



Flight-related body morphology shapes mating success in a damselfly

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A small-male mating advantage has been only rarely encountered in territorial species and may be an artefact of selection on covarying traits linked to flight-related body morphology. Here, we explicitly tested its occurrence in the territorial damselfly, *Lestes viridis*, while taking into account two key traits shaping flight performance: relative thorax mass and wing asymmetry. Morphological correlates of mating success were determined by comparing sets of mated and unmated males in a natural population at two different collection dates. We showed consistent morphometric differences between mated and unmated males across both sampling dates, suggesting consistent sexual selection on these traits. Mated males were smaller, had a higher relative thorax mass (proxy for flight-muscle ratio), and showed lower levels of fluctuating asymmetry in the hindwings compared with unmated males. Moreover, these patterns remained when taking their potential covariation into account, suggesting they were directly selected for. As such, we provided the first multivariate proof for a small-male mating advantage in a territorial species taking into account two other key traits related to flight-related body morphology. Given the assumed mechanistic base (low energy consumption and high flight manoeuvrability), we hypothesize that a small-male mating advantage may not be that rare in flying territorial species.

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Of all morphological traits, size is undoubtedly the one that has been most often the focus in sexual selection studies (Andersson 1994). Whereas the evidence for sexual selection favouring large body size is overwhelming, evidence for selection favouring small body size in males is relatively scant (Blanckenhorn 2000). This has been attributed to a bias towards studies on territorial species where there is typically a large-male mating advantage associated with the ability of defending a territory (Andersson 1994; Andersson & Iwasa 1996). This pattern is, however, not general. Several studies reported no effect of size (e.g. Marden 1989; Strohm & Lechner 2000) and other studies have even reported an apparently paradoxical small-male mating advantage in territorial species (Convey 1989; Hernandez & Benson 1998; Voigt et al. 2005).

In general, a small-male advantage in sexual selection can result from two mechanisms (Blanckenhorn 2000):

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(1) small males are more agile and manoeuvrable (Crompton et al. 2003), and (2) small males require less food to support themselves, and may therefore have more free energy and time for sexual activities (so-called small-male time-budget advantage, Blanckenhorn et al. 1995). While these mechanisms are probably more important in scrambling species, they may also operate in territorial species. This may be especially so for species that scramble or defend territories in flight because flight energy expenditure and manoeuvrability are likely to be of major importance (Voigt et al. 2005).

Size may, however, be only indirectly selected for as other variables may be more directly linked to flight performance and ultimately to mating success. One crucial morphological trait shaping flight performance is the flight-muscle ratio (Marden 2000). Males with a higher ratio of flight muscles to body mass have been shown to have a higher mating success (e.g. Marden 1989; Coelho & Holliday 2001). As flight muscles make up most of the thorax, the ratio of thorax mass to total body mass is often used as a proxy for flight-muscle ratio (e.g. Berwaerts et al.

2002; Stjernholm et al. 2005). Given that relative thorax mass may covary with size (e.g. Cordero 1994), it may be a confounding variable when relating body size to mating success. Fluctuating asymmetry of the wings, i.e. small random deviations from perfect symmetry between left and right wings, is another important morphological trait known to shape flight performance which may covary with size and hence be a more direct target of sexual selection. For example, in swarming midges small males have a better flight performance (Crompton et al. 2003) and a higher mating success, but this can be attributed to their more symmetrical wings (McLachlan & Cant 1995). Nearly all studies that could show a small-male mating advantage only included size, and none included both (a proxy for) flight-muscle ratio and wing asymmetry. Therefore, there is a need for studies on mating success of flying territorial species that besides size incorporate these two other variables that may mediate the size effect.

We tested for a small-male mating advantage in terms of sexual selection in the territorial damselfly, *Lestes viridis*, taking into account potential confounding effects of flight-muscle ratio and wing asymmetry. We compared mating success between field collections of mated and unmated males, a well-established method to study sexual selection on traits (see e.g. Bertin & Cezilly 2003). Given the importance of flight performance in this species we hypothesized that mated males should have a smaller size, a higher relative thorax mass and more symmetrical wings than unmated males. We specifically tested whether the expected small-male mating advantage was direct, or indirect and mediated by relative thorax mass and wing asymmetry.

METHODS

Study Species

Lestes viridis is quite unique among damselflies in that females oviposit in branches of trees at the waterside. Males of *L. viridis* typically perch in trees where they defend small territories by aggressively chasing away other males and where they adopt a sit-and-wait strategy to intercept passing females in flight (Dryer 1978; Cordero 1988). Although Dryer (1978) described that males gather at trees away from the waterside, males in our study population defended spots in trees at the pond itself, as was the case in a detailed study of this species in a large insectary that included both trees at a small pond and trees away from the pond (De Block & Stoks 2005, unpublished data). This perching strategy matches the territorial strategy described for *Pyrhosoma nymphula* (Gribbin & Thompson 1991), and contrasts with most other damselflies that are typical patrollers scrambling for females (e.g. Stoks 2000).

Field Collection

Adult males were sampled on two separate dates at a pond in Wilrijk (northern Belgium): 23 August and 15 September 2002. Both dates are well within the mating

season that runs from early August until mid-October. All males were caught when mating activity peaked, between 1300 and 1500 hours, on sunny days with intense reproductive activity. On 23 August we collected 40 mated and 37 unmated males, on 15 September we collected 49 mated and 48 unmated ones (total of 174 males). Only males that were collected in the copulation wheel were categorized as being mated. Unmated males were those not associated with a female but that were active at the reproduction site and were frequently harassing mating pairs. Care was taken to only collect males with intact wings to allow assessment of wing asymmetry. Males were stored individually at 70% ethanol in microcentrifuge tubes. Each time a mated male was caught, the female was kept in a cage to avoid that unmated males would start a mating with one of these females. Females were released after 1500 hours.

Morphometrics

In the laboratory we removed all wings and legs with scissors and separated head, thorax (including the prothorax) and abdomen. Body parts were individually weighed to the nearest 0.01 mg using a microbalance after drying them at 60°C for 60 h. From these measurements we obtained total mass and relative thorax mass. Flight muscles are situated in the thorax. Therefore, the ratio of thorax mass to total body mass is used as a proxy for flight-muscle ratio; and has been shown to positively correlate with flight performance (e.g. Berwaerts et al. 2002; Berwaerts & Van Dyck 2004). Replacing thorax ratio with the residuals of the regression of thorax mass against total mass did not affect which factors were significant in the analyses.

To relate our work to other studies on damselflies, we based wing asymmetry on the length of the hindwings (see e.g. Carchini et al. 2000, 2001; Stoks 2001). Wings were measured from the arculus towards the proximate corner of the pterostigma (see Fig. 1 in Carchini et al. 2000). Therefore, the hindwings of each individual were placed on plasticized paper, fixed with an object glass, and photographed with a digital camera mounted at a fixed position above the slide (28.4 cm). All photographs were taken during a single session and a piece of millimetre paper was added in the background to allow calibration. Digital images of each pair of wings were measured using the image analyser software Image-Pro Plus. Each wing was measured twice to obtain an idea of measurement error. As wing length, we took the overall mean of the two measurements of the left and right hindwings.

Statistical Analyses

Fluctuating asymmetry

To analyse wing asymmetry, we first checked for directional asymmetry and measurement error by performing a two-way mixed model analysis of variance (ANOVA) with individual as a random effect and side as a fixed effect (Palmer 1994). A significant side-effect would indicate directional asymmetry. A significant side*individual

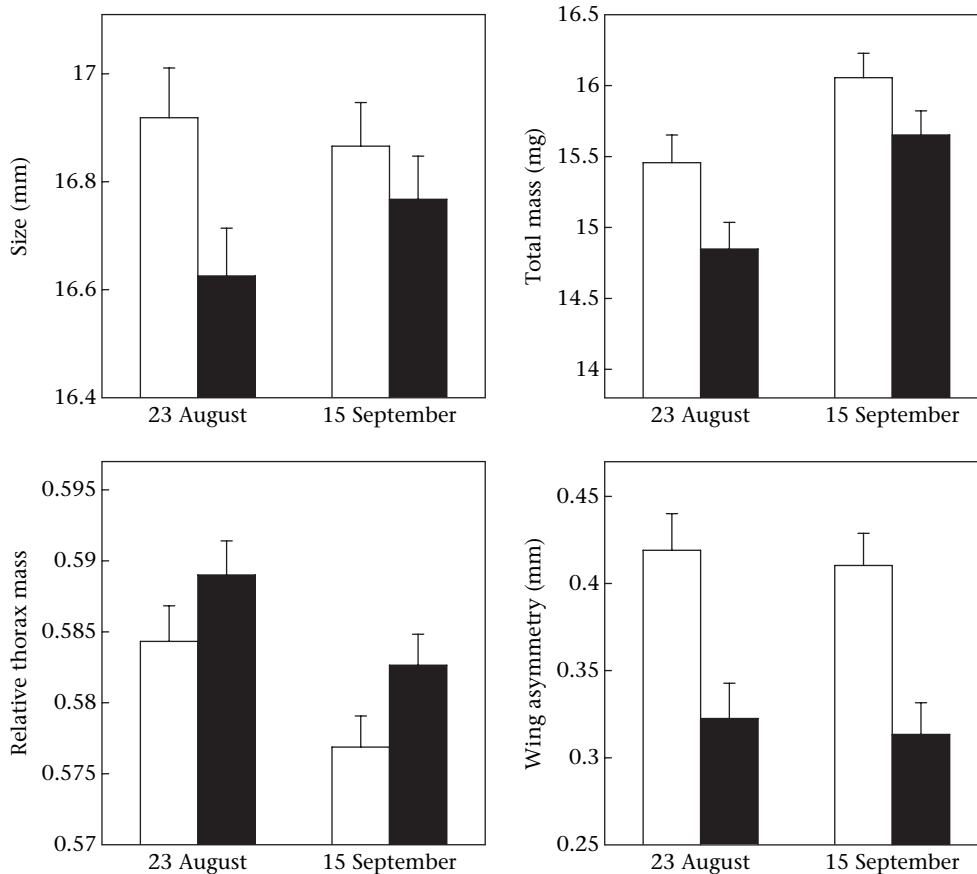


Figure 1. Morphometric correlates of male mating status of the damselfly *L. viridis* for the two collection dates (□: Unmated; ■: Mated). Means are given with 1 SE.

term would indicate that the between-sides variation is larger than the measurement error, indicative of true fluctuating asymmetry. To rule out antisymmetry, we also tested whether the distribution of the signed differences between left and right wing lengths were normally distributed. We chose a common fluctuating asymmetry index at the individual level based on the unsigned difference between left and right wing lengths instead of an fluctuating asymmetry index at the group level (i.e. mated versus unmated males) based on the variance of the signed differences as the former is suited for multivariate analyses (see below).

Correlates of mating success

In a first step, we tested for morphometric differences between mated and unmated males in a MANOVA with mating status (mated and unmated) and date (23 August and 15 September) as independent variables, and the four morphometric traits (hindwing length, total mass, relative thorax mass and hindwing asymmetry) as dependent variables. To interpret the MANOVA, this analysis was followed by separate ANOVAs per trait. Hindwing length, total mass and relative thorax mass were all normally distributed (Shapiro–Wilk's W -test: all $W > 0.97$), and were not transformed.

One potential pitfall when linking relative thorax mass with short-term mating success is that mated males may have expended more energy and eaten less during mating resulting in less gut content, hence less abdomen mass and a relatively higher relative thorax mass (Marden 1989). If the latter scenario were true, we would expect that at the individual level, males showing a larger mass reduction (hence a lower mass) to also show a higher relative thorax mass. We tested this potential effect of total mass (covariate) on relative thorax mass (dependent variable) with an analysis of covariance (ANCOVA) that included date and mating status as categorical variables. Further, if mated males had expended more energy and eaten less, one would expect a smaller mass for a given body size compared with unmated males. We evaluated this with an ANCOVA testing for the effects of mating status and date on body mass with size as a covariate.

The former statistical procedures do not allow evaluating the unique contribution of each morphometric trait to mating success. As covariation among traits may give misleading results about the contribution of individual traits to mating success (Carchini et al. 2000), we also analysed the traits combined in a multivariate regression framework. For this, we performed a generalized linear model with mating status as dependent variable and date and the morphological correlates as independent variables. As the response variable was binary we used

Table 1. Results of univariate ANOVAs testing for effects of collection date and mating status on four morphometric traits in the damselfly *L. viridis*

Source	df	Size		Total mass		Relative thorax mass		Hindwing asymmetry	
		F	P	F	P	F	P	F	P
Date (D)	1,170	0.27	0.60	14.89	0.00016	8.84	0.0034	0.21	0.65
Mating status (M)	1,170	5.25	0.023	7.76	0.0096	5.07	0.026	24.57	<0.0001
D*M	1,170	1.30	0.26	0.32	0.57	0.06	0.81	0.00	0.99

a binomial error structure and the logit link (Crawley 2002). This method evaluates the contribution of each individual morphometric trait to mating success, thereby taking into account the contribution of all other traits. Given the strong positive correlation between total mass and wing length (Spearman rank correlation: $r_s = 0.768$, $N = 174$, $P < 0.001$) we only included the latter in this model to avoid the problem of multicollinearity. Additionally, to evaluate the presence of nonlinear selection we also included the squared terms of the morphological traits in the full model. As none of the squared terms was significant (all $P > 0.14$), they were not included in the final model. All analyses were run in STATISTICA 6.0 (Statsoft Inc., Tulsa, OK, U.S.A.).

RESULTS

Fluctuating Asymmetry

There was no significant side-effect (ANOVA: $F_{1,348} = 1.69$, $P = 0.19$) indicating no directional asymmetry. A significant side*individual term ($F_{173,348} = 14.05$, $P < 0.0001$) indicated that the between-sides variation was larger than the measurement error. This, together with the fact that the distribution of the signed differences between left and right wing lengths was normally distributed (Shapiro–Wilk's W -test: $W = 0.995$, $P = 0.79$), indicated the presence of fluctuating asymmetry. There was no relationship between mean hindwing length and the absolute value of the signed left-right differences (Spearman rank correlation: $r_s = 0.148$, $N = 174$, $P = 0.051$). After square-root transformation, these unsigned differences were normally distributed (Shapiro–Wilk's W -test: $W = 0.992$, $P = 0.51$). Therefore, the square-rooted absolute values of the signed differences were taken as asymmetry values.

Correlates of Mating Success

The MANOVA showed morphometric differences between the males collected at both dates, and between mated and unmated males (Date: $F_{4,167} = 9.18$, $P < 0.00001$; Mating status: $F_{4,167} = 10.20$, $P < 0.00001$). The morphometric correlates of a male's mating status did not change with date (Date*Mating status: $F_{4,167} = 0.39$, $P = 0.81$). Univariate analyses showed that males only differed between dates in mass-related variables: males collected at the second date had a higher mass and a lower relative thorax mass compared with

males collected at the first date (Table 1, Fig. 1). Mated and unmated males differed in each morphometric trait measured. Compared with unmated males, mated males were smaller and less heavy, had a higher relative thorax mass, and had more symmetrical wings (Table 1, Fig. 1).

The ANCOVA testing for the effect of total mass on relative thorax mass showed no effect of total mass or its interactions with date and mating status (all $P > 0.12$). Further, the smaller mass of mated males disappeared when correcting for their smaller size (ANCOVA, mating status: $F_{1,169} = 2.45$, $P = 0.12$).

The generalized linear model that takes the covariation among traits into account, fitted the data well (dispersion parameter = 1.036). It showed that size, relative thorax mass and wing asymmetry all independently contributed to a male's mating status (Table 2). These contributions were consistent between both collection dates as indicated by the nonsignificant interaction terms with date. The regression coefficients showed that males with a smaller size ($\bar{X} \pm SE = -0.86 \pm 0.35$), a higher relative thorax mass ($\bar{X} \pm SE = 37.62 \pm 12.96$), and with more symmetrical wings ($\bar{X} \pm SE = -6.80 \pm 1.52$) had a higher mating probability.

DISCUSSION

We showed consistent morphometric differences between mated and unmated males across both sampling dates, indicating sexual selection on these traits. Alternatively, because morphometric traits covary with date of emergence, at a given collection date these differences may be confounded with age differences between mated and unmated males. This is unlikely in our data set as we only sampled males with undamaged wings, thereby reducing the range of ages included in the data set.

Table 2. Results of the generalized linear model testing for the effects of collection date and morphometric traits on the mating status of males of the damselfly *L. viridis*

Variable	Wald statistic	df	P
Date	0.69	1	0.41
Size	5.98	1	0.014
Relative thorax mass	8.38	1	0.0038
Hindwing asymmetry	19.90	1	<0.00001
Date*size	2.99	1	0.084
Date*relative thorax mass	0.22	1	0.64
Date*hindwing asymmetry	0.67	1	0.41

Moreover, no effect of age on mating efficiency was present in a detailed study of lifetime mating success of this species in a large insectary (M. De Block & R. Stoks, unpublished data).

Mated males were smaller than unmated males, thereby supporting the small-male mating advantage hypothesis in this territorial species. These results are in line with the few other studies showing a small-male mating advantage in territorial species (Convey 1989; Hernandez & Benson 1998; Voigt et al. 2005). Moreover, the multivariate analysis suggested that sexual selection favoured a smaller body size, irrespective of the apparent direct selection operating on a higher relative thorax mass and more symmetrical wings. Our data do not allow us to identify the mechanistic link between small body size and mating success. Small males may have a higher flight ability (Crompton et al. 2003), and lower energy costs (Blanckenhorn et al. 1995). The apparent direct selection on relative thorax mass and wing symmetry, however, indicates that at least the former mechanism contributes to mating success in this species. Clearly, our observational data need to be expanded with experimental data to firmly evaluate the direct targets of selection and to unravel their mechanistic link with mating success. Given the small-male mating advantage it is intriguing why males emerge at a larger than sexually selected optimal body size. One reason may be that lifetime mating success is positively linked with a longer reproductive life span and that larger males are favoured by survival selection (see e.g. Banks & Thompson 1985).

The higher relative thorax mass of mated males may indicate a higher flight-muscle ratio (e.g. Marden 1989; Stjernholm et al. 2005). Alternatively, mated males may have expended more energy and eaten less during mating resulting in less gut content, hence less abdomen mass and a higher relative thorax mass (Marden 1989). The latter scenario is, however, unlikely. First, at the individual level, males showing a larger mass reduction (hence a lower mass) did not show a higher relative thorax mass. Second, the smaller mass of mated males disappeared when correcting for their smaller size, indicating that their smaller mass was not due to a higher expense of energy or a lower food intake. As flight muscles make up the vast majority of the thorax mass in odonates (Marden 1989), our data indicate that the higher relative thorax mass in the study species reflects a higher flight-muscle ratio. Similarly, in the territorial dragonfly, *Platheimis lydia*, males with a higher thorax ratio had a higher short-term mating success (Marden 1989). This is in line with the finding that a higher relative thorax mass is associated with a higher flight performance (Berwaerts et al. 2002; Berwaerts & Van Dyck 2004). Likewise, in the territorial dragonfly, *Libellula pulchella*, male mating success showed a significant positive association with muscle power output (Marden & Cobb 2004). Interestingly, this was only the case in a population with a low burden but not in a population with a high burden of gregarine gut parasites. Unfortunately, we did not assess gregarine parasites in this study, but our results indicate that gregarine parasites if present did not cancel out the link between flight performance and mating success.

Also in line with their assumed better flight performance, mated males had more symmetrical wings. Alternatively, fluctuating asymmetry may reflect male quality and more symmetrical males may have been favoured by females. However, this seems unlikely as males of the study species quite aggressively intercept females in flight and almost all of these interceptions result in copulation (M. De Block and R. Stoks, unpublished data). Moreover, wing asymmetry may to a large extent be randomly determined in damselflies and therefore not reflect individual quality (Bonn et al. 1996; Leung & Forbes 1997). For example, in the damselfly *Coenagrion puella* hindwing asymmetry is positively linked to chance parasitism by water mites. In our study, no animals were parasitized by water mites. However, we cannot exclude they were infected by gregarine endoparasites whose levels may have covaried with wing asymmetry. Several studies in odonates and other taxa (overviews in Polak 2003) reported a mating advantage of more symmetrical males, however, relatively few of them considered potential confounding variables (but see e.g. Harvey & Walsh 1993; McLachlan & Cant 1995). Such multivariate approach is important as, for example, Carchini et al. (2000) showed that mated males of the damselfly *Ischnura elegans* had more symmetrical wings, but this effect disappeared when taking body size into account.

Taken together, our result gave strong support for sexual selection favouring morphological traits likely to affect flight performance in this territorial species. Although such mechanism is frequently invoked it has not often been rigorously shown in natural populations (but see Marden 1989; McLachlan & Cant 1995). Moreover, we could identify three independent targets of selection (small size, high relative thorax mass, low wing asymmetry) indicating that flight performance results from the combined contributions of several morphometric traits. This cautions against studies including one single trait, as the contribution of individual traits to flight performance may vary among species and populations, which may lead to false negative conclusions about the importance of flight performance in shaping mating success. It is striking that the few studies so far that showed a small-male mating advantage in territorial species, all did so in species that defend their territory in flight (Convey 1989; Hernandez & Benson 1998; Voigt et al. 2005, this study). This is not surprising as the assumed underlying mechanisms (low energy consumption and high manoeuvrability) should be especially important for such species. Therefore, we hypothesize the, at first sight counterintuitive, small-male mating advantage in territorial species may not be that rare in flying territorial species.

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