

**LIFETIME MATING SUCCESS, SURVIVORSHIP AND SYNCHRONIZED
REPRODUCTION IN THE DAMSELFLY *ISCHNURA PUMILIO* (ODONATA:
COENAGRIONIDAE)**

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This paper is dedicated to Philip S. Corbet on the occasion of his 70th birthday.

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Abstract

A small population of *Ischnura pumilio* in NW Spain was studied by marking and resighting in August-September 1996. A total of 142 males and 100 females were captured. Adults of *I. pumilio* appeared in two clear groups, starting on 31 August and 10 September. Population size was estimated about 1-2 individuals from 14 to 30 August but suddenly increased to 30-50 males and 40-120 females from 31 August to 13 September. A large fraction of males (43.6%) were never seen to mate, but only 13 females were never seen in copula. Androchrome females were rare (14 females) and did not differ from gynochrome females in fitness correlates. Copulation duration ranged from 1 to 5 h, and was dependent on time of day. The analysis of survival and recapture rates indicates that males and females have similar survivorship, but sex had a significant effect on recapture probability.

Introduction

Ischnura damselflies show several remarkable features in their mating behaviour. Females of some species seem to mate only once per lifetime after they mature (Fincke, 1987; Robinson *et al.*, 1996), in an immature stage (Hinneking & Dumont, 1989) or even immediately after emergence, when still teneral (Rowe, 1978). Other species are polygamous (Robertson, 1985; Cordero *et al.*, 1997; Cordero *et al.*, 1998). Copulation duration is extremely long in some species, reaching more than 6h in *I. elegans* (Miller, 1987) and depends on population density (Cordero, 1990). There are species with postcopulatory contact guarding (tandem) during oviposition (e.g. *Ischnura gemina* Hafernik *et al.*, 1986), but in most species females oviposit alone. This diversity of behaviour makes *Ischnura* a key genus to study the evolution of mating patterns in damselflies (Waage, 1984; Robinson *et al.*, 1996; Robinson *et al.*, 1997).

Ischnura pumilio is a widespread species in Europe (Askew, 1988), but never forms dense populations. It is an endangered species in most of its range due to its dependence on early successional water masses with low plant cover to maintain viable populations (Jurzitza, 1970; Fox, 1989; Fox *et al.*, 1994). Its biology is therefore poorly known. Here, we present a field study of a small population of *I. pumilio* inhabiting a coastal lagoon. We were able to mark and follow virtually every animal in the population, and therefore our results are useful to understand the population dynamics of this rare species and to test whether sexes differ in survival rates.

Methods

The population studied inhabits a small lagoon formed by a stream in the beach of Barra (Cangas, Pontevedra, Lat.: 42°16'. Long.: 8°50', NW Spain). The stream dries up during summer and a small fresh water mass of less than 50 cm deep remains behind a sand dune. The waterbody had a surface area of about 300 m² at the start of the observations, but was very reduced at the end, due to evaporation. The lagoon receives marine water at very high tides. Water conductivity on 31 August varied from 1652 μ S/cm in the exposed area to 916 μ S/cm in the area most protected from sea influence. The area sampled was about 2600 m² of grass vegetation, where adult damselflies aggregated. We did not find damselflies in nearby dune vegetation, despite an intensive search.

Marking and observations were carried out by one observer during 31 days from 14 August to 17 September 1996 (no sample on 19, 21, 22 August and 16 September). Observations started at 10-11h and ended at about 19 h, when activity was reduced (a total of 161h of observation, mean \pm SE: 5.2 \pm 0.37 h, range: 1-8 h). Legal time is used. Solar time is two hours earlier.

Animals were marked with a black number on their right hindwing (Staedtler Pancolor 303s) and measured with a digital caliper (precision 0.01 mm). They were released at the point of capture and most of them behaved normally immediately. We noted mating, feeding and oviposition activity of marked animals at every sighting.

To obtain population estimates we used POPAN4 software (Arnason *et al.*, 1995). Survival rates were analysed by the Cormack-Jolly-Seber model (CJS model) using SURGE (Cooch *et al.*, 1996), for the period 30 August-15 September, when enough animals were available to mark. We tested the adjustment of our data to a CSJ model using test 2 and 3 of the RELEASE program. Both tests use contingency tables and χ^2 tests. Test 2 analyses the probability of resighting animals at occasion $i+1$ depending on whether they were seen or not at the i th occasion. In a CJS model all animals, resighted or not at the i th occasion, must have the same recapture probability. Test 3 analyses whether all marked animals alive at the i th occasion have the same survival probability. The sum of Test 2 and Test 3 indicates the global adjust of the data to a CJS model (Lebreton *et al.*, 1992). The effect of sex on survival and recapture probabilities was analysed using maximum likelihood tests and deviances 'LRT' by means of the program SURGE. The comparison starts with a global model with enough parameters to fit the data (saturated model). The subsequent models are particular cases of this saturated model (are nested in the saturated model). For each model we calculated its deviance. The LRT test was calculated as the difference in deviance

between two models. It approximately follows a χ^2 distribution with number of degrees of freedom equal to the difference in parameters between the models. If there is a significant increase in deviance due to the reduction in the number of parameters of the model (the simplified model has a poorer fit to the data), the variable excluded from the simplified model has a significant effect on the model (see Lebreton *et al.*, 1992, for a detailed description of the method).

Temperature records were obtained from the station at Misión Biológica de Galicia, situated at about 30 km and 50 m.a.s.l.

Results

In total we marked 142 males and 100 females. Most males (67%) and half of females (48%) were resighted at least once. During the first half of the study the number of individuals was reduced: only 11 animals were found from 14 to 30 August. Figure 1 shows the daily number of different individuals observed, the number of copulating pairs and daily maximum temperature. The most surprising result is that adults of *I. pumilio* appeared in two clear groups, starting on 31 August and 10 September. The number of copulations was positively correlated with maximum temperature ($r_s=0.40$, $n=31$, $p=0.025$). As is usual in damselflies, males outnumbered females. Population size was estimated about 1-2 individuals from 14 to 30 August but suddenly increased to 30-50 males and 40-120 females from 31 August to 13 September. All animals were mature when first observed, but some males had an intermediate coloration (blue-green thorax) indicating that they were young.

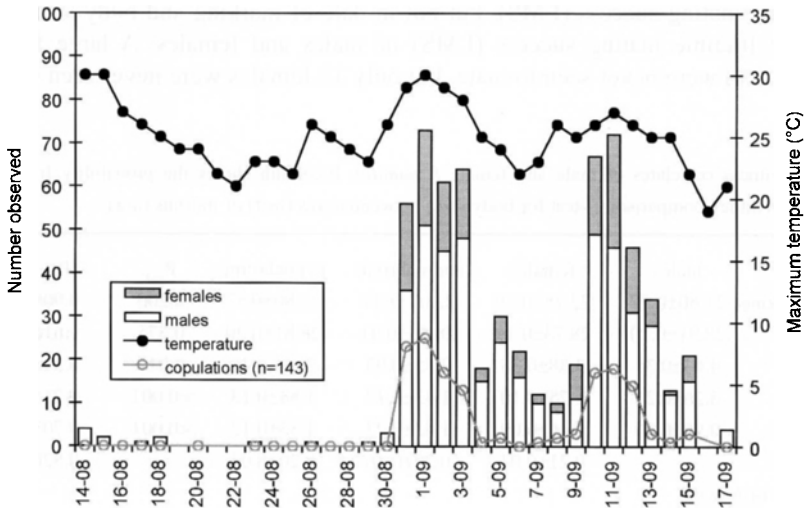


Figure 1. The number of individuals and copulations observed during the period of study. Note that animals arrived in two groups, starting at 31 August and 10 September.

Male body size did not correlate with the date of marking ($r_s=0.04$, $n=135$, $p=0.662$) but last-arrived females were smaller ($r_s=-0.31$, $n=60$, $p=0.017$; Fig. 2).

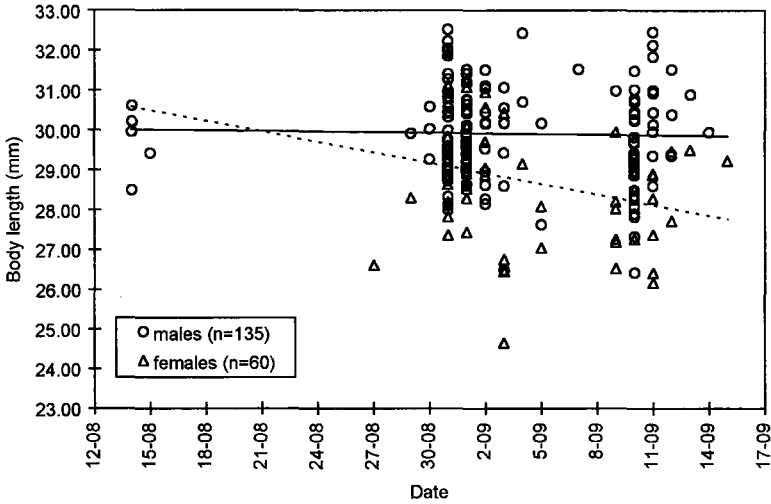


Figure 2. The relationship between body size and date of marking in male and female *I. pumilio*. Sexes did not differ in body size; male body size did not correlate with date but female body size did.

Table 1 shows fitness correlates for males and females. Sexes differed in estimated lifespan (due to differences in recapture probability, see table 2), number of observations and lifetime mating success (LMS), but not in date of marking and body size. Figure 3 shows the lifetime mating success (LMS) of males and females. A large fraction of males (43.6%) were never seen to mate, but only 13 females were never seen in copula.

Table 1. Fitness correlates of male and female *I. pumilio*. P-column shows the probability from a Mann-Whitney comparison (*t*-test for body size) between sexes (m-f) or morphs (a-g).

Variable	males	females	androchrome	gynochrome	P_{m-f}	P_{a-g}
Date of marking ¹	21.80±0.52	22.78±0.49	22.07±1.17	22.80±0.57	0.200	0.908
Body size	28.91±0.10	28.73±0.19	28.56±0.41	28.81±0.20	0.375	0.618
Lifespan ²	4.43±0.35	3.58±0.38	2.85±0.93	3.96±0.46	0.014	0.318
observations	3.26±0.21	1.75±0.10	1.43±0.17	1.84±0.13	<0.001	0.218
LMS	0.99±0.10	1.46±0.09	1.43±0.23	1.53±0.12	<0.001	0.703
ovipositions	-	0.21±0.04	0.29±0.16	0.20±0.04	-	0.826

¹ Days from 14 August.

² Lifespan = 1 day for unrecaptured animals.

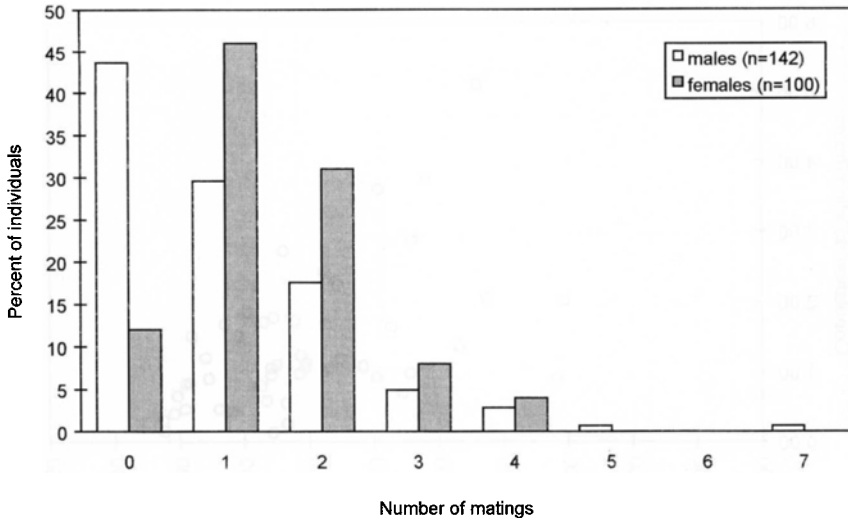


Figure 3. The lifetime mating success of male and female *I. pumilio*. Variance in mating success was significantly larger in males.

Variance in LMS was larger in males than in females ($F_{141,99}=1.596$, $p=0.007$). Most copulations were observed between 14 and 17 h (Fig. 4). Copulation duration of mating pairs that were observed at least twice averaged 1:19 h, but one pair was observed in copula during 5:06 h. Copulation duration was negatively correlated with time of day ($r_s=-0.51$, $n=51$, $p<0.001$; Fig. 5). The same pattern was observed in sympatric *I. graellsii* (pers. obs.).

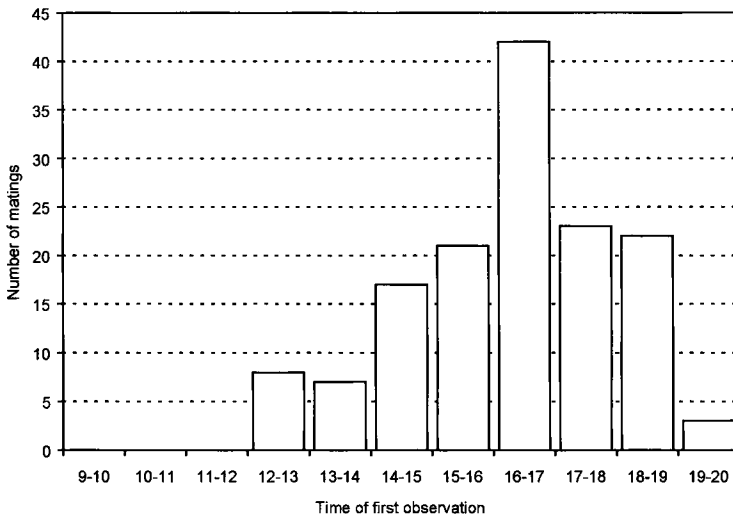


Figure 4. Diel distribution of copulations in *I. pumilio* by the time of first observation (legal time).

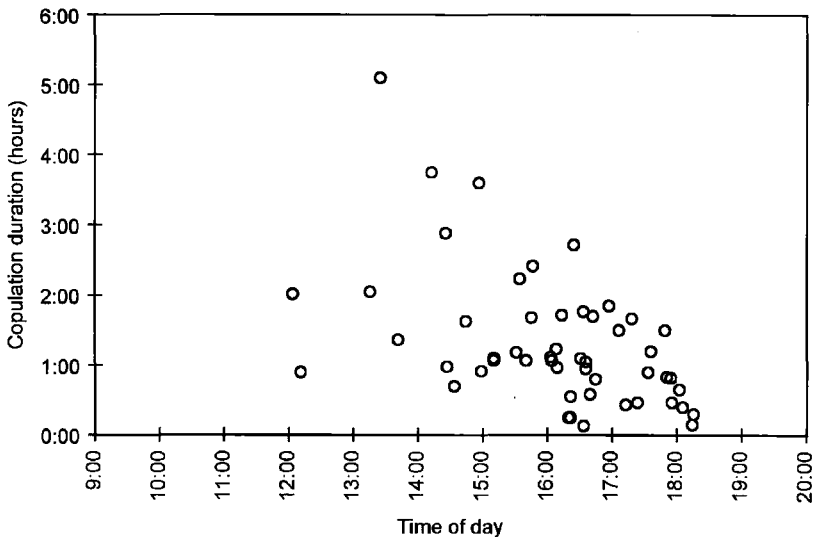


Figure 5. The relationship between time of first observation and copulation duration (time from first to last observation in mating) in *I. pumilio*.

Male lifetime mating success (LMS) was positively correlated with lifespan ($r_s=0.57$, $n=142$, $p<0.001$) and with the number of observations ($r_s=0.62$, $p<0.001$). Body size did not significantly correlate with LMS ($r_s=0.13$, $p=0.119$). Males that were marked in copula were more likely to mate again (60%) than males marked alone (36%, $\chi^2=7.14$, $d.f.=1$, $p=0.008$). Males marked in copula lived longer (Mann-Whitney U, $z=-3.08$, $p=0.002$) and were also observed more often than males marked alone ($z=-3.18$, $p=0.001$). Female LMS was also positively correlated with lifespan ($r_s=0.46$, $n=100$, $p<0.001$), and body size had no effect ($r_s=0.09$, $p=0.474$).

Table 2 shows the analysis of recapture and survival probabilities. Our data do not fit the CJS model due to the arrival of a large number of individuals in two clear groups producing several days with only recaptures (test 2+test 3 = 101.6, 70 d.f., $p=0.008$). Nevertheless, after excluding data of 6 September (when no new animals were observed) we obtained a reasonable fit (test 2 + test 3 = 86.46, 67 d.f., $p=0.055$). Results of this analysis indicate that time and sex had a highly significant effect on recapture probabilities (Table 2), but only time had a significant effect on survival rate.

Females in this population were polychromatic. Androchrome females were blue when fully mature (14 females, 16%) and gynochromes were green-brown (74 females, 84%). A small number of females (12) had intermediate coloration and were not included in morph comparisons. There were no significant differences in fitness correlates between morphs (Table 1).

Table 2. Results of capture-recapture models and of comparisons between models for *I. pumilio*. For each model we give the number of estimable parameters (np), the deviance (DEV) and the Akaike Information Criterion (AIC) (see Lebreton *et al.*, 1992). The model that minimises the AIC is shown in **bold**.

	np	DEV	AIC	Comparison
<i>Basic models</i>				
(1) $\phi_{st} p_{st}$ (CJS model by sex)	63	1337.637	1463.637	(fits the data)
(2) $\phi_t p_t$ (CJS model for pooled data)	32	1514.093	1578.093	Overall differences between males and females (2) vs. (1): $\chi^2_{31} = 176.456$, $p < 0.0001$
<i>Modeling capture rate</i>				
(3) $\phi_{st} p_{s+t}$	50	1363.856	1463.856	Parallelism over time in capture rates (3) vs. (1): $\chi^2_{13} = 26.219$, $p = 0.016$ Time effect in capture rates (5) vs. (3): $\chi^2_{14} = 133.119$, $p < 0.0001$ Sex effect in capture rates (4) vs. (3): $\chi^2_1 = 121.022$, $p < 0.0001$
(4) $\phi_{st} p_t$	49	1484.878	1582.878	
(5) $\phi_{st} p_s$	36	1469.975	1541.970	
<i>Modeling survival rate</i>				
(6) $\phi_{s+t} p_{st}$	51	1345.009	1447.009	Parallelism in survival rates (6) vs. (1): $\chi^2_{12} = 7.372$, $p = 0.679$
(7) $\phi_s p_{st}$	36	1380.952	1452.952	Time effect in survival rates (7) vs. (6): $\chi^2_{15} = 35.94$, $p = 0.002$
(8) $\phi_t p_{st}$	49	1350.577	1448.577	Sex effect in survival rates (8) vs. (6): $\chi^2_2 = 5.568$, $p = 0.0618$
ϕ = survival rate; p = recapture rate, t = time, s = sex.				

Discussion

Our results indicate that adults of *I. pumilio* did not mature near water. We were unable to find a single teneral specimen, in spite of almost daily sampling. In contrast, tenerals of *I. graellsii* were common. There are three possibilities to explain the synchronised arrival of large numbers of mature individuals on 31 August and 10 September (Fig. 1). First, adults could be immigrants that arrived at the study pond due to favourable weather conditions (*I. pumilio* makes up flights on windy days; Fox, 1989). This possibility is unlikely because the study pond is at the end of a peninsula, and we do not know of any waterbody suitable for *I. pumilio* in the area. Furthermore, the species has been observed mating at the pond in 1995, and some adults were observed in the spring of 1996. The second possibility is that animals were of local origin, but had emerged before the start of our study and returned when temperatures were specially high. Adults of *I. pumilio* take 6-12 days to change colour (mature), depending on temperature (Langenbach, 1993). Therefore it seems unlikely that they took up to three weeks to mature. Finally, individuals could have emerged early in the morning, before we started observations, especially in the period 19-22 August, when no morning samples were collected. The absence of tenerals could have been due to their exclusion by aggressive interactions with mature individuals, as suggested for *I. elegans* (Hinneking & Dumont, 1989). Nevertheless this seems not to be the case, because on some days we started observations before damselflies could fly. The available information does not allow to reject any of the above possibilities. In any case, this result indicates that a population of *I. pumilio* can “appear” in just one day. To protect habitats of this rare species a long-term monitoring of suitable sites to detect its presence is therefore necessary.

The mating behaviour of *I. pumilio*, with long copulations of up to 5 h, was similar to *Ischnura elegans* (Krieger *et al.*, 1958; Miller, 1987) and *I. graellsii* (Cordero, 1989). Copulations of 3-4h of duration were also observed by Wellinghorst *et al.* 1979) in *I. pumilio*. Our results indicate that this species is polygamous (Fig. 3) and the distribution of LMS is similar to other damselflies that show greater variance in males than females (Fincke, 1982; Banks *et al.*, 1985; Cordero, 1995). We found that males marked in copula were more likely to mate again than males marked alone. This result, also found in *I. graellsii* (Cordero, 1995) and *I. elegans* (Cordero *et al.*, 1997), suggests that male LMS is dependent on male phenotype. In *I. pumilio* it could be due to age differences between both groups of males, because males marked in copula lived longer. However, this is unlikely because almost all the males were marked in their first day of reproduction. Therefore this result suggests that males marked in copula were more skilled in survival **and** reproduction.

There were no significant differences in fitness correlates between androchrome and gynochrome females (Table 1). One adaptive hypothesis to explain the maintenance of female colour polymorphism in damselflies assumes that androchromes are male mimics (Robertson, 1985; Hinneking, 1987). But androchrome *I. pumilio* are not a perfect mimic of males (see Sandhall (1987) for colour pictures of female morphs) and are usually extremely rare (Seidenbusch, 1995). They seem absent from the British Isles (Corbet *et al.*, 1985), and none was observed by Krieger & Krieger-Loibl (1958). These facts suggest that density-dependent or frequency-dependent mechanisms based on the avoidance

of male harassment cannot explain the maintenance of female morphs in this species (see also Fincke, 1994). To address this question we need an analysis of the genetics of this polymorphism and a detailed study of male responses to female morphs. Unfortunately such experiments are difficult because of the rarity of this species.

The analysis of recapture and survival rates indicate that sexes do not differ in survivorship, but in recapture probabilities. Many studies conclude that marked male damselflies usually live longer, but many authors also suggest that this may appear so because females are recaptured less often than males (Cordero, 1994). The use of models that take into account recapture and survival probabilities allows a better understanding of population dynamics of damselflies (Anholt, 1997). We can therefore show that females do not live shorter, but simply are not recaptured as often as males. The same has been found in a population of *Lestes disjunctus*, where males were 2.5 times more likely to be recaptured than females (Anholt, 1997). Anholt (1997) predicts that sexes should differ in survival in the pre-reproductive period: females and males with the greater mass gain have the lowest survival until sexual maturity (Anholt, 1991). He suggests that if immatures are raised in the absence of predators, sex-based differences in survival until sexual maturity should disappear. This prediction has been tested by Cordero (1994), who found that females live longer than males in laboratory colonies and confirms what was found in *I. elegans* (Hinneking, 1987). We suggest that the male-biased sex-ratio of mature adults is due to greater female dispersal, before and after sexual maturity. No differences in survival between sexes should be expected to occur in most populations (e.g. Fincke, 1986).

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