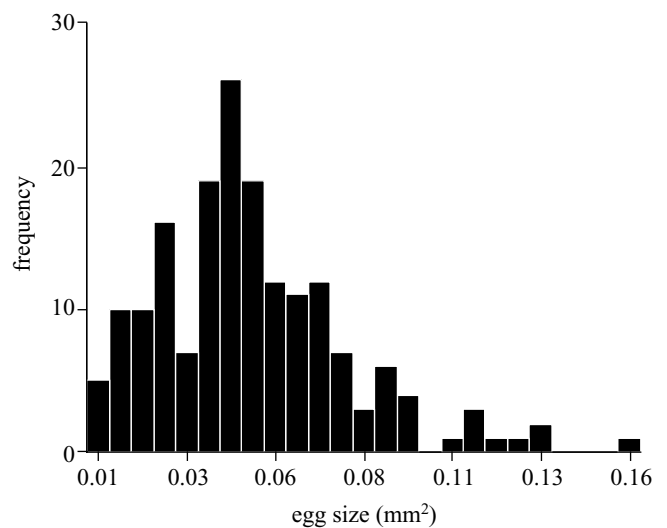


Figure 3. Egg size distribution from females collected from the lek and mating pairs.

#### (d) *Fitness consequences of selection*

The evolutionary benefit, rather than a cost, to males of their choice of females is demonstrated by the higher fecundity of chosen females (mean egg number of chosen females =  $40.16 \pm 0.84$ , mean egg number of lek females =  $34.98 \pm 1.55$ ,  $t_{(174)} = -2.9$ ,  $p = 0.004$ ). Paired females also had more mature eggs than those in the lek (mean egg size chosen females =  $0.052 \pm 0.002$ , mean egg size lek females =  $0.043 \pm 0.004$ ,  $t_{(174)} = -2.14$ ,  $p = 0.03$ ).

#### (e) *OSR and sexual selection on males*

The sex ratio in the lek, representing the operational sex ratio (OSR), did not differ from equality (mean =  $2.3 \pm 0.90$ ,  $t_{(1,8)} = 1.47$ ,  $p = 0.18$ ) or change over the season ( $n = 9$ ,  $p = 0.32$ ). These tests have low power, but the tendency is to an OSR biased towards males rather than females, indicating that this is not a completely role-reversed mating system. There was also directional sexual selection on male size (selection differential =  $0.27 \pm 0.065$ ,  $n = 224$ ,  $p < 0.001$ ) and weight (selection differential =  $0.246 \pm 0.065$ ,  $n = 222$ ,  $p < 0.001$ ).

#### (f) *Nuptial gift size*

There was no relationship between male body size and gift size (partial correlation controlling for date:  $r = 0.07$ , d.f. = 107,  $p = 0.47$ ) nor assortative mating for body size ( $r = 0.14$ , d.f. = 114,  $p = 0.14$ ). Within pairs, males with the largest gifts were paired to females with the most eggs ( $r = 0.24$ , d.f. = 108,  $p = 0.01$ ). If males exert more stringent choice when they possess a valuable gift, their criteria for this choice are unclear as although there is a trend for males with larger nuptial gifts to pair with heavier females ( $r = 0.16$ , d.f. = 108,  $p = 0.09$ ) there were no relationships with any other morphological variable. High-quality, fecund females may exert stronger preferences for larger nuptial gifts.

## 4. DISCUSSION

This study reveals that female pinnate scales in *R. tarsata* are currently subject to nonlinear and correlational sexual selection and that pinnate scales honestly reflect

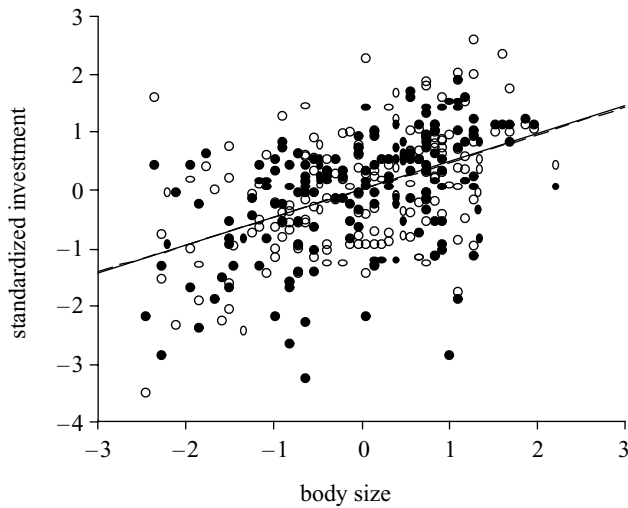


Figure 4. Female investment in ornaments and offspring. With increasing body size (tibia length) females invest equally into fecundity, egg number (filled circles) and ornament size, pinnate length (open circles). All traits are standardized. Fecundity regression:  $F_{1,174} = 49.56$ ,  $\beta = 0.471 \pm 0.067$ ,  $p < 0.001$ . Pinnate length regression:  $F_{1,174} = 51.38$ ,  $\beta = 0.477 \pm 0.067$ ,  $p < 0.001$ . Regression lines for egg number (solid line) and pinnate length (dashed line) on body size overlay so precisely that they are indistinguishable.

female fecundity. We also show correlational selection on pinnate scale size and fecundity. This correlational selection may select for a genetic correlation between these traits and hence maintain honesty of the female ornament.

Neither body nor abdomen size were targets of sexual selection. The multivariate selection analysis revealed that the total selection acting on tibia length and abdomen area was a consequence of these traits' phenotypic correlations with female weight and pinnate area. These analyses support the importance of pinnate scales rather than body size as a target of sexual selection. A comparison of mating and courting swarms of another empidid with pinnate scales, *R. sociabilis*, also found that body size did not influence mating success (Funk & Tallamy 2000). The form of the nonlinear sexual selection on female pinnate scales is particularly noteworthy. Very few studies have documented this form of selection on a secondary sexual trait (Kingsolver *et al.* 2001), though tests for nonlinear sexual selection are infrequent. It has been proposed that this form of selection may contribute to the genetic variance in secondary sexual traits, as variance effective selection will favour modifier genes acting on the variance rather than the mean value of the trait (Pomiankowski & Møller 1995).

Female traits such as pinnate scales and abdominal sacs in empidids have been considered to exaggerate abdomen size and thus deceive males about egg maturity so as to obtain matings (Funk & Tallamy 2000). The selective pressures and potential sexual conflicts that led to the evolution of such female traits are unknown. It is possible that in *R. tarsata* the positioning of the pinnate scales around the abdomen also disguises the state of egg maturation (Funk & Tallamy 2000). Males, however, do not have the option of choosing females that lack pinnate scales. Of current selective importance is whether males choosing females on the basis of pinnate scales bear a cost

as a result of that choice. We have shown that in *R. tarsata* pinnate scales honestly reflect female fecundity. As it is likely that males can only assess female weight once in the paired descent flight, relative pinnate length is actually the best trait a male could use to select a fecund mate from the lek.

Variation in egg maturity is expected to have large fitness consequences for males. Abdomen size predicted egg maturity yet was not a target of sexual selection. The lack of selection on abdomen size may indicate that the pinnate scales on female legs do mask abdomen size. However, provided that there is no negative relationship between female pinnate scale size and egg maturity, any masking of abdomen size is only likely to introduce random variation into male fitness rather than selecting against a male preference. In *R. tarsata* there was no evidence for a negative relationship between pinnate scales and egg size and indeed, even in *R. longicauda* there was a positive relationship between inflated abdomen size and egg maturity (Funk & Tallamy 2000). These relationships will not select against male preferences for female pinnate scales, particularly when coupled with a fecundity benefit. Instead of assessing females in the lek on the basis of abdomen size, male assessment of female weight in the descent flight may ensure that males obtain females with mature eggs. The success of this preference is borne out in the more mature eggs of selected compared to lekking females. In addition, the distribution of egg sizes within the lek suggests that females with mature eggs may actually stop visiting the lek. Females with mature eggs are less likely to need nuptial gifts as a food resource as their eggs are already developed. These females are also more likely to face higher predation in the lek owing to reduced mobility and pay higher energetic costs when lekking because of their increased weight. Males then may often only have females with immature eggs as potential mates.

Selection analyses reveal that pinnate area is subject to quadratic selection and pinnate length is subject to correlational selection. It is only pinnate length, however, that is related to female fecundity. Pinnate length and area are clearly related traits and it may be that males chose primarily on the larger visual signal, the total area of the pinnates. The significant correlational selection indicates that males also chose on female pinnate length, but it is in conjunction with female weight. The correlational selection between pinnate length and female weight may be indicative of a two-stage male choice process. Pairs have been observed to split up in the descent flight that follows pairing in the lek. Males may initially choose females from the lek on visual cues such as large pinnate scales, but only remain paired with these females if they are heavy. Splitting up with light females may be particularly beneficial for males when they carry a high value nuptial gift. It is the nature of this correlation selection that most probably explains why there is no significant overall directional selection on pinnate length. It is only females that were heavy as well as having long pinnates that were selected. This selection, with a trend towards negative selection on body size, may prevent any overall selection on pinnate length.

Strong sexual selection on male size and an equal OSR in *R. tarsata* leks indicates that this species has mutual mate choice rather than sex role reversal. In *R. tarsata* it

appears that male nuptial gifts are of sufficient value for females to compete and invest in ornamentation that increases their chance of obtaining a gift. Female investment in reproduction also appears to be sufficiently costly for females to be choosy. Mutual mate choice is rare (Andersson 1994), though this may reflect a lack of studies that have investigated male choice of females (Amundsen 2000a). However, recent models show that the rarity of mutual mate choice may be expected, as it is hindered by the reduction in mating rate of the chosen sex when the opposite sex becomes choosy (Kokko & Johnstone 2002). Further empirical studies are required, although determining the role of female ornamentation may be more difficult than of male ornamentation. Even under equivalent selection pressure, the degree of elaboration in ornamentation is likely to be more constrained in females than in males. This is due to the competing demands of reproduction (Fitzpatrick *et al.* 1995) and the high fitness returns females obtain from directly investing in offspring for which they have guaranteed maternity. Lower selection pressures on female ornamentation and expectations for reduced elaboration even with equivalent selection pressures, will require more sensitive testing to detect sexual selection on female ornamentation. *Rhamphomyia tarsata* provides evidence that elaborate female ornamentation, that is absent in males, can evolve within the constraints of high investment in gametes, and with simultaneous selection for female choosiness.

How females invest in ornamentation and offspring will determine the honesty of female ornamentation as a signal of female quality. Females that invest in ornamentation may be less able to invest in offspring than females of equivalent resources that only invest in offspring (Fitzpatrick *et al.* 1995; Berglund *et al.* 1997). Competing demands of offspring and ornaments in females may result in an unstable, dishonest signal. Species in which females rely on nutrition from nuptial gifts, however, may actually benefit from investing in ornamentation if it increases their resources more than the cost of the ornamentation. Honesty may also be maintained in female ornamentation if the cost of the ornamentation does not restrict female fecundity (Fitzpatrick *et al.* 1995). Support for this hypothesis has been found in the sex-role-reversed pipefish *Syngnathus typhle*. Females develop a highly contrasting striped pattern during social interactions and this pattern honestly signals female egg number (Berglund *et al.* 1997). The ornamentation does not impose any detectable energetic costs and honesty may instead be maintained by social costs or predation (Berglund *et al.* 1997). In *R. tarsata*, pinnate scales are a morphological trait of fixed size in the adult; however, pinnate scales may divert female resources from reproductive organs during development (Emlen 2001; Roff & Gelinas 2003) or increase susceptibility to predation (Cumming 1994). Such potential costs of the ornamentation in *R. tarsata* are unknown; however, we have shown equivalent allometry for offspring and ornaments.

The honest relationship between female fecundity and pinnate scales in *R. tarsata* may also arise because females with larger pinnate scales gain more matings and with the increased nutrition from nuptial gifts make more eggs. The latter is likely to establish honest signalling within a season, and may also maintain honesty across generations

via maternal and indirect genetic effects (Wolf *et al.* 1998). If the fecundity variation targeted by correlational selection is not purely environmental, correlational selection may further select for genetic covariance between pinnate scales and fecundity. Pinnate scales may also play an aerodynamic role by increasing surface area and reducing the costs of flight for lekking females. Increased flight efficiency may also allow females to divert more resources to eggs, again potentially generating a relationship between pinnate scale size and fecundity. None of these potential scenarios alters the conclusion that males obtain a fecundity benefit rather than a cost by choosing females with larger pinnate scales. Pinnate scales may have exploited a pre-existing male preference for females with large abdomens, but current selection is not expected to remove such a preference now that pinnates reliably indicate fecundity.

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