

Correlates of male mating success in two natural populations of the damselfly *Ischnura graellsii* (Odonata: Coenagrionidae)

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Abstract. 1. Two natural populations of *Ischnura graellsii* were studied in north-west Spain by means of mark–release–recapture techniques. Recaptured males were a random sample of the original marked population with regard to date of marking. At O Rosal a greater proportion of young males than old males disappeared after marking; at Lourizán recaptured males were larger than unrecaptured ones.

2. The number of matings observed in both populations showed great daily variation. Most of the variation is accounted for by climatic variables. Most males (56–65%) and many females (41–45%) were never observed to mate.

3. Male LMS was highly correlated with lifespan in both populations. At O Rosal, male LMS was also positively correlated with body length, and mated males were larger than unmated males. This surprising result for a non-territorial species was due to the positive correlation between date of marking and size. There was a positive correlation between body size and mobility for males at O Rosal, but mobility was not correlated with male LMS.

4. As predicted by sexual selection theory, the standardized variance in male LMS was greater than in female LMS. Variation in mature lifespan explained 16% of variance in male LMS at Lourizán and 28% at O Rosal.

Key words. Dragonflies, *Ischnura*, body size, mobility, lifetime mating success, sexual selection.

Introduction

In recent years, many studies have shown that variance in reproductive success is greater in males than females, but variation in female reproductive success is substantial in all species (Clutton-Brock, 1988). The importance of measuring lifetime rather than short-term mating success has been noted, because the latter could produce erroneous conclusions due to tradeoffs between selection episodes (Lande & Arnold, 1983; Arnold & Wade, 1984; Banks & Thompson, 1985a; Fincke, 1986; Clutton-Brock, 1988; Thompson & Banks, 1989).

Damselflies are particularly suitable for studies of lifetime reproductive success because (1) they are often aggregated near ponds, lakes or rivers, (2) they are very easy to observe in the field, (3) their adult maximum longevity is about 5–8 weeks (Corbet, 1980), so they can be studied throughout their reproductive lives, and (4) different species show very diverse

mating systems, making them ideal for comparative studies. Previous studies of LMS of Odonata have concentrated on one population, and no comparative studies of several populations have been published. In this paper I report the study of lifetime mating success (LMS) at two natural populations of the damselfly *Ischnura graellsii* Rambur, 1842. Males of this species are non-territorial and are involved in scramble competition searching for mates (Cordero, 1989). Females of *I. graellsii* are polymorphic in body coloration, with one male-like form (androchromotypic), coloured and patterned like the male and two different kinds of gynochromotypic females, very diverse from males in coloration (*infuscans* form) or pattern and coloration (*aurantiaca* form) (Cordero, 1992b). Females lay eggs alone, usually before the start of mating activity in the afternoon (Cordero, 1989). The existence of last-male sperm precedence (Cordero & Miller, 1992) and long copulations (a method of ‘*in-copula* guarding’; Cordero, 1990) suggest a great influence of sexual selection on the evolution of male reproductive behaviour.

The aim of this study is to describe how mating success is distributed among individuals in two natural populations, and to determine what phenotypic variables (if any) are correlated with

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male LMS. This study was designed to answer the following questions. Is variation in mating success greater in males than in females, as is currently assumed for polygamous species? To what extent is variation in mating success caused by phenotypic differences, by chance or by short-term environmental variation (Clutton-Brock, 1988)? How similar are results obtained by studying several populations of the same species?

Methods

Lourizán population. The population inhabits a small tidal marsh of about 4000 m² with a dense vegetation of *Juncus* and grasses, situated at Lourizán (Pontevedra, north-west Spain). Adults of *I. graellsii* were concentrated in the shoreline of a small stream, resulting in very high density of specimens in this area. *I. graellsii* was the commonest species in this marsh, with only a small population of *Ischnura pumilio* and *Ceriagrion tenellum* present during the study period. The closest conspecific population was at a small artificial pond about 700 m from the marsh, but during the study period it was almost dry and just two or three specimens were observed over several visits. Another population existed 3 km away on the other side of Pontevedra estuary. Thus the study population was isolated and it is reasonable to suppose that animals breeding at this site bred nowhere (see Banks & Thompson, 1985b).

Sampling occurred daily from 15 August to 20 September 1987 (155 h of observation). Adults were individually marked by writing a number in their wings with indelible ink (Staedtler Pancolor 303s), measured (total body length, from head to tip of the abdomen to the nearest 0.1 mm), and their activity (mating, alone, etc.) and thoracic coloration (an estimate of age) were registered at every sighting. I marked individuals (979 males and 672 females) from 15 to 30 August (mean 6.3 h of observation per day, SE 1.2), and from 31 August to 20 September I visited the marsh during the afternoons only to record matings by marked individuals (2.6±0.3 h/day). Rainy days were not excluded, because in *I. graellsii* mating activity continues even in light rain (personal observations). Due to the high number of individuals present and the complexity of the shoreline in the stream, there was insufficient time to follow ovipositing females and therefore no attempt was made to record ovipositions. Individuals were aggregated near the shore, so that I was able to capture and mark specimens in groups of fifteen to twenty. The habitat was an open field, and 2 days before the start of the study most grasses were cut by farmers, and this probably increased the rate of encounter between individuals. From Jolly's method (as described in Begon, 1979), I estimated that the average daily proportion of the male population that was marked was about 49% (range 37–65%). This was therefore a high density population. The relationship between thoracic colour and age was estimated from a set of specimens marked during first days of adulthood (Cordero, 1987).

O Rosal population. I repeated the study in a population with contrasting density at O Rosal, in order to compare mating success of female phenotypes (Cordero, 1992a). I chose the population with the lowest density of *I. graellsii* I could find. This population was at an artificial pond (300 m perimeter) formed in the early 1960s in a clay pit (Pontevedra, north-west Spain). I sampled this population daily in 1990 from 11 August to 8

September (286 h of observation). The water surface was 2–4 m below the ground level, and the shoreline had a continuous band of the grass *Molinia caerulea*, which provided protection from wind. Adults of *I. graellsii* were aggregated in this area (1–3 m wide), and no individuals were observed in the vicinity, probably due to the intense winds common during most days. This pond supported large populations of *Enallagma cyathigerum*, *Cercion lindenii* and *Ceriagrion tenellum*. *I. graellsii* was the fourth most abundant damselfly. The closest conspecific population was at Miño river, about 1.2 km to the south of the pond, separated by woods of *Quercus*, and plantations of *Pinus* and *Eucalyptus*. Individuals were scarce compared to Lourizán. To mark specimens I had to search for them and I could rarely capture more than one unmarked male at any time. On the other hand, the complexity and three-dimensional structure of shoreline vegetation probably reduced the rate of encounter between specimens. The daily proportion of male population that was marked was about 70% (range 43–84%). From all these observations I conclude that this was a low-density population compared to that at Lourizán.

I made 9.8±0.2 h of observation per day until 23 August, and marked and measured 615 males and 479 females. To have estimates of population size I continued marking (471 males and 618 females) until 8 September. These individuals were not measured (except for androchromotypic females) and are excluded from the analysis of mating success, because most of them would be still alive at the end of the sampling period. I tried to record all ovipositions, slowly walking by the shore and recording the identification codes of females seen in the typical egg-laying behaviour.

For every sighting of a marked specimen I registered the identification code, time of day, thoracic coloration, shore zone and activity. The perimeter of the pond (300 m) was divided into fifty-nine zones of 5 m each. An index of mobility was calculated only for males as follows (the low number of recaptures of females prevented this analysis). The distance between consecutive observations was calculated by counting the minimum number of 5 m pond sections between observation points. I assumed that males moved by the shore and did not cross the pond from one shore to the other. From these movements I calculated the average mobility index of the male.

Analysing data. *Ischnura graellsii* has a prolonged flight period in north-west Spain, from the end of March to the first days of October, with at least two generations per year (Cordero, 1988). I analysed mating success in a cohort of individuals whose mature lifespan was included in the sampling period. To select this group of individuals, I estimated the date of emergence as date of marking minus age at marking, and excluded all individuals that had emerged more than 6 days before the start of the sampling period (I assume a maturation period of 6 days, as in Cordero, 1987). In O Rosal I also excluded individuals marked after 23 August. At the end of sampling, no selected male was still reproductively active in any population. This procedure reduced the sample size to 746 males and 516 females in Lourizán and 365 males and 217 females in O Rosal.

Estimates of population size were obtained using all data from marked specimens using Jolly's method (as described in Begon, 1979; see Cordero, 1992a). Values are presented as means ±SE. Climatic data were obtained from the station at the Centre of

Forest Research of Lourizán, which is 700 m from Lourizán and at the same altitude, and from the station at Vigo airport, which is 26 km from O Rosal.

Results

The effect of marking

There was a clear effect of marking on the probability of recapture. At Lourizán, 46% of males and 52% of females were never resighted after marking, whereas at O Rosal these figures were 38% and 52%. These values contrast markedly with the average daily proportion of individuals which disappeared in the following 10 days after marking (Lourizán: 18% of males and 19% of females; O Rosal: 15% and 18%). This fact could be due to increased mortality or dispersal induced by the marking procedure, or both. Indirect evidence suggests greater dispersal rather than mortality as the likely cause. First, laboratory specimens marked in the same way showed no increased mortality the day after marking (Cordero, 1994). Second, one male that had been marked on 2 September at O Rosal and had not previously been resighted, was found at River Miño, 1.2 km away from its marking place, in a search made on 15 September.

Table 1 compares date of marking, age at marking, and body length of recaptured and unrecaptured individuals. Recaptured individuals were a random sample of the original marked population with respect to date of marking. At O Rosal recaptured males were older at marking than recaptured ones. Young males tended to disappear in a greater proportion after marking: 48% (59/122) of males marked when immature (<6 days old) were never recaptured, whereas this proportion was 28% (69/243) for mature males (age at marking ≥ 6 days, $\chi^2=14.22$, $P<0.001$). The average body length of recaptured and unrecaptured individuals was significantly different for the male population at Lourizán, with recaptured males being larger than unrecaptured ones (Table 1). For the female population no differences were found between recaptured and unrecaptured individuals.

The effect of weather on mating activity

In both populations the observed number of matings showed great daily variation (Fig. 1). By means of a stepwise multiple

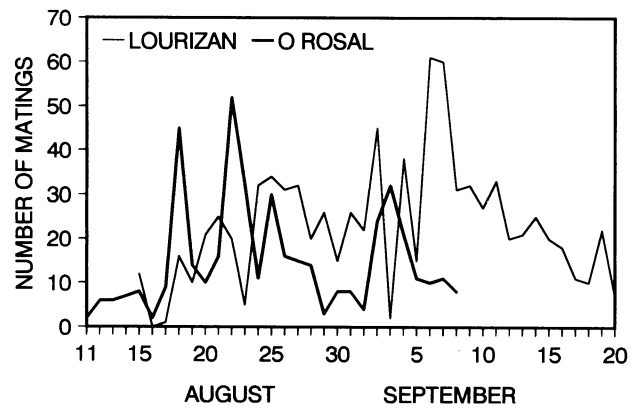


Fig. 1. Daily variation in the number of copulations observed at two natural populations of *Ischnura graellsii*. Most of this variability is accounted for by climatic variables.

regression procedure, I investigated the ability of climatic variables to predict the daily number of matings observed. The dependent variable was the number of matings, and the independent variables were minimum and maximum daily temperatures, hours of sunshine, lunar cycle (varying from 0 in new moon to 1 in full moon), wind (in km/day), rain (in mm/day), and the estimates of population size after Jolly's method (which were entered to control for changes in male and female density). At Lourizán, lunar cycle, number of females and maximum temperature explained 88% of the variance in number of matings, whereas at O Rosal three variables, namely the number of hours of sunshine and the numbers of females and males, accounted for 76% of the variance. Therefore most of the variation in the daily number of matings is accounted for by climatic variables.

Mating success

The following analyses of LMS are made for individuals that lived at least 6 days, and therefore achieved sexual maturation. Fig. 2 shows the distribution of LMS for males and females at both populations. Most males (65% in Lourizán and 56% in O Rosal) and a large fraction of females (41% at Lourizán and 45% at O Rosal) were never observed to mate. Excluding individuals

Table 1. Comparison of phenotypic variables of recaptured and unrecaptured individuals. Values are presented as means \pm SE (n). Probability after a two-tailed Mann-Whitney U test (t -test for body length).

Variable	Lourizán			O Rosal		
	Unrecaptured	Recaptured	P	Unrecaptured	Recaptured	P
Males						
Date of marking*	22.7 \pm 0.26 (340)	22.5 \pm 0.23 (406)	0.575	18.6 \pm 0.28 (128)	18.2 \pm 0.25 (237)	0.774
Age at marking	6.8 \pm 0.20 (340)	7.1 \pm 0.16 (406)	0.350	6.0 \pm 0.48 (128)	7.3 \pm 0.29 (237)	0.002
Body length (mm)	26.6 \pm 0.06 (296)	26.8 \pm 0.05 (388)	0.029	26.8 \pm 0.12 (116)	27.0 \pm 0.08 (233)	0.118
Females						
Date of marking	22.8 \pm 0.30 (258)	22.5 \pm 0.29 (258)	0.519	19.8 \pm 0.28 (111)	19.5 \pm 0.28 (106)	0.277
Age at marking	6.0 \pm 0.27 (258)	6.1 \pm 0.24 (258)	0.667	6.6 \pm 0.42 (110)	6.3 \pm 0.39 (106)	0.693
Body length (mm)	27.4 \pm 0.08 (210)	27.5 \pm 0.07 (242)	0.662	28.0 \pm 0.14 (76)	28.0 \pm 0.11 (104)	0.927

* Days from 1 August.

Table 2. Mean \pm SE of phenotypic variables for all individuals that lived at least 6 days and never mated or mated at least once. Probability after a two-tailed Mann-Whitney *U* test (*t*-test for body length).

Variable	Lourizán			O Rosal		
	Unmated	Mated	<i>P</i>	Unmated	Mated	<i>P</i>
Males	<i>n</i> = 404	<i>n</i> = 219		<i>n</i> = 164	<i>n</i> = 127	
Date of emergence ¹	14.2 \pm 0.22	15.5 \pm 0.32	<0.001	10.3 \pm 0.33	10.5 \pm 0.39	0.630
Body length (mm) ²	26.8 \pm 0.05	26.8 \pm 0.07	0.365	27.0 \pm 0.09	27.4 \pm 0.10	0.008
Age at marking ³	7.8 \pm 0.13	8.5 \pm 0.18	<0.001	7.3 \pm 0.34	9.4 \pm 0.39	<0.001
Mature lifespan ⁴	5.3 \pm 0.18	8.7 \pm 0.30	<0.001	7.3 \pm 0.44	11.0 \pm 0.52	<0.001
Observations ⁵	1.8 \pm 0.05	2.7 \pm 0.10	<0.001	3.4 \pm 0.19	4.4 \pm 0.29	0.003
Females	<i>n</i> = 149	<i>n</i> = 216		<i>n</i> = 81	<i>n</i> = 98	
Date of emergence	14.4 \pm 0.37	16.0 \pm 0.33	0.001	12.3 \pm 0.36	12.4 \pm 0.30	0.487
Body length (mm) ⁶	27.6 \pm 0.09	27.5 \pm 0.09	0.928	28.2 \pm 0.11	28.2 \pm 0.15	0.706
Age at marking	8.4 \pm 0.26	7.7 \pm 0.23	0.249	7.5 \pm 0.43	7.7 \pm 0.32	0.755
Mature lifespan	4.8 \pm 0.24	7.7 \pm 0.29	<0.001	6.9 \pm 0.51	6.9 \pm 0.49	0.871
Observations	1.5 \pm 0.07	2.7 \pm 0.11	<0.001	2.1 \pm 0.16	2.5 \pm 0.20	0.327

¹ Days of August. ² Sample size is 571, 404, 167, 275, 164 and 111. ³ Age estimated from thoracic coloration, in days. ⁴ Calculated as age at marking+observed lifespan-6 days of maturation period. ⁵ Number of days an individual was resighted. ⁶ Sample size is 312, 148, 164, 144, 81 and 63.

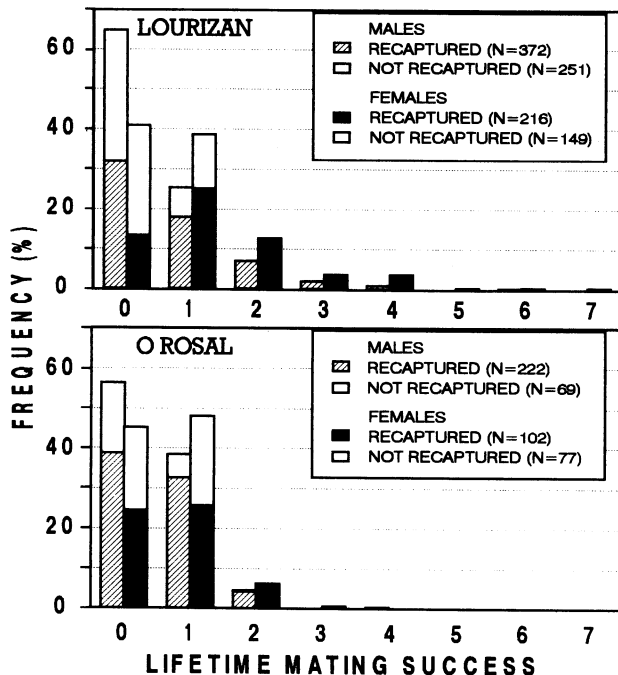
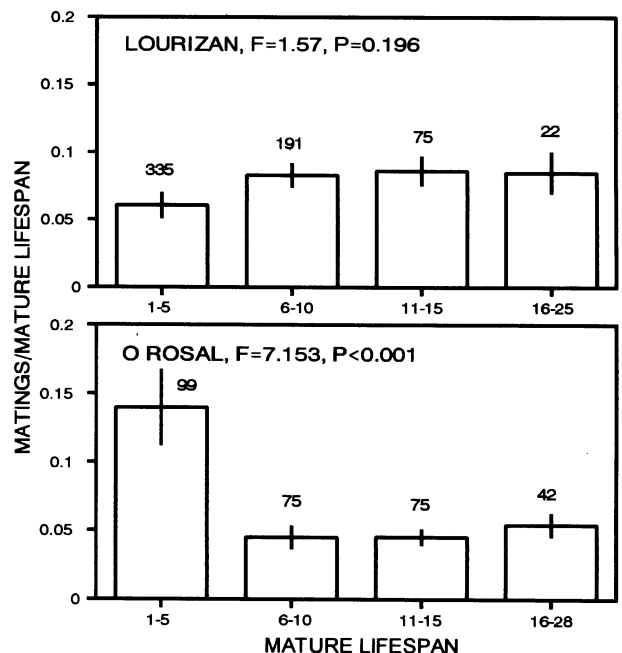
never resighted after marking, the proportion of unmated males was similar between populations (54% and 51%), but a greater proportion of females remained unmated at O Rosal (43%) than at Lourizán (23%), probably due to the low density of males at O Rosal (Cordero, 1992a).

Table 2 presents means and standard errors of phenotypic variables for individuals that achieved maturation but never mated and for those that mated at least once. Mated males were significantly different from those unmated in all variables except body length in Lourizán and date of emergence in O Rosal. Mated females emerged later, lived longer and were observed more times

than unmated ones in Lourizán. In contrast, for females at O Rosal no differences were found between mated and unmated individuals.

Lifespan

Male LMS was highly correlated with mature lifespan in both populations (Lourizán: Spearman $r_s = 0.42$, $n = 623$, $P < 0.001$; O Rosal: $r_s = 0.34$, $n = 291$, $P < 0.001$). In Lourizán, daily mating

**Fig. 2.** Lifetime mating success (number of matings) of male and female *I. graellsii* in two natural populations.**Fig. 3.** The average mating rate (\pm SE) for males with different mature lifespan (in days). Numbers are sample size.

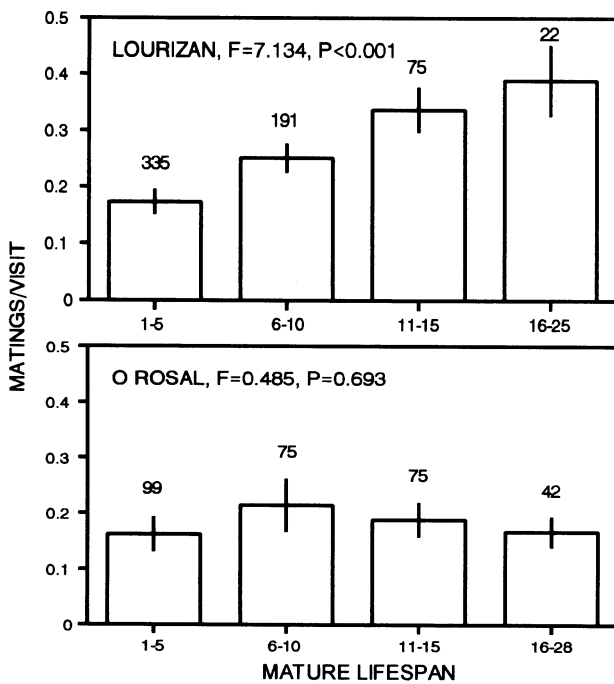


Fig. 4. Mating efficiency (\pm SE) for males with different mature lifespan (in days). Numbers are sample size.

rate (matings/mature lifespan) was similar for short-lived and long-lived males, but in O Rosal short-lived males had a greater daily mating rate (Fig. 3). The difference between the two populations is due to the fact that mating efficiency (matings/visit) increased with mature lifespan in Lourizán but was similar for short- and long-lived males at O Rosal (Fig. 4).

The interval between observations when a male mated (Lourizán: 2.1 ± 0.18 days, $n = 189$ intervals; O Rosal: 2.2 ± 0.22 , $n = 93$) and did not mate (Lourizán: 2.2 ± 0.11 , $n = 534$; O Rosal: 2.0 ± 0.07 , $n = 624$) calculated for all mature males that lived at least 3 days after marking was not significantly different (Lourizán: Mann-Whitney $U = -0.45$, $P = 0.65$; O Rosal: $U = 0.88$, $P = 0.38$). Therefore males remained near the water independent of their mating history. Furthermore, for males that had at least 3 days of mature lifespan there was no significant correlation between LMS and the proportion of mature lifespan that males spent near the water (observations/mature lifespan; Lourizán: $r_s = -0.06$, $n = 338$, $P = 0.288$; O Rosal: $r_s = -0.08$, $n = 192$, $P = 0.254$).

Body length

No significant correlation between male body length and LMS was found at Lourizán ($r_s = 0.03$, $n = 571$, $P = 0.453$), but a significant positive correlation was found at O Rosal ($r_s = 0.18$, $n = 275$, $P = 0.004$). Furthermore, mated males were larger than unmated males at O Rosal but not at Lourizán (Table 2). Body length was not significantly correlated with mature lifespan in either population (Lourizán: $r_s = 0.04$, $n = 571$, $P = 0.308$; O Rosal: $r_s = 0.10$, $n = 275$, $P = 0.104$). At Lourizán there was no correlation between body length and date of marking ($r_s = -0.00$, $n = 571$, $P = 0.975$), but a significant positive correlation was found at O Rosal ($r_s = 0.38$, $n = 275$, $P < 0.001$). The difference

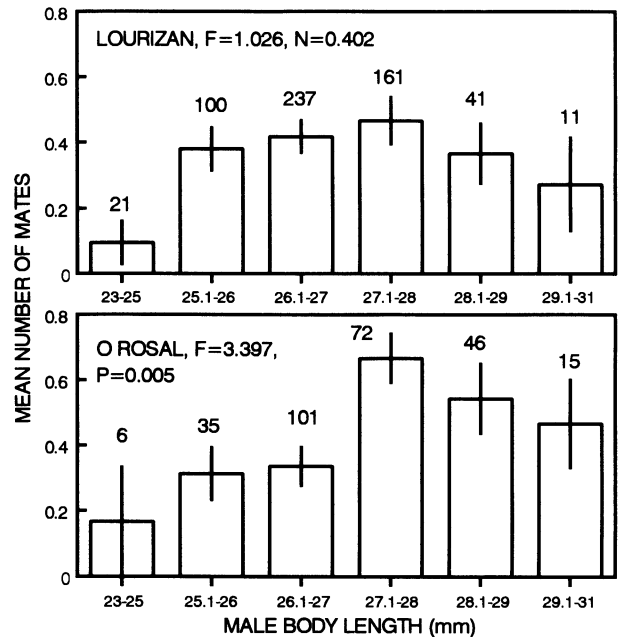


Fig. 5. Lifetime mating success (\pm SE) of males of different size. Numbers are sample size.

in body length between mated and unmated males at O Rosal is not significant when date of marking is entered as a covariate (ANCOVA, covariate: $F = 35.608$, $df = 1$, $P < 0.001$; main effects: $F = 1.37$, $df = 1$, $P = 0.243$). Mating was not assortative by size (Lourizán, $r = 0.04$, $n = 186$ pairs, $P = 0.621$; O Rosal, $r = -0.03$; $n = 106$, $P = 0.74$). Fig. 5 shows the relationship between LMS and body size for males at both populations. Very small and very large males had smaller LMS, suggesting the existence of

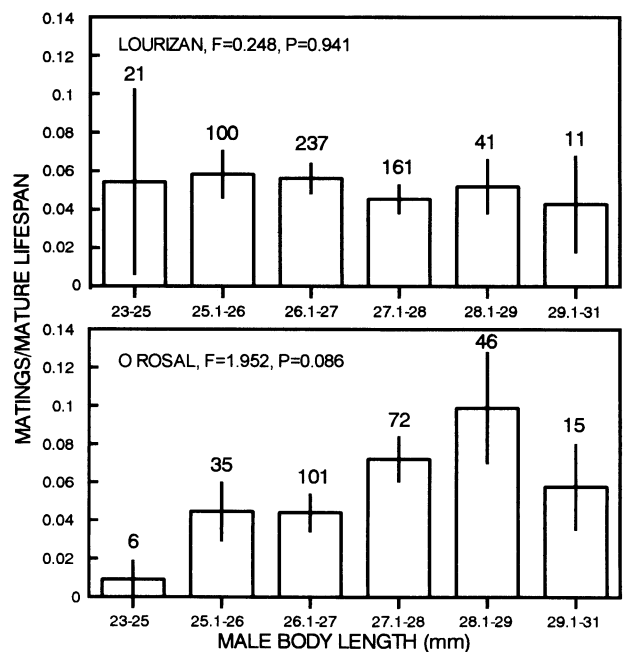


Fig. 6. The average mating rate (\pm SE) for males of different size. Numbers are sample size.

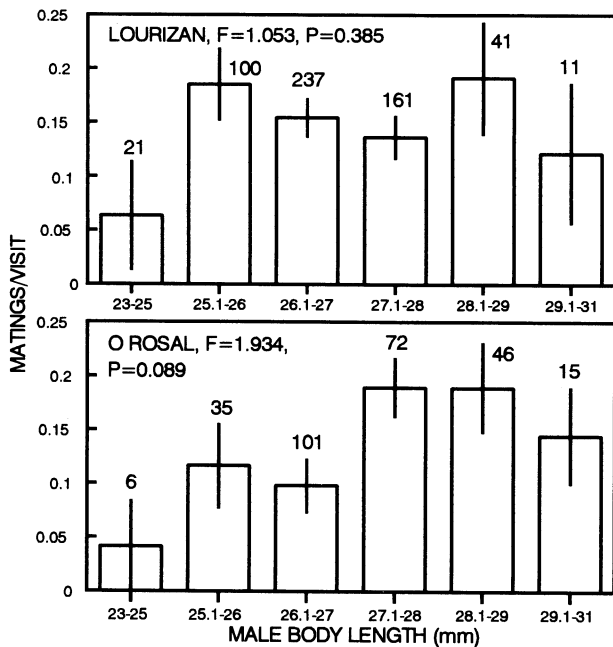


Fig. 7. Mating efficiency (\pm SE) for males of different size. Numbers are sample size.

stabilizing selection for body size. Nevertheless, variance was similar for mated and unmated males in both populations (F-tests, $P > 0.05$). Daily mating rate (matings/mature lifespan) was similar for males of all sizes in Lourizán (Fig. 6), but a tendency for greater mating rate of larger males existed at O Rosal (Fig. 6). No significant differences in matings/visit were found for males of different size (Fig. 7), although a tendency for greater success of larger males was again found at O Rosal.

Mobility

This variable was studied only in O Rosal. Some males showed high site fidelity, whereas others were resighted at different shore zones. The correlation between LMS and the mobility index is

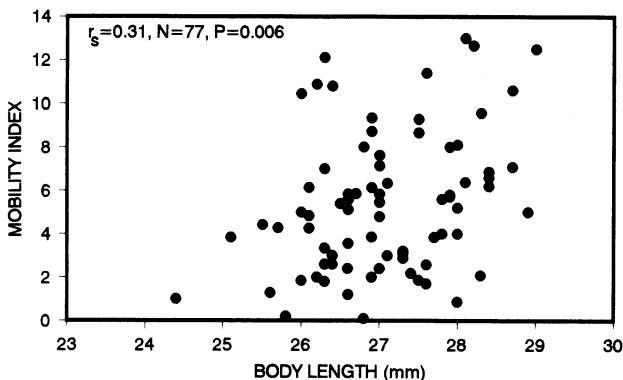


Fig. 8. The relationship between male body length and mobility for O Rosal males that were resighted at least six times. The mobility index averages the minimum number of 5 m pond sections between consecutive recaptures.

not significant ($r_s = 0.00$, $n = 291$, $P = 0.975$), but a positive correlation between mobility and body length was found ($r_s = 0.18$, $n = 275$, $P = 0.014$). Although the probability that a male moves from one pond section to another increases with the number of recaptures, the relationship between body length and mobility for males that were resighted at least six times (five or more movements) is still significant (Fig. 8). Fig. 8 indicates that small males are rather sedentary. The correlation between LMS and mobility is not significant when the effect of body length is accounted for (partial $r = 0.06$, $n = 211$, $P = 0.389$).

The effect of previous experience

Table 3 compares frequencies of males obtaining 0, 1 or 2+ matings with a Poisson distribution based on the number of days that a male visited the water during its mature lifespan. In all cases where enough degrees of freedom are available, no significant difference was observed, although the long mating duration (which effectively prevents two matings in the same day) was not considered. Nevertheless, some variation in mating probability seems non-random with respect to male phenotype. In Lourizán, 36% (48/134) of mature males marked *in copula* remated, whereas only 15% (67/440) of mature males marked alone subsequently obtained a copulation ($\chi^2 = 27.2$, $P < 0.001$). This could be explained by learning, but given the positive relationship between LMS and lifespan, the greater mating success of males marked *in copula* could be also due to their longer lifespan (4.6 ± 0.35 days versus 3.7 ± 0.19 days for males marked alone; Mann-Whitney U , $P = 0.001$). In contrast with this result, in O Rosal males marked *in copula* were less likely to obtain a mating (9/73 or 11%) than mature males marked alone (37/161 or 23%; $\chi^2 = 5.1$, $P = 0.024$). The average lifespan after marking was the same for males marked *in copula* (5.1 ± 0.47 days) and alone (6.2 ± 0.49 days, $P = 0.907$) in this population, and males marked *in copula* (27.6 ± 0.12 mm, $n = 67$) were not significantly larger than males marked alone (27.3 ± 0.09 , $n = 160$), although it is close ($t = 1.93$, $P = 0.054$).

Female mating success

In females LMS was positively correlated with date of emergence ($r_s = 0.17$, $n = 365$, $P < 0.001$), mature lifespan ($r_s = 0.47$, $P < 0.001$) and number of observations ($r_s = 0.59$, $P < 0.001$) at Lourizán, but only with number of observations ($r_s = 0.15$, $n = 179$, $P = 0.0498$) at O Rosal.

The opportunity for selection

Table 4 presents means, variances and the opportunity for selection (variance/mean²) for selection components. In both populations the opportunity for natural selection on lifespan was similar for both sexes. Nevertheless, the opportunity for sexual selection on daily mating rate (matings/lifespan) was nearly twice as high on males than females in both populations. Variation in mature lifespan explained 16% (0.439/2.690) of variance in male LMS at Lourizán and 28% at O Rosal. Variance in LMS was smaller than variance in matings/lifespan in all cases, indicating

Table 3. Comparison of the observed mating distribution with the Poisson distribution (expected values in parentheses) for males visiting the water an equal number of days in their mature lifespan. n = number of males; P = probability after one χ^2 goodness of fit test; df: degrees of freedom. Classes with expected frequency less than five were grouped.

	Visits	n	Mean	No. of matings			P	df
				0	1	2+		
Lourizán	1	275	0.20	220 (226.0)	54 (44.0)	0 (4.6)	–	0
	2	183	0.44	121 (118.2)	44 (51.7)	18 (13.1)	0.083	1
	3	92	0.85	38 (39.4)	34 (33.4)	20 (19.2)	0.777	2
	4	46	1.02	18 (16.6)	16 (16.9)	12 (12.5)	0.657	1
	5	14	1.29	3 (3.9)	8 (5.0)	3 (5.1)	–	0
	6–9	13	2.23	3 (1.4)	2 (3.1)	8 (8.5)	–	0
O Rosal	1	76	0.26	57 (58.4)	18 (15.4)	1 (2.2)	–	0
	2	57	0.47	32 (35.5)	23 (16.8)	2 (4.7)	–	0
	3	42	0.45	23 (26.7)	19 (12.1)	0 (3.2)	–	0
	4	33	0.64	13 (17.5)	19 (11.1)	1 (4.4)	–	0
	5	22	0.41	14 (14.6)	7 (6.0)	1 (4.4)	–	0
	6–16	61	0.80	25 (27.3)	26 (21.9)	10 (11.8)	0.273	1

Table 4. Means and variances for components of reproductive success in mature male and female *I. graellsii*. I = variance/mean². Lourizán: n = 623 males and 365 females; O Rosal: n = 291 males and 179 females.

Population	Fitness component	Males			Females		
		Mean	Variance	I	Mean	Variance	I
Lourizán	Observed lifespan	4.39	19.03	0.985	4.56	18.10	0.869
	Mature lifespan	6.46	18.30	0.439	6.52	16.57	0.390
	Matings/observed lifespan	0.15	0.09	3.706	0.27	0.12	1.664
	Matings/mature lifespan	0.07	0.02	3.575	0.16	0.04	1.680
	Visits to pond	2.02	1.55	0.382	2.08	1.86	0.430
	Matings/visit	0.22	0.12	2.460	0.42	0.17	0.970
	Visits/mature lifespan	0.43	0.10	0.506	0.40	0.08	0.498
	LMS	0.49	0.65	2.690	0.94	1.21	1.375
O Rosal	Observed lifespan	6.71	35.57	0.790	5.25	30.96	1.125
	Mature lifespan	8.94	35.64	0.446	6.87	22.34	0.473
	Matings/observed lifespan	0.15	0.08	3.686	0.31	0.17	1.761
	Matings/mature lifespan	0.08	0.03	4.507	0.13	0.03	1.567
	Visits to pond	3.58	7.60	0.592	2.06	2.97	0.704
	Matings/visit	0.18	0.09	2.634	0.39	0.18	1.185
	Visits/mature lifespan	0.56	0.15	0.469	0.35	0.04	0.339
	LMS	0.49	0.39	1.588	0.62	0.39	1.025

the existence of a negative covariance between matings/lifespan and lifespan, which accounts for the difference. Although in O Rosal, 56% (164/291) of mature males never mated, the mates of ninety-one males did not oviposit, increasing the proportion of non-breeding males to 88% (255/291). The most successful male mated four times, and this male was also the most successful in fertilizing eggs because the females mated by him oviposited eleven times. The second most successful male achieved only four ovipositions. Therefore LMS underestimates variance in reproductive success, particularly in males (Table 4).

Discussion

Reliability of the estimates of LMS

I have assumed that individuals never observed to mate remained unmated. Nevertheless, the proportion of unmated

individuals in *I. graellsii* (56–65% for males, 41–45% for females) is surprisingly high. How confident can I be that I actually observed most of the matings that occurred each day? Two sources of error are possible: matings that occurred near the water but remained unnoticed and matings that occurred far from the water.

With regard to the first source of error, I am confident that I have observed most of the matings that took place near the water for the following reasons. First, mating pairs are much more conspicuous and have a slower flight velocity than single individuals, and for this reason they are very easy to detect. Second, male *I. graellsii* prolongs copulation mainly to prevent sperm competition, and consequently mating duration is often about 2–3 h (maximum 5 h; Cordero, 1990). Such long-lasting copulations are unlikely to be missed. Indeed, most mating pairs were observed several times, although I concentrated the search on previously unrecorded pairs.

With regard to the second source of error, Van Noordwijk (1978) indicates that in *Ischnura elegans* mating is not restricted to the water, and suggests that by copulating far from the water this species avoids interactions with other species, returning females to oviposit in the evening. This fact could explain the low mating rate observed by Parr & Palmer (1971) for this species (95% of unmated males). At the time I was doing the field work I thought that mating was restricted to the water in *I. graellsii*, but I have recently observed a copulating pair which was several hundred metres from the nearest water body. At the O Rosal population, where oviposition was also recorded, three out of nine females marked as tenerals and resighted as mature adults were never observed to mate but were observed in typical oviposition behaviour, indicating that some matings were not detected. It is likely that some individuals mated far from the water, and therefore my estimates are biased for individuals that remained near the water. Another source of bias is the fact that recaptured males were older (O Rosal) or larger (Lourizán) than unrecaptured ones. These facts should be considered in the interpretation of my results.

Notwithstanding the above considerations, I think that my estimates of LMS are valuable. Taking into account the long duration of mating in *I. graellsii* that prevents males from obtaining a second mating in the same day, and the short mature lifespan (average of 5–9 days), the maximum number of matings per lifetime a male can obtain is clearly limited: six matings at Lourizán and four at O Rosal (Fig. 2). This contrasts with *Coenagrion puella* (up to eighteen matings; Banks & Thompson, 1985a) and *Ischnura gemina* (fifteen matings; Hafermik & Garrison, 1986), but is similar to *Enallagma hageni* (five matings; Fincke, 1982) and *Argia chelata* (six matings; Hamilton & Montgomerie, 1989). Even the high proportion of unmated males in *I. graellsii* (56–65%) has been exceeded in other studies: 76% in *Enallagma civile* (Bick & Bick, 1963), 95% in *Ischnura elegans* and *Enallagma cyathigerum*, and 81% in *C. puella* (Parr & Palmer, 1971). This great proportion of unmated males also occurs in other insect orders: 73% in the butterfly *Atrophaneura alcinous* (Suzuki & Matsumoto, 1992). My data are therefore in the range of previous studies of non-territorial damselflies.

Correlates of male mating success

Climatic variables had a strong influence on male mating probability: if one male achieves sexual maturation at the start of a period of cold or wet weather its LMS will be reduced, because bad weather reduces reproductive activity in most damselflies (Thompson, 1990; but see Wasscher, 1990). The intensity and even the direction of selection (Anholt, 1991) can change from one reproductive season to another, depending on weather conditions. This is very important in *I. graellsii*, because this species has at least two generations per year (Cordero, 1988). In the spring generation, when rainy days are common, the effect of selection is likely to be different from its effect on the summer generation.

In the present study the best predictor of male LMS was lifespan. The probability of mating increased with the number of days that a male visited the water. For this reason, the observed distribution of male LMS is not significantly different from a

Poisson distribution based on the number of visits to the water (Table 3). The same occurred in two other damselfly species (Banks & Thompson, 1985a; Fincke, 1986). Nevertheless, there are many indications of non-random mating with regard to male phenotype (Table 2).

Several studies have shown a relationship between body size and mating or reproductive success in odonates (Fincke, 1984, 1992; Harvey & Corbet, 1985; Koenig & Albano, 1985; Tsubaki & Ono, 1987; Moore, 1990; Anholt, 1991), and other studies have shown no relationship (Koenig & Albano, 1987; Van Buskirk, 1987; Marden, 1989; Forbes, 1991; Gribbin & Thompson, 1991). Large size has been demonstrated to be advantageous in mating efficiency only in three odonates, all of whose males defend oviposition sites (Miller, 1983; Fincke, 1984, 1992; Moore, 1990). In non-territorial damselflies large size is not advantageous, but recently Harvey & Walsh (1993) found a positive correlation between size and LMS in *C. puella* (in contrast with previous studies on this species; Banks & Thompson, 1985a). They suggest that in *C. puella* large size produces increased longevity, and in rainy summers large males could obtain greater LMS because they survive longer. In this study I have also found a positive correlation between male size and LMS in the O Rosal population. Nevertheless, this relationship is not significant if date of marking is entered as a covariate, indicating that the greater success of larger males was probably due to the fact that they lived when more matings occurred. Large size *per se* seems not influence LMS of non-territorial damselflies. Nevertheless, I also found a positive correlation between male size and date of marking, in contrast with most studies of temperate-zone dragonflies (e.g. Banks & Thompson, 1985a), and between male size and mobility. Given this last correlation, if some matings occurred away from the pond, it is likely that in these matings were involved more large than small males, increasing the positive correlation between male size and LMS. This interesting possibility, together with the relationship between fluctuating asymmetry and LMS (Harvey & Walsh, 1993), merit examination in future studies.

The probability of obtaining a mating was different for males marked in *copula* and males marked alone in both populations. Surprisingly, at Lourizán males marked in *copula* had a higher probability of remating, whereas at O Rosal males marked in *copula* were less likely to remate than males marked alone. The greater mating probability of males marked in *copula* at Lourizán could be due to learning or to their longer lifespan. Perhaps the rate of encounter with receptive females at O Rosal was so low that learning was not possible. Learning could explain why mating efficiency (matings/visit) increased with mature lifespan in Lourizán but was similar for short- and long-lived males at O Rosal (Fig. 4). Learning could also explain the increase in mating rate for the first 6 days of mature life in *Coenagrion puella* (Banks & Thompson, 1985a).

I used lifetime mating success (LMS) of males as an estimate of reproductive success. This is appropriate, because males can remove most of the sperm from females, resulting in virtually complete last male precedence in the subsequent clutch (Cordero & Miller, 1992). Nevertheless, this estimate ignores the variation in fertilizations/mating and female fecundity (Fincke, 1986). Variation in fertilizations/mating could in part be due to the fact that some females could oviposit without remating, resulting in

great differences in the number of eggs that males could fertilize depending on the number of subsequent ovipositions and matings by their females (even for males that mated the same number of times). Therefore variance in LMS underestimates variance in LRS, particularly in males. Since female fecundity is mainly affected by female longevity and size (Cordero, 1991; see also Banks & Thompson, 1987), and mating was not size assortative (see Results), variation in female fecundity is probably of minor importance in male reproductive success.

The existence of variance in LMS has been considered as an estimate of the potential for sexual selection (Wade & Arnold, 1980), but this view has been questioned because variance in LMS includes non-heritable random effects and is very dependent on how much time is invested in mating (Sutherland, 1985; Koenig & Albano, 1986). This index is also problematic, because LMS is not a good correlate of reproductive success for females of many species, and this is particularly true for *I. graellsii*. In this species the ratio between variance/mean² ranges from 1.025 for females at O Rosal to 2.690 for males at Lourizán and, as predicted by sexual selection theory (Alcock, 1989), standardized variance in LMS was greater in male than female *I. graellsii* (Table 4). Greater variance in male LMS occurred also in *C. puella* (Banks & Thompson, 1985a) and *E. hageni* (Fincke, 1982), but Hafernik & Garrison (1986) found similar variance in both sexes of *I. gemina*. Recently, Nishida (1992) has proposed a new index of the opportunity for sexual selection for interspecific comparisons, avoiding problems generated by different mortality schedules and longevities. Nishida (1992) compared published estimates of the opportunity for selection in number of matings divided by reproductive lifespan and found that the opportunity for sexual selection clearly increases from monogamy to polygyny, whereas this pattern is unclear if LMS rather than matings/lifespan is considered. The values of this index found in the present study for *I. graellsii* (2.128 at Lourizán and 2.876 at O Rosal) are in the range of the values reported for other species which show scramble competition polygyny (Nishida, 1992). I think that this index is the best now available for comparative purposes. The difference in the potential for sexual selection between both populations could be due to the fact that male density was very low at O Rosal compared to Lourizán. It is also possible that these differences are unimportant, or caused by other ecological variables which changed between populations (for instance, species composition).

Acknowledgments

Several anonymous referees have greatly improved previous versions of this paper. This work was supported by a fellowship from the Spanish Ministry of Education and Science (Plan de Formación del Personal Investigador).

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Accepted 30 January 1995