Sexual size dimorphism in the American rubyspot: male body size predicts male competition and mating success

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Sexual differences in body size are widespread among animals, and various explanations for the evolution and maintenance of sexual size dimorphism have been proposed. We investigated the effects of sexual selection and fecundity selection on the sizes of males and females, respectively, in American rubyspots, *Hetaerina americana*. Males are larger than females and have large red spots at the base of each wing that are sexually selected via male–male contests. Mating success is determined by the ownership of a territory. Large males held territories for longer and sustained longer territorial fights than small males. Territorial males obtained more copulations than nonterritorial ones. Large males also had more wing pigmentation and mated with large females. Large territorial males had high energy reserves, whereas nonterritorial males appeared to have depleted reserves. Selection analyses of body size showed disruptive selection acting on male body size, suggesting that both small and large males may be favoured in terms of mating success. We also tested whether fecundity selection acts on female size. However, female body size was unrelated to the number of eggs carried. Taken together, our results suggest that in this territorial damselfly species male-biased size dimorphism is driven by large male size in male–male competition being selectively advantageous in territory acquisition and/or maintenance. We also suggest that small size is advantageous in nonterritorial males to improve their agility in courting (or subduing) females.

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Differences in body size between males and females are widespread in the animal kingdom. The degree and direction of body size difference, termed sexual size dimorphism (SSD), varies across different animal taxa (Andersson 1994; Teder & Tammaru 2005). Several hypotheses have been advanced to explain the interspecific variation in SSD (reviewed in Shine 1989; Andersson 1994; Blanckenhorn 2005). First, increased female body size relative to male size (female-biased SSD) may be the result of selection

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for fecundity (Andersson 1994). This is likely to happen if large females have higher reproductive success because of their higher capacity for producing eggs (Ridley & Thompson 1979; Wiewandt 1982; Honěk 1993), and/or if large females are preferred by males (Sandercock 1998, 2001). For instance, a positive relation between female size and fecundity has been found in frogs, spiders and insects (Shine 1979; Head 1995; Prenter et al. 1999; Legaspi & Legaspi 2005).

Second, differential exploitation of resources may reduce the competition between the sexes, and drive their sizes to different optima (differential niche utilization, Selander 1966; Hedrick & Temeles 1989; Shine 1989; Thom et al. 2004). If resources are scarce and a differential exploitation between the sexes arises, then changes in morphology and body size may follow (Shine 1989; Sandercock 2001; Temeles & Kress 2003).

Third, sexual selection acting on either sex may select for SSD (Raihani et al. 2006). For instance, male–male

competition may favour large body size in those species in which males compete intensely for females (Mitani et al. 1996; Dunn et al. 2001; Lindenfors et al. 2003; Raihani et al. 2006). Thus, large size may be advantageous for males in polygynous species (Clutton-Brock & Harvey 1977; Owens & Hartley 1998).

Finally, the selective advantage of body size may depend on whether the competition occurs on the ground or in the air (Payne 1984; Jehl & Murray 1986). If males compete or display in the air then small male size may be advantageous (Andersson & Norberg 1981; Blomqvist et al. 1997; Székely et al. 2000, 2004; Serrano-Meneses & Székely 2006), whereas large size may be beneficial in those species where males display or compete on the ground (Clutton-Brock et al. 1982; Anderson & Fedak 1985; Lindenfors & Tullberg 1998). These selection processes may be reinforced via female choice (reviewed in Thornhill & Alcock 1983; Choe & Crespi 1997).

The effect of sexual selection on SSD may vary across insect taxa. Different mating strategies (e.g. territoriality, nonterritoriality) may promote changes in the degree and direction of SSD (Andersson 1994). For example, small size is often advantageous to nonterritorial individuals in situations where agility is important (Fincke 1988; Neems et al. 1990), whereas large size is often linked to territorial advantages (Alcock 1979; Fincke 1984; Tsubaki & Ono 1987; Crespi 1988; Villalobos & Shelly 1991; Polak 1993), presumably because large males store more fat to fuel aerial fights (Marden & Waage 1990; Plaistow & Siva-Jothy 1996; Plaistow & Tsubaki 2000; Contreras-Garduño et al. 2006).

Odonates (dragonflies and damselflies) are an ideal group for investigating the selection and physiological processes underlying SSD. They have a variety of mating tactics, strategies and habitats (e.g. Forsyth & Montgomerie 1987; Plaistow & Tsubaki 2000), causing different selection pressures on body sizes of males and females (Conrad & Pritchard 1992; Thompson & Fincke 2002); their SSD ranges from female to male biased (Anholt et al. 1991). Females are usually the larger sex in adult odonates (Anholt et al. 1991), but this difference can be less evident, or even the opposite, in territorial species (Anholt et al. 1991; Fincke et al. 1997). What selection processes influence male- or female-biased SSD? On the one hand, it is possible that male body size is under selection towards large size in species with territorial mating systems (Anholt et al. 1991), since male–male competition is known to select for large male body size (relative to female size, Blanckenhorn 2005). However, the relative strength of different selection processes may be difficult to detect. For example, stabilizing selection may also act on body size across odonates (reviewed in Thompson & Fincke 2002). When stabilizing selection acts, fitness is not a linear function of size. For instance, males of intermediate size of the nonterritorial damselfly *Enallagma hageni* have higher lifetime reproductive success than large males (Fincke 1982). Furthermore, disruptive selection may also occur if, for example, both large and small males are favoured. The conditions of this selection are variable although it often accompanies assortative mating (e.g. Jones et al. 2003). On the other hand, selection for increased female fecundity may result in selection for increased female body size relative to male body size, if fecundity increases with body size. Nevertheless, the relation between female fecundity and body size is poorly understood in odonates (Corbet 1999).

In territorial odonates, males fight to acquire a territory (Corbet 1999). Having a territory is often a prerequisite for males to obtain copulations, because females are attracted to these areas for copulation and/or oviposition (Corbet 1999; Córdoba-Aguilar & Cordero Rivera 2005). Fights over a territory may be short (e.g. 3–5 s) or long (from 20 min to over 2 h); however, territory acquisition is usually determined by prolonged encounters (reviewed by Córdoba-Aguilar & Cordero Rivera 2005). Particularly in the Calopterygidae the acquisition of a territory is usually determined by the outcome of aerial encounters between territory holders and intruders (Córdoba-Aguilar & Cordero Rivera 2005). In these prolonged encounters, males with higher energy reserves in the thoracic muscles (metabolic fat) have an advantage over males with low fat reserves (Marden & Waage 1990; Plaistow & Siva-Jothy 1996; Koskimäki et al. 2004; Contreras-Garduño et al. 2006).

We investigated a damselfly, the American rubyspot, *Hetaerina americana*, to reveal whether male-biased SSD is driven by sexual selection operating on male body size. First, we predicted that large body size is advantageous for males. The American rubyspot's mating system is resource defence polygyny, so that males compete intensely over the possession of a territory (Grether 1996a, b). Soon after emergence, males develop a large red-pigmented spot at the base of each wing. Grether (1996a, b) showed experimentally that the red pigmentation is involved in male–male interactions, since males with larger wing spots held territories for a greater proportion of their reproductive life span and, therefore, mated at higher rates. Grether (1996b) also found that body size was positively selected, but only in nonterritorial males, possibly because they were able to subdue females in the precopulatory stage. Nevertheless, the relations between body size, wing pigmentation and male mating success have not been investigated. In this study we explored the interactions of these variables, and the role of fat reserves and muscle mass in the context of the advantage of large body size in territoriality. We also used selection analyses to quantify the direction and mode of selection acting on body size of males in relation to their mating patterns. Second, since fecundity selection has not been investigated in American rubyspots, we also investigated whether the number and size of the eggs are related to female size. These relations may be linear suggesting directional selection for increased female body size, or females of intermediate body sizes may be more fecund than large or small females, which would be consistent with stabilizing selection.

METHODS

Study Site

Fieldwork was carried out in Tehuixtla, Morelos, Mexico (18°32′56″N, 99°16′23″W, elevation 840 m) between

17 December 2003 and 27 February 2004, and between 12 November and 15 December 2004. We worked along the shore of the Amacuzac River in a section approximately 300 m long. Since American rubyspots avoid areas with shade or cover (M. A. Serrano-Meneses, personal observation), we divided our study site into three areas that were not shaded by trees and held the largest concentrations of individuals.

Marking, Morphometrics and Body Size

On each day we caught unmarked individuals, and marked them with an indelible marker on the right anterior wing with a unique combination of three digits. These numbers were easily readable through binoculars from a few metres, and allowed us to identify individuals during behavioural observations and daily surveys. First, for each captured male we measured its body length (from the head to the tip of the abdomen), head width and wing length (right anterior wing) using a digital calliper (± 0.01 mm). Second, we photographed the wings of 211 randomly chosen marked males at a constant distance with a digital camera (Olympus 765UZ). Third, we categorized males as either territorial or nonterritorial. In our study site, territorial males defended an area against conspecifics and remained faithful to their area after an aggressive dispute, whereas nonterritorial males did not establish an area, wandered along several sections of the river and were chased off by territory owners (for a review of the territorial behaviour see Corbet 1999). Finally, we assigned males to three age classes: (1) juvenile mature, (2) mature and (3) old (see Córdoba-Aguilar (1994) for a detailed description of this procedure). These age classes were estimated from morphological cues (Córdoba-Aguilar 1994): (1) juvenile mature individuals had bright intense colours and highly transparent wings (2) mature individuals showed less brightness and intensity in body colour and their wings were less transparent than those of the juvenile mature individuals; (3) old individuals usually had dark body coloration and their wings tended to be broken at the tips.

We used body length as a proxy for body size for two reasons. First, wing length and head width were highly correlated with body length (see Results). Second, we argue that measuring SSD from differences in wing length may not be appropriate, since it leads to the false conclusion that females are larger than males in this species (see Results).

We assumed that body size is fixed after adult emergence, although one may argue that male body length may change so that it reflects feeding condition. To test this assumption, we captured 44 adult males in our study site on 27 May 2006, measured their total body length, and put them into individual plastic tubes. The tubes were transported to a laboratory at the Universidad Nacional Autónoma de México inside a plastic cooler to keep males alive but inactive. In the laboratory we randomly chose 22 individuals, and fed these males whereas the remaining 22 males were not fed. Males in the fed group were manually fed with fruit flies, *Drosophila melanogaster*, until they ate no more (they usually took 6–11 flies before satiation). Males were fed once a day for 2 days. After 48 h of capture we remeasured their body length.

Male Behaviour, Territory Tenure and Survival

We recorded male behaviour daily between 1000 and 1500 hours (Central Standard Time) when American rubyspots are most active (M. A. Serrano-Meneses, personal observation). Each male was observed for 15 min by scan sampling. Behavioural units were recorded every 10 s using a digital timer. We then estimated the proportion of time the males spent fighting. Prior to analyses, these proportions were log transformed, and we refer to these data as 'fighting rate'.

During behavioural observations and daily surveys we also recorded copulations, and noted whether the observed male was territorial. We used the number of copulations as an indicator of male mating success.

To estimate male territory tenure (the number of days a male held a territory) and survival (the number of days a male was seen alive) we searched for marked animals from 1200 to 1400 hours. Both territory tenure and survival were log transformed. Survival analyses included only those males that were marked during the first 15 days of the first field season (December 2003–February 2004), to exclude those individuals whose lifetime was not fully covered by the study time span.

Wing Pigmentation

Pigmented patches and total wing areas were measured on digital photographs of 211 males, with ImageJ 1.34s (National Institutes of Health, http://rsb.info.nih.gov/ij/). We measured the total area (in pixels) of the four wings and the area of their respective pigmented patches. Since we were interested in the relation between wing pigmentation and body size, we controlled in two ways for the allometric relation that large wings bear large pigmented patches. First, we estimated the average proportion of wing pigmentation for four wings (see similar approach by Córdoba-Aguilar et al. 2003). Second, we calculated the log (mean areas of the pigmented patches) and the log (mean wing areas), and used these log-transformed values in the analyses (see below).

Fat Extractions and Flight Muscle Mass

Weights of metabolic fat and flight muscle were measured for 22 territorial and 22 nonterritorial males that were captured in the field. To avoid the use of chemicals, we killed these males by twisting their heads. We used the thorax of these individuals to weigh both metabolic fat and flight muscle since they are mostly found in this cavity (Plaistow & Siva-Jothy 1996; Corbet 1999). Fat extractions were based on the method described by Marden (1989), where available fat is measured as the difference between thorax dry weight and thorax weight after fat extraction by petroleum ether (see Marden (1989) for full

details); therefore, fat load refers to fat weight (g). The dry, fatless thorax was later immersed in 0.2 M potassium hydroxide for 24 h (Plaistow & Siva-Jothy 1996) to digest the flight muscle and the remaining cuticle was washed in distilled water, dried and reweighed. We used the difference between the weight of thorax cuticle with muscle and the dry muscleless cuticle as an estimate of muscle mass (g).

Fecundity

We captured 45 females in the field. We killed them by twisting their heads and stored them in 70% ethanol. We later dissected them in the laboratory and measured their head width, body length and wing length (± 0.01 mm). We captured only those females that attempted oviposition after copulation; these females had presumably matured a batch of eggs that were ready to be laid. In the laboratory, each female was placed in a petri dish, filled with water, for 2 h and dissected under a stereomicroscope by removing the abdominal sternites and gut. Since clutch size is often traded off against egg size (Roff 2002), we also measured the length and width of 10 eggs per female, using a $10\times$ measuring eyepiece, and used the average size of these eggs in the analyses. We estimated egg size by calculating an egg index based on egg length $\times$ width^2.

Statistical Analyses

To compare the body sizes of males and females we used Student's t tests. To test whether body length changes with feeding regime and thus with body condition, we used a paired t test to compare the body length before and after treatment in both fed and food-deprived groups. We investigated the relations between male size (i.e. body length or wing length) and fighting rate, territory tenure and survival by using Pearson correlations. We constructed two general linear models (GLMs) that initially included either body length or wing length as the dependent variable, and male fighting rate, territory tenure and survival as explanatory variables, and then removed the nonsignificant variable(s) by using backward elimination. All first-order interactions were tested in the initial models, but none was significant ($P > 0.3$), so statistical interactions were not considered further.

To test the relation between wing pigmentation and body size, we first investigated whether the proportion of wing pigmentation was related to body length in a Pearson correlation. Second, we fitted a major axis (MA) regression (model II regression, Sokal & Rohlf 1981) between log area of pigmented patches (dependent variable) and log area of wing. We used major axis regression instead of least-squares regression since the latter does not take into account that both X and Y are estimated with error, and the magnitude of errors was likely to be different between the X and Y variables (Sokal & Rohlf 1981). An MA slope significantly greater than one would suggest that large males have a higher proportion of wing pigmentation. The MA slope and its 99% confidence intervals (lower CI–upper CI) are given in the Results. The confidence

intervals of the slope were calculated by bootstrapping the log-transformed data using R (R Development Core Team 2004, http://www.R-project.org).

We investigated the relations between either fat load or muscle mass (as the dependent variable) and body length (independent variable) by considering the possession of a territory (i.e. male status) using two GLMs. In model 1 fat load was the dependent variable, body length was a covariate and male status was a factor. We found a significant interaction between male status and body length ($P = 0.001$). Thus, we investigated further the association between fat load and body length separately for territorial and nonterritorial males by using bivariate least-squares regressions. In model 2 muscle mass was the dependent variable, body length was a covariate and male status was a factor. Since the interaction between male status and body length was not significant ($P = 0.488$), this interaction was not included in model 2.

We tested assortative mating with regard to body size by fitting an MA regression using the body lengths of 54 males and females found in copula. We used MA regression for two reasons. First, body size is usually estimated with error so least-squares regressions may not be appropriate. Second, least-squares regression often underestimates the slope and the confidence intervals when both variables are measured with error (Fairbairn 1997). The slope of the MA regression and its 99% confidence intervals (lower CI–upper CI) are given in the Results. Confidence intervals were calculated by bootstrapping the body length data using R (R Development Core Team 2004, http://www.R-project.org).

To test the relation between female body length and egg number we used Pearson correlation. Unexpectedly, egg size was not normally distributed (skewed towards the left, Kolmogorov–Smirnov test: $Z = 2.26$, $N = 45$, $P = 0.001$), so we used a Spearman rank correlation for the relation between female body length and egg size. Data are shown as mean $\pm$ SD and the analyses were carried out with SPSS version 12 (SPSS Inc., Chicago, IL, U.S.A.) with the exception of those mentioned above.

Selection Analyses

In selection analyses we used two measures of body size: body length and wing length. Prior to the selection analyses we carried out a principal components analysis (PCA) to reduce the number of variables. Nevertheless, the eigenvectors of both body length and wing length were high (both 0.707) suggesting that body length and wing length were similarly represented in the PCA. Wing pigmentation was not included in the selection analysis because of the low sample size ($N = 16$ mated males).

To estimate the direction and mode of selection acting on body length, wing length and male age we used a multiple regression analysis (Lande & Arnold 1983). To estimate directional (β_i coefficients) selection and curvilinear (stabilizing/disruptive and correlational: γ_{ij} coefficients) selection, we used partial linear regression and quadratic multivariate regression, respectively, of relative fitness against standardized body length, wing length

and age (mean $= 0$, variance, $S^2 = 1$) as independent variables. Relative fitness (w_i) of a given male was estimated as $w_i = W_i / \widehat{W}$, where W_i is the number of matings obtained by a male i throughout the season and $\widehat{W}$ is the mean number of matings of all males in the population.

Ethical Note

All individuals were released immediately after marking and measuring. The total handling time of every individual was usually less than 3 min. Marking was apparently not harmful since shortly after release most territorial males returned to their territory, whereas nonterritorial males and females returned to perching sites near the river.

RESULTS

Sexual Size Dimorphism

Males were significantly larger than females as measured by body length (Student's t test: $t_{844} = 35.04$, $P = 0.001$), head width ($t_{844} = 9.65$, $P = 0.001$) and body mass ($t_{23} = 2.15$, $P = 0.042$). Females, however, had longer wings than males ($t_{844} = 4.58$, $P = 0.001$; Fig. 1). Wing length and head width were highly correlated with body length (Pearson correlation: wing length: males: $r_{738} = 0.76$, $P = 0.001$;

females: $r_{104} = 0.71$, $P = 0.001$; head width: males: $r_{738} = 0.84$, $P = 0.001$; females: $r_{104} = 0.78$, $P = 0.001$).

Male body length did not change in either feeding regime; male length was not different before and after treatment either in the fed group (paired t test: $t_{21} = 0.48$, $P = 0.634$) or in the food-deprived group ($t_{21} = 1.04$, $P = 0.309$).

Territoriality and Survival

Although territorial males were not significantly larger than nonterritorial males (Student's t test: $t_{384} = 1.33$, $P = 0.183$), both territory tenure and male fighting rate increased with body length (Pearson correlation: tenure: $r_{83} = 0.34$, $P = 0.002$; Fig. 2a; fighting rate: $r_{54} = 0.44$, $P = 0.001$; Fig. 2b). These relations were weaker with wing length (tenure: $r_{83} = 0.15$, $P = 0.175$; fighting rate: $r_{54} = 0.26$, $P = 0.056$). Territory tenure was unrelated to the age of males (age estimated at capture, one-way ANOVA: $F_{2,84} = 2.46$, $P = 0.092$), and it was invariable across areas within the study site ($F_{2,84} = 0.39$, $P = 0.678$).

Body size was unrelated to survival (Pearson correlation: body length and survival: $r_{211} = 0.07$, $P = 0.316$; wing length and survival: $r_{211} = 0.07$, $P = 0.281$). These results were consistent with the GLM of body length, since survival was not retained in the final model, whereas both territory tenure and male fighting rate were correlated
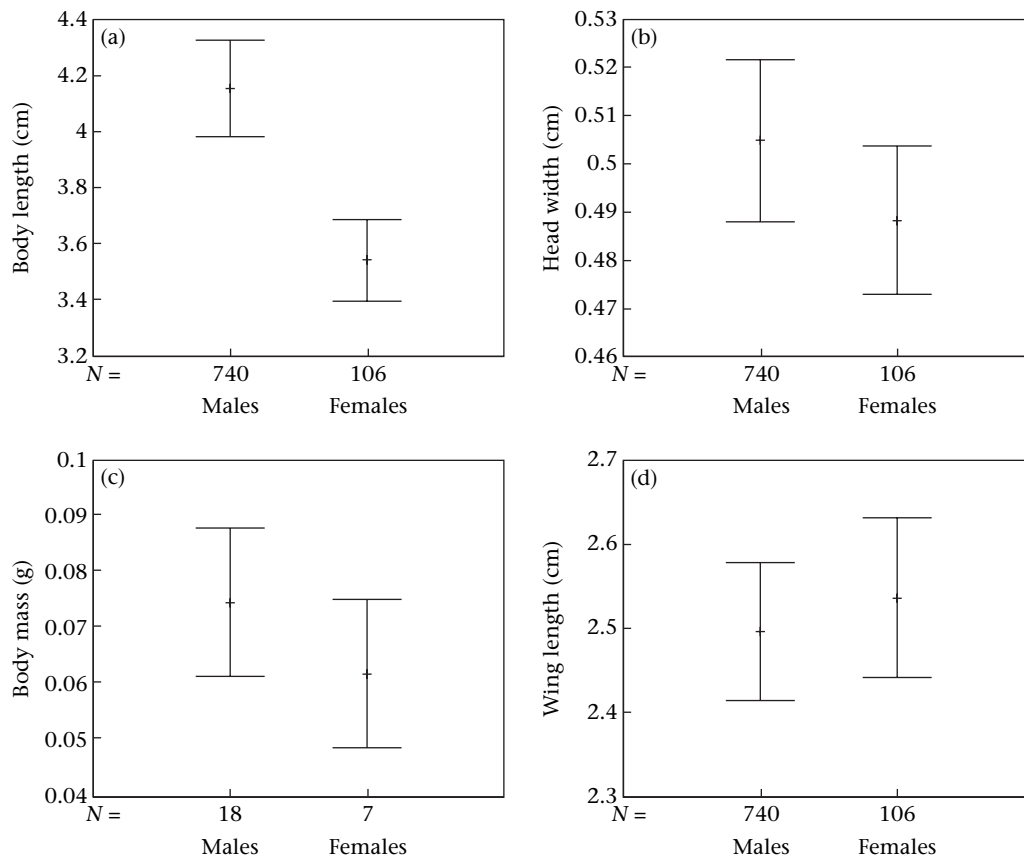

Figure 1. Body sizes of male and female American rubyspots ($\overline{X} \pm$ SD). (a) Body length, (b) head width, (c) body mass and (d) wing length. N refers to the number of males or females.
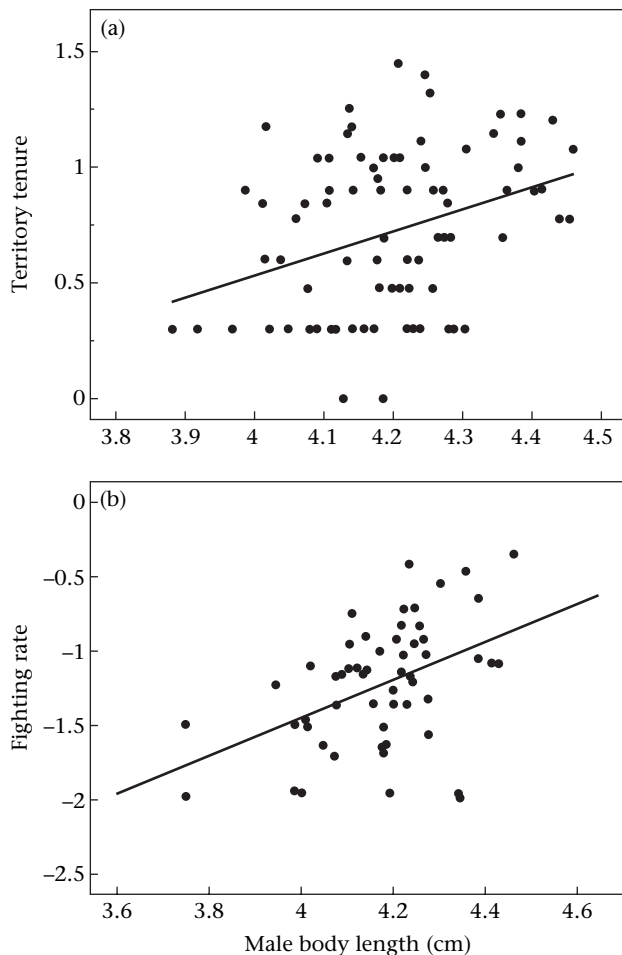
Figure 2. Body length of territorial males in relation to (a) territory tenure (log days) and (b) fighting rate (log proportion of time spent fighting).

with male body length (tenure: $F_{1,33} = 4.64$, $P = 0.039$; fighting rate: $F_{1,33} = 11.33$, $P = 0.002$). None of the explanatory variables were significantly related to wing length ($P > 0.155$ in all cases).

Wing Pigmentation and Body Size

The mean proportion of wing pigmentation was 0.130 ± 0.021 ($N = 211$ males). Large males had a higher proportion of wing pigmentation than small males as measured by body length (Pearson correlation: $r_{209} = 0.29$, $P = 0.001$; Fig. 3) or wing length ($r_{209} = 0.25$, $P = 0.008$).

The log (area of pigmented patches) and log (area of wings) were highly correlated ($b = 1.31$, $N = 211$). The slope of the MA regression was significantly greater than one (lower 99% CI–upper 99% CI: 1.25–1.37).

Fat Load and Flight Muscle Mass

The relation between fat load and body length differed between territorial and nonterritorial males (model 1,
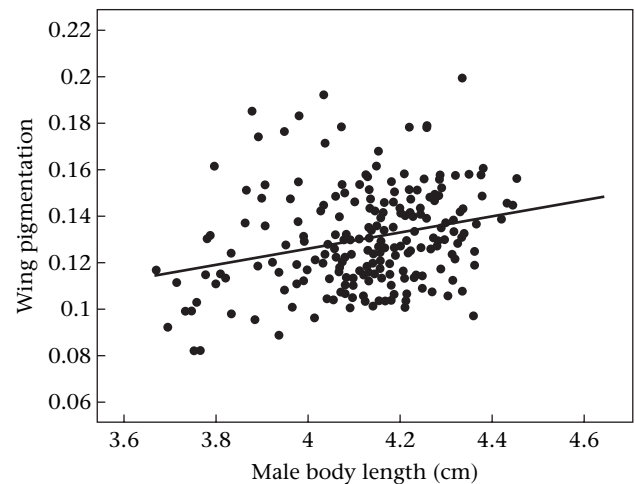

Figure 3. Wing pigmentation in relation to male size. Wing pigmentation is expressed as a proportion, i.e. pigment area/wing area.

male status ∗ body length: $P = 0.001$; Fig. 4a): it increased with body length in territorial males ($r_{20} = 0.69$, $P = 0.001$), but was unrelated to body length in nonterritorial males ($r_{20} = 0.27$, $P = 0.215$).

Flight muscle mass increased with body length (model 2: $F_{1,41} = 59.89$, $P = 0.001$), but it was not different between territorial and nonterritorial males ($F_{1,41} = 0.50$, $P = 0.484$; Fig. 4b).

Mating Rate and Selection Analysis

Males mated 0.014 ± 0.006 times per day, with a maximum of three observed copulations per male. Of 206 territorial males, 49 were seen in copula, whereas only 13 of 180 nonterritorial males were seen copulating. Thus territorial males obtained more copulations than nonterritorial males (chi-square test: $\chi^2_1 = 19.55$, $P = 0.001$).

We found directional selection on male body length, but not on wing length or age (Table 1). The positive and significant gradient of selection on male body length (β_i) suggests that larger males had higher mating success. The gradients of nonlinear selection (γ_{ii}) were not significant except for male body length (Table 1). This gradient of selection was positive indicating that disruptive selection was acting on male body length. Thus, both large and small body sizes were being selected for. No correlational selection was significant.

The body lengths of males and females found in copula were highly correlated ($b = 0.77$, $N = 54$ pairs; Fig. 5). The slope of the MA regression was not different from one (lower 99% CI–upper 99% CI: 0.47–1.19).

Female Fecundity

Females had 676.94 ± 118 eggs ($N = 45$ females), and their egg size was 0.048 ± 0.001 mm^3 ($N = 45$ females). Female body length was not related either to the number (Pearson correlation: $r_{43} = 0.04$, $P = 0.774$) or
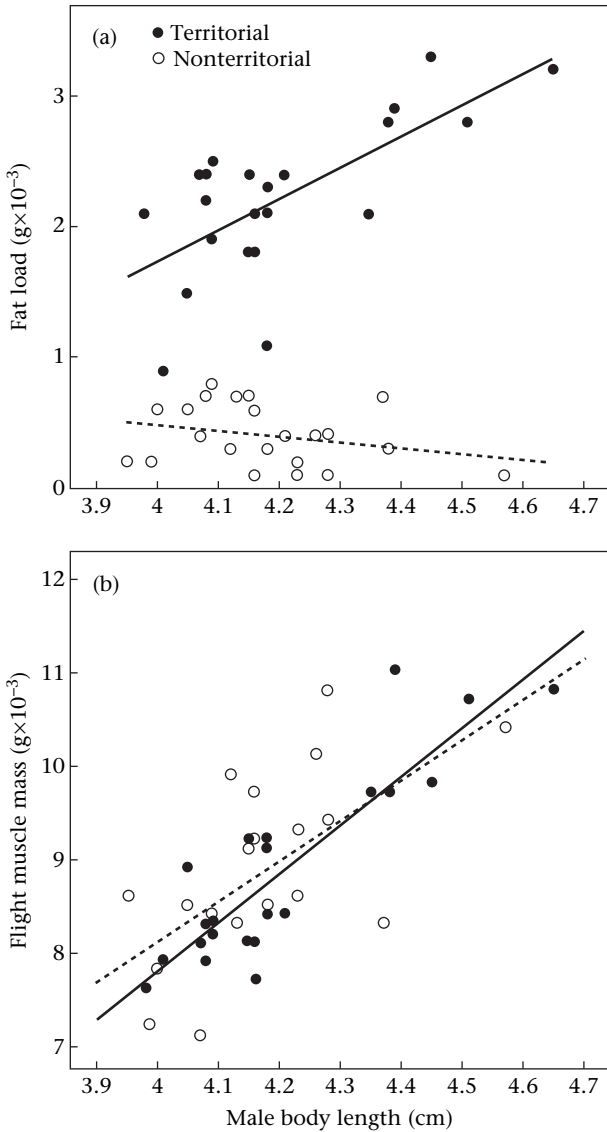
Figure 4. Body length in relation to (a) fat load and (b) muscle mass in territorial and nonterritorial males.

the size of eggs (Spearman correlation: $r_S = -0.04$, $N = 45$, $P = 0.752$).

DISCUSSION

Our study suggests that body size does not reflect feeding condition in adult male American rubyspots. We also found that large body size is selectively advantageous in this territorial damselfly. Males were larger than females in some of the traits we measured. Despite American ruby-spot females having longer wings than males, all other morphological measurements indicated that males are the larger sex. Although it is not known why male and female rubyspots show interspecific differences in wing length, there may be two explanations to why this pattern occurs in odonates. (1) Ecological processes may influence body size and wing length differentially. For instance, Taylor & Merriam (1995) found that long-winged male and female *Calopteryx maculata* were more likely to occur in open hab-itats, such as grasslands, than in forests and they proposed that large wings may reduce manoeuvrability in dense habitats such as forests. (2) The type of flights made by males and females may differ. For instance, females may make more prolonged flights and males more forward flights; long (and wider) wings seem to be used for pro-longed flights (Marden 1987) rather than for forward flight (Wootton 1992).

Territorial and nonterritorial males were similar in body length; nevertheless, larger males had a greater proportion of fat reserves and flight muscle than smaller males. The latter result may be expected in territorial odonates. Males start building up fat reserves soon after emergence, and these reserves are burned during sexual activities and territorial disputes (Plaistow & Siva-Jothy 1996). Perhaps large size at emergence provides the opportunity for males to produce a large muscular mass and store more fat in the days following eclosion (Plaistow & Siva-Jothy 1999). Once a male has lost his territory, there is a large decrease in fat storage (Marden & Waage 1990; Plaistow & Siva-Jothy 1996). Low fat reserves (although not as low as in evicted territorial males) are seen in nonterritorial males that have never defended a territory (Contreras-Garduño

Table 1. Directional (β_i), quadratic (γ_{ii}) and correlational (γ_{ij}) selection gradients for body size and age on mating success in males

Character	β_i	γ_{ii}	γ_{ij}
Body length	0.519±0.189**	0.393±0.178*	
Wing length	0.132±0.189	0.016±0.153	
Age	−0.007±0.125	−0.080±0.104	
Body length×Wing length			−0.123±0.272
Body length×Age			0.182±0.207
Wing length×Age			0.019±0.197
ANOVA for the linear model			
Model	Sum of squares=290.250, F=8.437, df=3, P=0.001, R^2_{adj}=0.029		
Error	Sum of squares=8451.875, df=737		
ANOVA for the quadratic model			
Model	Sum of squares=486.403, F=4.785, df=9, P=0.001, R^2_{adj}=0.044		
Error	Sum of squares=8255.721, df=731		

Gradients are given ± SE.
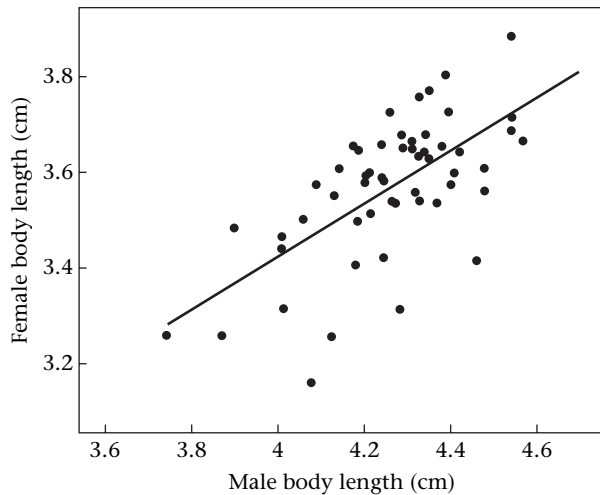*P = 0.028; **P = 0.006.

Figure 5. The relation between body sizes of males and females found in copula. The continuous line represents the relation fitted by major axis regression.

et al. 2006). This pattern has been found in other *Calopteryx* species (Marden & Waage 1990; Plaistow & Siva-Jothy 1996) as well as in *H. americana* (Contreras-Garduño et al. 2006). The decrease in fat reserves after energy-demanding contests, despite large male size, is therefore inevitable. Thus after a male is evicted from a territory, large size is no longer an indicator of fat reserve storage although it is before eviction. In American rubyspots non-territoriality includes both males that were once territorial and males that tried to obtain a territory but failed to do so. We are currently looking at whether these two types of nonterritorial animals differ in size.

Large body size is advantageous for male rubyspots since it enhances territory tenure, fighting rate, wing pigmentation and mating. Large males held territories for longer possibly because of higher fighting ability (e.g. large males had higher fighting rates, perhaps as a result of having large fat stores in their flight muscle). Territory tenure was unrelated to the age of males, suggesting that the ability of males to remain territorial did not depend on age. Grether (1996b) found that males with extensive wing pigmentation held territories for a higher proportion of their reproductive life in both an observational study and an experimental study in which the wing spot of a number of males was artificially enlarged. However, and unlike our results, Grether (1996b) reported that body size was unrelated to territory tenure. We argue that these discrepancies between studies arise from (1) the differences in estimating body size between Grether (1996b) and our study, and (2) ignoring the relation between wing pigmentation and body size. Whereas Grether (1996b) estimated body size from wing length, wing width and thorax width, we used body length. Large size may allow males to put on more muscle mass and fat (Plaistow & Siva-Jothy 1999) that may be honestly signalled to other rivals by using wing pigmentation during territorial contests (since large males are more ornamented). Grether (1996a, b) argued that wing pigmentation has evolved via male—male interactions, as the pigmentation is displayed by males during agonistic encounters. In territorial males, fat reserves are positively correlated with wing pigmentation, whereas the same is not true for nonterritorial males (Contreras-Garduño et al. 2006). The fact that fat reserves are related to wing pigmentation in territorial males strengthens the idea that wing pigmentation is an honest signal of body condition only in territorial males. However, to assess the relative significance of these processes one needs to evaluate carefully the costs and benefits of pigmentation in both female choice and male—male competition.

Male survival was unrelated to body size. We suggest three explanations for this. (1) More ornamented individuals (i.e. with large wing spots) may be spotted sooner by their prey, so that their foraging success and survival are reduced (Grether & Grey 1996): Grether & Grey (1996) found that experimental females marked with red spots in the wings (like those of males), captured fewer prey than control females, thereby gaining less weight. Thus, according to Grether & Grey (1996), wing pigmentation enhances the prey's ability to detect and escape from the approaching damselfly. This may apply particularly to large damselfly males in which strong selection may operate against large spots. (2) Large territorial males may fight until exhausted and be more likely to die than a small animal, which makes it difficult to correlate survival estimates with size. Our study supports this notion since large males spent more time fighting. (3) We may have underestimated survival because some males dispersed rather than died. Ideally, survival should be estimated from mark—recapture data, taking into account differences in resighting rates (reviewed in Lebreton et al. 1992). In American rubyspots, however, survival is difficult to measure accurately given their strong flying capacity.

Territoriality was related to mating success since territorial males obtained more copulations than nonterritorial males. One may argue, however, that we underestimated mating success, particularly of nonterritorial males, by failing to observe copulations. However, in our study both territorial and nonterritorial males were highly visible suggesting that our estimates of copulation rates are not biased (both could be seen crossing the river, looking for oviposition sites, as females do not lay eggs in the male's defended space; M. A. Serrano-Meneses, unpublished data). Furthermore, nonterritorial males obtained few copulations in other studies of *Hetaerina* species (e.g. Córdoba-Aguilar 1995; Grether 1996a). Females visit the territories once they are ready to mate, and although precopulatory events in rubyspots have not been described in detail (but see Johnson 1963), it seems that matings are more likely to occur with territorial males as occurs in other calopterygids (Plaistow & Siva-Jothy 1996; Córdoba-Aguilar & Cordero Rivera 2005). One explanation for the differential mating success of territorial and nonterritorial males is that only a territorial male may provide good oviposition sites for females (Alcock 1987; Waage 1987; Meek & Herman 1990) and protection from other males' interference (Siva-Jothy 1999). In *Hetaerina*, unlike *Calopteryx*, the pair goes to a different place to that defended by the mating male to lay eggs (Córdoba-Aguilar & Cordero Rivera 2005). In fact,

female visit rate to males is not affected by the presence of oviposition sites (Alcock 1987). In this situation, the pair faces aggressive attacks by other males when crossing over these males' territories (M. A. Serrano-Meneses, unpublished data). A territorial male may be able to hold the female firmly and prove his ability to fly to the oviposition resource with her (Córdoba-Aguilar & Cordero Rivera 2005), whereas a nonterritorial male may be unable to do this.

Our selection analysis corroborated our previous findings that large size is selectively advantageous in males. However, it also detected disruptive selection (both extremes of male body length are selected in mating success) which is unusual in odonates. Among odonates, directional selection on body size is expected in resource defence polygamist species such as *H. americana* (Fincke et al. 1997), although the males defend a site only before pairing; once the pair is formed, they look for an oviposition site. Although stabilizing selection has been found in nonterritorial species (e.g. Fincke 1988), it is also in these species that selection for small males has been found (e.g. Banks & Thompson 1985; Anholt 1991) presumably because of advantages via better flight manoeuvrability (Fincke et al. 1997). In *H. americana*, better manoeuvrability could be advantageous during territorial fighting and chasing or while evading other males when the male is in tandem and looking for a place for the female to lay eggs. Theoretical studies suggest that disruptive selection is expected to be accompanied by assortative mating (e.g. Bürger & Schneider 2006), and this prediction is consistent with our results. There may be three explanations for assortative mating. First, large and successful males may prefer to mate with large females, perhaps because these are more fecund. However, our results do not support a positive relation between female body size and fecundity. It is therefore not possible to draw any conclusions on whether linear or stabilizing selection acts on female body size. Perhaps a better estimate of female fecundity would be lifetime fecundity. Studies (Corbet 1999) have reported associations between female body size and lifetime fecundity in *Ischnura graellsii* (Cordero 1991) and *Coenagrion puella* (Banks & Thompson 1987). However, contrary to the hypothesis that female fecundity increases with body size, females of intermediate size produce the most eggs over their lifetime (Banks & Thompson 1987). More studies are needed using lifetime fecundity, but these will be difficult to do given that many calopterygids do not survive in the laboratory. Second, assortative mating may emerge from a simple mechanical rule, for instance if only males and females of similar sizes can copulate (mechanical barrier, Arnqvist et al. 1996). An effective fit of the structures involved in tandem connection (male abdominal appendages and female mesostigmal plates) would be advantageous again during those flights that the pair takes to reach an oviposition site. A third explanation for assortative mating would be related to the lower energy requirements and better manoeuvrability for a small male when flying with a small female than with a large female. Reasons 1 and 3 however, would not explain why small males should pair with large females and large males with small

females, respectively. The second possibility, tandem fitting, is currently under investigation.

In conclusion, sexual selection is likely to select for large size in male–male competition in American rubyspots, since large males hold territories for longer than small males and can store more fat. Fighting ability is likely to be signalled by the size of the wing spot. However, when we looked at mating success, we found disruptive selection on male body size, although the reasons for this remain unclear. The advantage of large size is less apparent in females, since we found no relation between female size and fecundity. Further research should estimate fecundity from the number of eggs deposited in all oviposition events. To quantify lifetime selection on male and female body size, studies should use quantitative genetic protocols using selection differentials (Preziosi & Fairbairn 2000; Blanckenhorn 2005).

Odonates show an excellent range of mating strategies and ecological traits (Corbet 1999). Thus future work should test functional hypotheses of SSD (e.g. fecundity selection, niche division and sexual selection) using phylogenetic comparative methods. Recent advances in phylogenetic methods now allow researchers to test whether evolutionary changes towards territorial mating systems are related to changes towards male-biased SSD. Furthermore, we can test whether male body size has changed around female body size to produce the observed patterns of SSD or vice versa.

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