

**THE EFFECT OF HANDLING DAMAGE, MOBILITY,
BODY SIZE, AND FLUCTUATING ASYMMETRY ON LIFETIME
MATING SUCCESS OF *ISCHNURA GRAELLSII* (RAMBUR)
(ZYGOPTERA: COENAGRIONIDAE)**

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Several spp. of odonates have been the subject of sexual selection studies. In non-territorial species most variance in lifetime mating success (LMS) is accounted for by lifespan and specially by the number of visits, and random factors (like rainy weather) can have strong effect on reproductive success. Here we present the study of 2 natural populations of *I. graellsii* by marking-recapture methods. Our results show that ♂ mating success is related to body size, mobility and handling damage, but not to fluctuating asymmetry. Larger ♂ had greater success in both populations, a result in agreement with previous findings on the same sp. Nevertheless, multivariate analyses indicate that body length was a significant correlate of LMS in just one of the studied populations. We estimated a mobility index for ♂ averaging the distance between consecutive resightings. For long-lived ♂, we found a positive relationship between mobility and LMS. There was a clear effect of leg loss during marking on survivorship, and a marginally significant negative effect on LMS. Finally, we studied the effect of wing fluctuating asymmetry (FA) on LMS by capturing a sample of marked individuals at the end of field work. Results suggest that FA is not an important correlate of LMS in this sp.

INTRODUCTION

Non-random variation in reproductive success is a prerequisite for the action of sexual selection (BRADBURY & ANDERSSON, 1987; ANDERSSON, 1994). If successful and unsuccessful individuals differ in phenotypic variables and there is heritability, then phenotypic characters will show an evolutionary change due to selective

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pressures. In many animal species male mating success is a positive function of body size, and this is specially true for territorial species (CLUTTON-BROCK, 1988). Female fecundity is also positively correlated with body size, either because larger females produce larger clutches or because larger body size increases lifespan and hence fecundity (WICKMAN & KARLSSON, 1989). Body size is therefore one of the most commonly measured variables in sexual selection studies. In odonates a recent meta-analysis suggests that body size is positively related to reproductive success in territorial and non-territorial species (SOKOLOVSKA et al., 2000, but see THOMPSON & FINCKE, in press). Nevertheless, there is no clear biological reason to expect a positive effect of body size in male mating success in non-territorial species. In fact, some studies have shown that small males are more successful (BANKS & THOMPSON, 1985; ANHOLT, 1991; CORDERO et al., 1997; CARCHINI et al., 2000), which is in agreement with studies in other small flying insects (McLACHLAN & NEEMS, 1989).

Fluctuating asymmetry (FA) is defined as random deviations from perfect symmetry in bilateral characters, and is supposed to be related to the individual's developmental stability (PALMER & STROBECK, 1986). FA studies are common in recent years. The first papers reported a significant relationship between FA and fitness, but recent studies are more likely to show non-significant effects (SIMMONS et al., 1999). This situation is similar in odonates, because the first FA studies showed significant associations between FA and male mating success in long-term (HARVEY & WALSH, 1993) and short-term data (CÓRDOBA AGUILAR, 1995), but recent papers failed to find this relationship (LEUNG & FORBES, 1997; FORBES et al., 1997; JENNIONS, 1998; CARCHINI et al., 2000, 2001).

In this paper we present the results of two long-term studies in natural populations of *Ischnura graellsii*, a small non-territorial damselfly common in the Iberian peninsula. CORDERO (1995) studied male mating success in two populations of this species and found evidence for non-random mating success, but the phenotypic variables related to fitness were not identified. More recently CORDERO (2000) using multivariate techniques showed that non-linear selection might be more important than directional selection on shaping male phenotype. Our aim is to test the effect of body size, FA, mobility and marking effects (leg loss during handling) on reproductive success. Furthermore, given that this species has been intensively studied, we provide comparative data on the repeatability of correlates of mating success.

METHODS

Two populations of *Ischnura graellsii* were studied by means of mark-recapture methods. All individuals were marked with a black number on the wing, using a permanent marker (Staetdler Pancolor @303 S pen). In 1995 we marked damselflies at a pond in the Campus of the University of Vigo (UTM: 29TNG2568), and in 1996 we followed a population inhabiting a small coastal lagoon at the beach of Barra (Cangas, Pontevedra, UTM: 29TNG1279), both in NW Spain. At every sighting of a marked specimen, we recorded time, shore section (only at Campus), sex, age (from thoracic coloration (CORDERO, 1987), and body length (to the nearest 0.1 mm). During handling for marking some specimens lost 1-3 legs, because we

tried not to damage wings and retained individuals by their legs. At Campus population we counted the number of legs lost, to see if leg loosing had an effect on reproductive success.

During the period of study, the Campus pond had 220 m of perimeter and a maximum depth of approximately 1.2 m. The shoreline had scarce or no vegetation, with the exception of three small areas covered by *Eleocharis* and a big patch of *Potamogeton*. The community of odonates was composed of *Cercion lindenii* (very common), *Orthetrum cancellatum* (common), *Sympetrum striolatum* (common), *Anax imperator* (common), *Ceragrion tenellum* (rare), *Calopteryx virgo* (two observations) and *Ischnura pumilio* (one observation). Field work was done during 29 days between 11 July and 12 August, with a total of 234 h of observation (8.1 h/day, range: 1-10.3 h). No observations were made on 15 and 25 July and 4 and 5 August, due to rainy weather. Marking was made daily until 7 August, but we continued recapturing after that date. The shoreline was divided into 44 sections of 5 m each, to have a spatial reference for mating activity. We estimated male mobility between resightings calculating the average number of shore sections between consecutive recaptures, assuming that males did not cross the pond (CORDERO, 1995). We marked 464 males and 440 females, and resighted 254 and 284 respectively.

The Barra lagoon was about 300 m² at the moment of the study. The emergent vegetation was scarce due to high evaporation, and maximum depth was about 0.5 m. Damselflies were concentrated on a grass field at the shore, and perched on *Juncus* and some Cyperaceae. At this habitat *I. graellsii* was the dominant species, but a small population of *I. pumilio* was also present (CORDERO & ANDRES, 1999). Other species were *Ceragrion tenellum* (common), *Enallagma cyathigerum* (rare), *Ischnura elegans* (5 individuals), *Cercion lindenii* (6 individuals), *Lestes virens* (1 individual), *L. viridis* (1 individual), *Sympetrum striolatum* (common), *Anax imperator* (common), *Aeshna mixta* (common) and *A. affinis* (one individual). We visited the pond during 31 days from 14 August to 17 September, with a total of 161 h of observation (5.2 h/day, range: 1-8 h). We marked 863 males (599 recaptured) and 766 females (526 recaptured).

To test the effect of fluctuating asymmetry on mating success we captured 31 marked males and 22 females on 12 August at Campus population. This allowed us to have data on lifetime mating success (LMS) of this sample of individuals and also to measure their wing length with an image analysis system. Unfortunately this method might produce biased estimates because captured animals are not able to obtain any more matings. We measured fore- and hindwing length on digitized images of dissected wings using GlobalLab 3.0 © software. Wing length was measured from the first antenodal to the distal end of pterostigma. Each wing was measured three times to estimate measurement error. This was done with a one-way ANOVA on absolute right-left differences with individuals as the factor (MERILÄ & BJÖRKLUND, 1995). Following LEUNG & FORBES (1997) we calculated measurement error as $(s^2_{\text{within}}/3)/(s^2_{\text{within}}/3 + s^2_{\text{among}}) - 100$, where s^2_{within} is the variance within sides (due to measurement error) and s^2_{among} is the variance between sides (FA variation).

To compare between age groups, we divided animals into 3 categories: teneral (0-1 days old), young (3-5 days) and old (more than 5 days). Means are presented with SE and sample size. Statistical tests were performed with GenStat®, SPSS® and BIOMStat®.

RESULTS

HANDLING AND LEG LOSS

About 10% of individuals (9.7% of 413 males and 10.9% of 339 females) lost one or more legs during marking. This fact had no effect on the probability of recapture (62% recaptured in both groups). We tested the effect of legs lost on lifespan (only for resighted individuals) with generalized linear methods (GLM), with observed lifespan as the dependent variable, sex as a fixed effect, number of legs lost as a random effect and date, age of marking and body length as covariables. Results indicate a significant

effect of age at marking on lifespan ($p < 0.001$), no effect of date of marking ($p = 0.141$), body length ($p = 0.612$) and sex ($p = 0.919$) and a significant effect of the number of legs lost ($p = 0.018$). There was no significant interaction legs*sex ($p = 0.864$). The average lifespan was 10.4 ± 0.32 (419) days for intact animals, 9.4 ± 1.04 (37) for animals that lost one leg and 5.0 ± 0.98 (12) for animals that lost two legs. None of three males that lost three legs was resighted.

A second GLM tested the effect of sex (fixed effect) and the number of legs lost (random) on the number of matings, including date of marking, lifespan and body length as covariables, for resighted animals that lived long enough to achieve sexual maturation. Results indicate significant effects of lifespan ($p < 0.0001$) and sex ($p = 0.008$), a marginally significant effect of the number of legs lost ($p = 0.091$) but no effect of date ($p = 0.965$), body length ($p = 0.893$) or the interaction legs*sex ($p = 0.814$).

MOBILITY

We estimated the minimum number of shore sections between consecutive observations of mature males. Mobility is difficult to estimate for males observed only

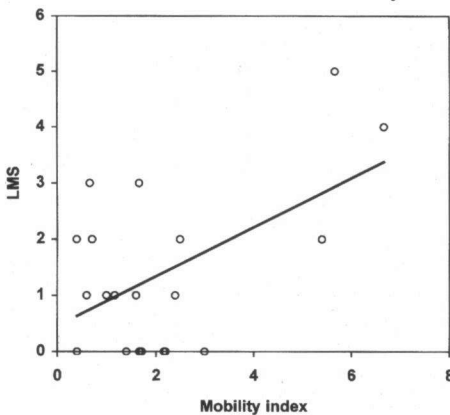


Fig. 1. The relationship between mobility and lifetime mating success in 20 males that were observed at least 6 times.

Some males showed high site-fidelity, whereas others were observed at different locations at every sighting. The effect of mobility on LMS was tested with a GLM with Poisson errors and log link (CRAWLEY, 1993), with LMS as the response variate and mobility index as the predictor variable. A significant positive effect was found ($p = 0.032$, $n = 20$ males; Fig. 1). Lifespan, number of visits and body length did not have a significant effect. This result might be sensitive to the particular set of animals selected. Changing the criterion to males that were recorded at least 5 times (at least 4 movements, $n = 43$ males) gave non-significant results.

BODY SIZE

At Campus population, there was no correlation between body length and date of marking (males, $r = -0.04$, $n = 387$, $p = 0.457$; females, $r = 0.01$, $n = 336$, $p = 0.822$) but

Table I

Body length comparison between mated and unmated individuals. — [mean \pm SE (N); P after t-tests]

Population	age	Mating status unmated	mated	P
Campus, ♂	teneral	25.19 \pm 0.16 (45)	25.83 \pm 0.28 (15)	0.048
	young	25.41 \pm 0.12 (96)	25.67 \pm 0.17 (60)	0.193
	mature	26.19 \pm 0.11 (110)	26.55 \pm 0.16 (57)	0.065
	all	25.71 \pm 0.08 (252)	26.08 \pm 0.11 (135)	0.006
Campus, ♀	teneral	25.73 \pm 0.27 (34)	26.62 \pm 0.20 (32)	0.012
	young	26.25 \pm 0.20 (46)	26.09 \pm 0.19 (49)	0.551
	mature	27.01 \pm 0.17 (64)	27.17 \pm 0.16 (74)	0.508
	all	26.48 \pm 0.12 (148)	26.66 \pm 0.10 (188)	0.229
Barra, ♂	teneral	27.06 \pm 0.08 (160)	27.18 \pm 0.17 (30)	0.561
	young	27.16 \pm 0.09 (123)	27.24 \pm 0.14 (85)	0.603
	mature	27.11 \pm 0.08 (191)	27.39 \pm 0.08 (229)	0.016
	all	27.11 \pm 0.05 (344)	27.33 \pm 0.06 (344)	0.004
Barra, ♀	teneral	28.01 \pm 0.09 (162)	27.92 \pm 0.14 (57)	0.589
	young	28.05 \pm 0.11 (93)	27.56 \pm 0.11 (121)	0.003
	mature	27.76 \pm 0.12 (127)	27.82 \pm 0.11 (167)	0.701
	all	27.94 \pm 0.06 (382)	27.75 \pm 0.07 (345)	0.038

a positive correlation between body length and age at marking (males, $r = 0.31$, $n = 383$, $p < 0.001$; females, $r = 0.27$, $n = 299$, $p < 0.001$). Mated males were significantly larger than unmated males, but in females this effect was only significant for individuals marked as tenerals (Tab. I). At Barra population, there was a positive correlation between body length and date of marking (males, $r = 0.29$, $n = 818$, $p < 0.001$; females, $r = 0.23$, $n = 727$, $p < 0.001$) but no correlation between body length and age at marking (males, $r = 0.07$, $n = 818$, $p = 0.059$; females, $r = -0.07$, $n = 727$, $p = 0.072$). As in the previous population, mated males were larger than unmated males (Tab. I).

The effect of body length on LMS was tested with a GLM with Poisson errors and log link, with LMS as the response variate and body length, lifespan and number of visits as independent variables. Due to non-random residuals in the complete sample, we restricted our analyses to individuals that were observed at least twice. Nevertheless we could not obtain a model with random residuals for females at Campus population. Results are presented in Table II. Body length had a significant effect on male LMS at Barra population, and in all cases, the number of visits to the pond was the best predictor of LMS in males and females.

FLUCTUATING ASYMMETRY

Measurement error was 21% and 20% for fore- and hindwing, but by using the mean of three measurements, the contribution of measurement error was reduced to 8.3% for forewing and 7.8% for hindwing. For both wings signed right-left differences

Table II

Results of a GLM analysis with Poisson errors and log link. LMS is the response variable, and body length, lifespan and number of visits are the independent variables. – [Individuals never resighted were excluded]

Population	Variable	Coefficient (S.E.)	p
Campus, ♂	intercept	-1.42 (1.90)	0.457
	body length	0.0205 (0.0728)	0.779
	visits	0.2184 (0.0770)	0.005
	lifespan	0.0045 (0.0181)	0.804
Campus, ♀	intercept	1.44 (1.06)	0.178
	body length	-0.0670 (0.0396)	0.092
	visits	0.2326 (0.0311)	<0.001
	lifespan	-0.0215 (0.0105)	0.043
Barra, ♂	intercept	-4.16 (1.06)	<0.001
	body length	0.1335 (0.0380)	<0.001
	visits	0.1773 (0.0214)	<0.001
	lifespan	-0.0121 (0.0111)	0.275
Barra, ♀	intercept	0.66 (0.99)	0.507
	body length	-0.0407 (0.0357)	0.255
	visits	0.1862 (0.0163)	<0.001
	lifespan	-0.0183 (0.0094)	0.051

were normally distributed around a mean of zero and positive kurtosis (Fig. 2; Kolmogorov-Smirnov test, forewing: 0.865, $p = 0.703$; hindwing: 0.443, $p = 0.706$). This indicates that the distribution is an example of fluctuating asymmetry (FA). There was no correlation between size (estimated as the mean of both wings) and absolute asymmetry (forewing: $r = 0.003$, $n = 53$, $p = 0.985$; hindwing: $r = 0.23$, $n = 53$, $p = 0.093$), and therefore no correction for allometry was necessary (LEUNG, 1998). There was no correlation between absolute asymmetry of fore and hindwing (males: $r = 0.12$, $n = 31$, $p = 0.516$; females: $r = -0.14$, $n = 22$, $p = 0.531$).

The correlation between absolute FA and LMS was not significant (Spearman's rank correlation, males forewing: $r_s = -0.30$, $n = 31$, $p = 0.104$, hindwing: $r_s = -0.05$, $n = 31$, $p = 0.797$; females forewing: $r_s = -0.12$, $n = 22$, $p = 0.600$; hindwing: $r_s = 0.05$, $n = 22$, $p = 0.820$). Figure 3 shows the relationship between FA and LMS in males and females. None of the individuals included in this sample lost legs during marking. In males, there was a tendency for a reduction in FA with increasing success. Given that LMS is also affected by lifespan, number of visits to the pond and body size, we tested the effect of FA with a GLM with Poisson errors and log link, with LMS as the response variable and body length, lifespan, number of visits and asymmetry (adding up the asymmetry value for both wings) as independent variables. Results indicate that male LMS is not predicted by the above variables ($p > 0.10$ in all cases, and $p = 0.185$ for FA). In females, LMS was predicted by the number of visits to the pond ($p = 0.017$), but not by FA ($p = 0.810$), and lifespan ($p = 0.066$), and body size ($p = 0.073$).

had marginally significant effects. A model with a quadratic term for body length yielded similar results.

DISCUSSION

Our results indicate that handling during marking can have a significant effect on fitness if several legs are lost, which in our experience, is not a rare event with very

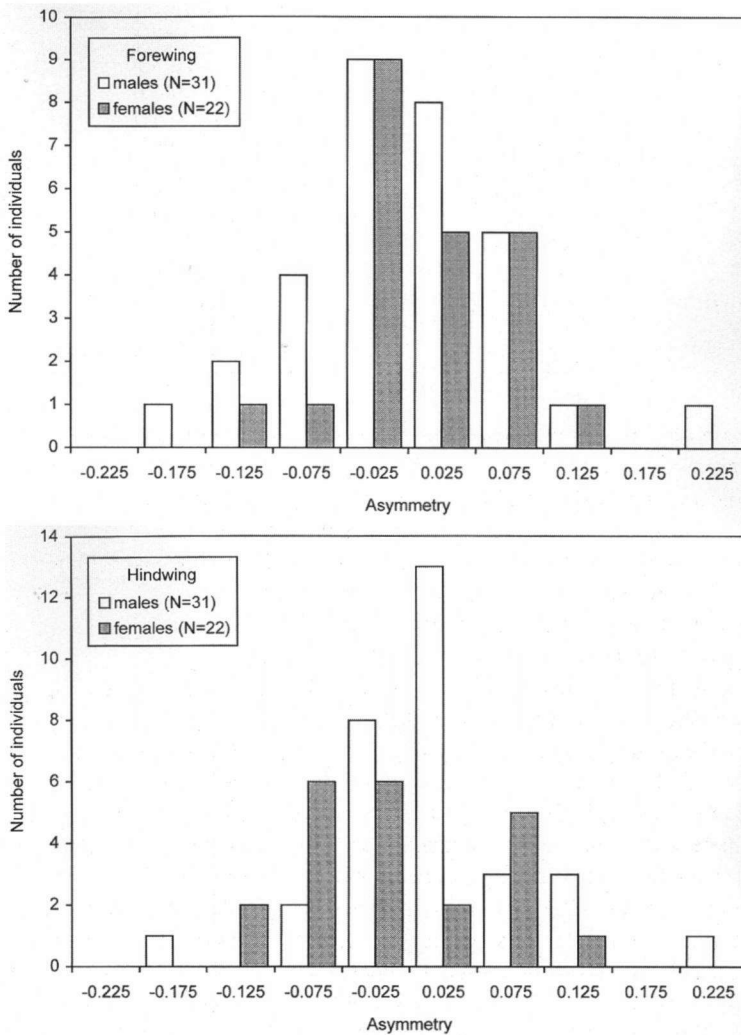


Fig. 2. The distribution of FA in fore and hindwing of *Ischnura graellsii*.

small damselflies. Loosing one leg is probably not a great problem for damselflies, specially if it is a median leg. This is important for applied studies that use legs removed surgically from adults to obtain DNA. FINCKE & HADRY (2001) removed one median tibia from a territorial damselfly and found no evidence for any effect of leg loss on fitness. In our case the difference between 6 and 5-legged animals is also not significant. Nevertheless, the loss of more than one leg, particularly from the same

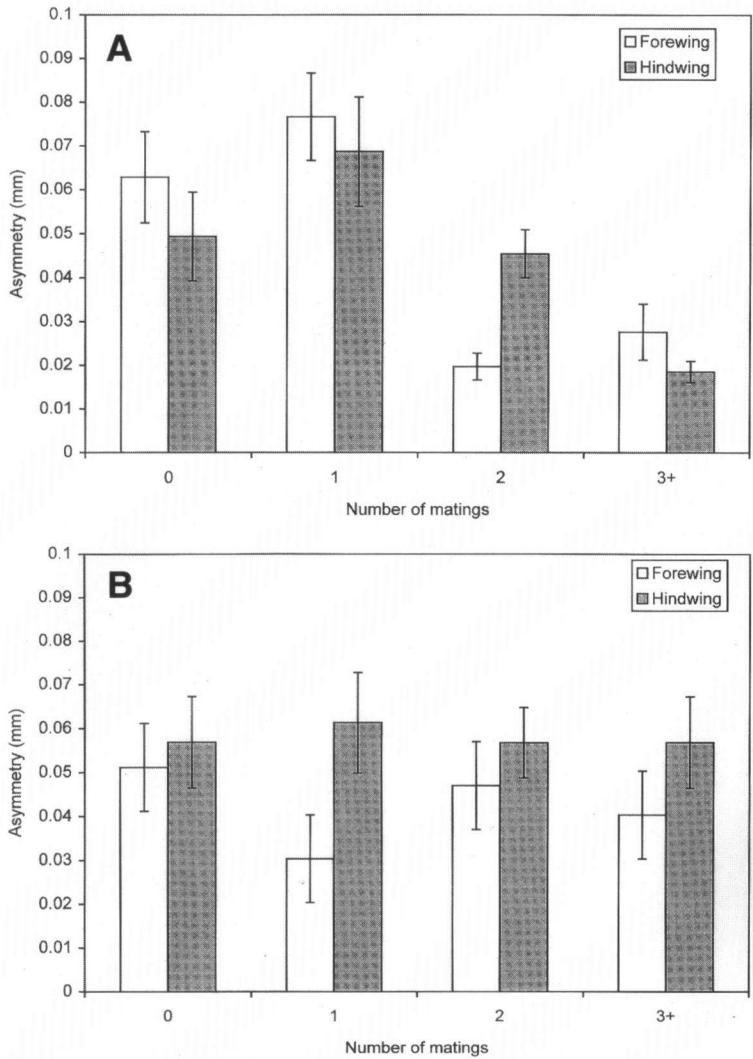


Fig. 3. The relationship between FA and LMS in *Ischnura graellsii*. A: males; – B: females.

side, should significantly reduce feeding and perching performance, and perhaps also the efficiency of mating attempts. Our results are clear and to our knowledge are unique in the literature. Future studies should record leg loss if LMS is to be related to phenotypic variables in small coenagrionids.

Studies of sexual selection in damselflies have found that lifespan is the most important correlate of male LMS (FINCKE et al., 1997), but random factors (SUTHERLAND, 1985; SUTHERLAND, 1987), specially climatic variables are also very important (THOMPSON, 1997). In *Ischnura graellsii*, CORDERO (1995) found evidence for non-random variation in male LMS, but no phenotypic variable was identified as the target for selection. This study shows that mating efficiency for long-lived males is related to mobility. It is possible that males employ two mate-finding strategies: sit-and-wait and active searching, and under some circumstances the second strategy might be more profitable. This trait is exactly the kind of mate-seeking ability predicted by CONRAD & PRITCHARD (1992) as the target of sexual selection on male scrambling damselflies. Furthermore, ANDERSSON (1994) suggested that sexual selection should favour male traits related to mate-finding and mobility in scrambling species, which is in agreement with the results of this study. Male mating efficiency in *I. graellsii* was shown to generate non-linear selection on wing length in a previous field study (CORDERO, 2000). Nevertheless, there might be biases introduced by selecting only animals that were resighted at least 6 times. In fact, for animals resighted at least 5 times this effect is not significant, and therefore these results are to be interpreted with caution.

Our main objective was to test the effect of body size on male and female reproductive success. It has been claimed that in Odonates fitness and body size are positively correlated. SOKOLOVSKA et al. (2000) performed a meta-analysis of 33 studies and claimed to have found evidence for a positive effect of size on male reproductive success, specially in territorial species. In non-territorial species, the effect was weak or non existent. They also pointed out that more studies are needed because the data set is small. Nevertheless the results of this meta-analysis are weak because they included erroneous data in the analysis and did not control for non-linear selection or phylogeny (THOMPSON & FINCKE, in press). Taking into account the present work, four populations of *I. graellsii* have been studied (see CORDERO, 1995). Male body size was positively correlated with LMS in three populations, but in all but one, multivariate analyses have ruled out the effect of body size on mating success (see also CORDERO, 2000). The only exception is the Barra population (Tab. I), where a positive relationship between male body length and LMS is clearly significant only for males marked after sexual maturation. If body size were important in mating success, then this effect should be clear in all age groups. CORDERO (1995) found evidence for greater mobility in larger males, but no effect of mobility on LMS. It is possible that larger males are more successful because they have greater mobility. On the other hand, we have also found a negative correlation between female body size and mating success at Barra population. In a closely related species, *Ischnura elegans*, three independent studies

suggest that small males are more successful than large males (GITTINGS, 1988, as cited by CORBET, 1999; CORDERO et al., 1997; CARCHINI et al., 2000). We see no reason for sexual selection to favour large males in *I. graellsii* but small males in *I. elegans*. The relationship between size and fitness is not easily described with a single correlation (CORDERO, 2000; THOMPSON & FINCKE, in press), and our results indicate that there is no consistent effect in different populations/years. Furthermore, several studies have shown non-linear selection (specially stabilizing) on male body size in non-territorial species (BANKS & THOMPSON, 1985; CORDERO, 2000; STOKS, 2000).

We found weak evidence for the use of FA as an indicator of individual quality. Although in males there was a tendency for more successful males to be more symmetrical (Fig. 3), this relationship was not significant. Given that we captured males at the end of the field season, our method to estimate LMS might have excluded unsuccessful short-lived males, and this could reduce the power of our test. Our results are questionable because our method of capturing marked animals at the end of sampling period impeded us to obtain a large sample, and also impeded animals to obtain more matings. Nevertheless if wing FA were a reliable indicator of flight performance, we cannot explain the difference between males and females. Furthermore, if FA is a good indicator of quality, then we should expect FA of fore and hindwing to be positively correlated, but no correlation was found in this study. Therefore individuals that are highly asymmetric for forewing are not asymmetric for hindwing and viceversa, suggesting that conclusions might depend on the measured trait. A common claim in the literature is that FA is negatively correlated with heterozygosity, but a recent meta-analysis suggests a weak relationship between both variables (VOLLESTAD et al., 1999). Furthermore, FA seems not to be a reliable measure of "quality" in many other animals (SIMMONS et al., 1999; BJORKSTEN et al., 2000). A recent paper on *Coenagrion scitulum* found no correlation between FA and heterozygosity, body size and short-term mating success (SMS), while heterozygosity was positively correlated with body size and SMS (CARCHINI et al., 2001).

In conclusion, our results suggest that lifespan and the number of days spent close to the water explain the greater part of variance in male LMS in *I. graellsii*, a pattern typical of non-territorial damselflies (FINCKE et al., 1997). The possible effect of FA needs a closer examination, specially with experimental phenotypic manipulations (see ANHOLT, 1991).

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