

**MALE MATING SUCCESS IN A NATURAL POPULATION
OF *ISCHNURA ELEGANS* (VANDER LINDEN)
(ODONATA: COENAGRIONIDAE)***

A. CORDERO¹, S. SANTOLAMAZZA CARBONE¹, C. UTZERI²

¹ Area de Ecoloxía, Universidade de Vigo, E.U.E.T. Forestal, Campus Universitario,
ES-36005 Pontevedra, Galicia, Spain; e-mail: acordero@uvigo.es

² Dipartimento di Biologia Animale e dell'Uomo, Università "La Sapienza",
Viale dell'Università 32, I-00185 Roma, Italy

Received 29 September 1996 / Revised and Accepted 27 March 1997

A natural population of *I. elegans* was studied by mark-recapture techniques in Rome (Italy) during 25 days in June-August 1994. We marked 1043 ♂ and 957 ♀ and recaptured one third of them. Recaptured ♂♂ were similar to unreaptured ones in age at marking, date of marking and body size. Recaptured ♀♀ were similar to unreaptured ones in age and size, but were marked earlier. 53% of mature recaptured ♂♂ and 34% of ♀♀ were never observed to mate. The maximum number of matings obtained by a ♂ was 3, but 1 ♀ mated 7 times. The best predictor of male lifetime mating success (LMS) was mature lifespan. Mated ♂ were smaller than unmated ones but body length was not correlated with LMS. The probability that ♂♂ marked in copula obtained a second copulation was 7% higher than for ♂♂ marked alone. We conclude that *I. elegans* ♀♀ are clearly not monogamous in central Italy.

INTRODUCTION

In recent years, several studies of lifetime mating success (LMS) in natural populations of damselflies have been published (FINCKE, 1982; BANKS & THOMPSON, 1985; HARVEY & WALSH, 1993; CORDERO, 1995). Long-term studies are particularly useful to test evolutionary theories, because the possible trade-offs between selection episodes are controlled for by observing the lifetime success of individuals. A current interest in sexual selection research is the relationship between phenotypic characters and reproductive success. If successful individuals are those with particularly "good" phenotypes, selection will help the

* This paper is dedicated to the memory of Peter L. Miller, who made substantial contributions to understand the behaviour of *Ischnura elegans*.

spread of these phenotypic characters, provided that they are (at least partially) heritable. On the other hand, if successful individuals are a random sample of the original population, then the average phenotypic distribution of the population will remain the same if numbers are high enough to avoid the effect of genetic drift.

Ischnurans are particularly interesting animals in this context, because many of them are rarely seen in mating. ROBINSON & ALLGEYER (1996) discussed the rarity of mating in several *Ischnura* species, and proposed that some species were monogamous, with females mating only at the time they reach sexual maturity. For instance, ROBINSON (1983) studied a population of *I. posita* and after marking 2215 individuals no single mature female was observed in mating. ROWE (1978) indicated that female *I. aurora* only mated when teneral, but never during their mature phase and were therefore monogamous, and FINCKE (1987) proposed that female *Ischnura verticalis* were also monogamous. PARR & PALMER (1971) were the first to study mating success in *I. elegans* in the field. They marked 1642 males in three years at several ponds in England but only observed 156 males mating, and all but two mated only once (the remaining two mated twice). Parr and Palmer's data suggested that mating in *I. elegans* was a very rare event, and therefore sexual selection on males should be very intense. Nevertheless, in southern France, copulating pairs of *I. elegans* were very common in a high density population, achieving densities of 2-3 pairs m⁻² in some places (MILLER, 1987). The aim of this paper is to discuss the incidence of mating in a natural population of *I. elegans* in central Italy, and to search for phenotypic correlates of male mating success.

METHODS

We studied a natural population of *Ischnura elegans*, inhabiting a small pond located at Castel Porziano (Rome, Italy). From June to August 1994 we marked as many individuals as possible, and followed them in sessions of 5 consecutive days, with two days without sampling between marking sessions. Marking and observations were carried out by 1 to 3 observers. The dates of sampling were: June 30, July 1, 4-8, 11-15, 18-22, 25-28, August 1-3, and 5. Given that we did not observe every day, our estimates of mating success underestimate lifetime mating success. We made 3.6 hours of observation per day (SE=0.30, range=1-5.7 hours, n=25 days) and marked a total of 1043 males (349 were resighted at least once), and 957 females (325 resighted).

The study pond was of natural origin, formed by a spring, but was recently enlarged to its present size (perimeter 140 m). The dominant vegetation consisted of *Juncus*, *Typha*, and *Digitaria* sp. Other species of odonates at this site during the period of study were *Ceragrion tenellum* (abundant), *Ischnura pumilio* (rare), *Coenagrion mercuriale* (rare), *Erythromma viridulum* (rare), *Libellula fulva* (rare), *L. depressa* (rare), *Orthetrum brunneum* (abundant), *O. coerulescens* (rare), *Crocothemis erythraea* (abundant), *Anax parthenope* (rare) and *A. imperator* (rare). The pond was bounded by agricultural fields (clover), that we inspected occasionally in search of copulating pairs of *I. elegans*. The pond has a drainage channel that ends in a larger pond at about 100 m away. The latter was not sampled.

Insects were netted, marked with a number in black ink (Staedtler® Pancolor 303 S pen) on the right hindwing, measured (from the end of the abdomen to the head) to the nearest 0.1 mm and released at the site of capture. At the time of marking and in each subsequent observation, we recorded number, sex, thorax colour (an indicator of age, (VAN NOORDWIJK, 1978)), hour of observation and

activity (in copula, tandem, feeding, oviposition, etc).

We estimated age at marking into three broad categories, using thoracic colour as a cue. Age groups were: 0, teneral (0-2 days old; pale pink colour, violaceous or very clear orange, soft body and glistening wings), 1, immature (2-5 days old; yellow-green, violet or pink-orange thorax), and 2, mature (at least 6 days old; turquoise, blue, olive green, orange-ocher or brown thorax, deepening with age).

Throughout the text, values are presented as mean \pm SE (n). Integer variables (e.g. number of copulations, longevity, etc) were square root transformed (after adding 0.5) before being entered into parametric tests.

RESULTS

As is usual in mark-recapture studies with damselflies (CORDERO, 1994), marking had an important effect on the probability of recapture. Most individuals (67% of males and 66% of females) were never resighted after marking, but the daily disappearance rate was only about 20% in subsequent days. We suspect that this difference between the day after marking and subsequent days was due to dispersal rather than mortality, because our marking procedure does not increase mortality of laboratory-reared individuals (CORDERO, 1994). Recaptured males were similar to unreaptured ones in age at marking (Mann-Whitney $U=-0.85$, $p=0.393$), date of marking ($U=-0.96$, $p=0.339$) and body size ($t=0.38$, $p=0.886$). They therefore represent a random sample of the original population. Recaptured females were marked earlier than unreaptured ones ($U=-2.99$, $p=0.003$), but they were of similar age at marking ($U=-1.18$, $p=0.237$) and size ($t=1.23$, $p=0.219$).

The mean age at first copulation of females that were marked as tenerals, was 6.1 ± 0.6 (22) days. Two males, also marked as tenerals, mated at the age of 7 days. We consider a period of 6 days as the maturation time, although a few females have mated at an estimated age of 4 days, in their violet or pink-orange colour phase.

Figure 1 shows the distribution of male and female mating success for mature individuals that were resighted at least once. Half of males (53%) were never observed to mate, as well as one third

of females (34%). If unreaptured individuals are also included, the proportion of unmated males achieves 64% and that of females 50%. The maximum number of matings by a male was only 3 per lifetime, but one female mated 7 times.

The following analyses include all males that reached sexual maturity, whether they were recaptured or not. Mated males had a longer mature lifespan (3.8 ± 0.3 (351)

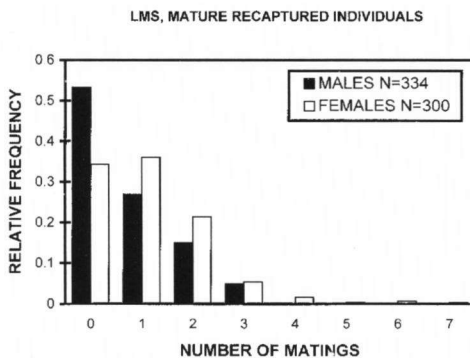


Fig. 1. The distribution of lifetime mating success in mature male and female *I. elegans* that were resighted at least once.

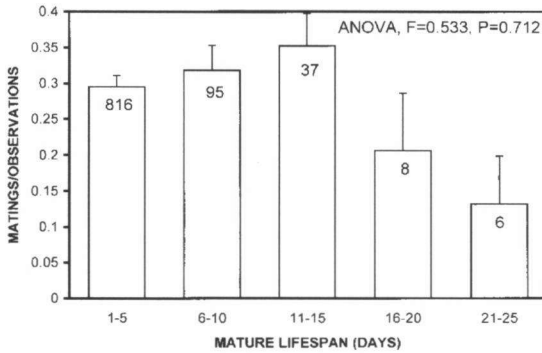


Fig. 2. The average mating efficiency (+SE) for males with different mature lifespan. Numbers are sample size.

days) than unmated males (2.2 ± 0.1 (611), $U=5.92$, $p < 0.001$), and were observed at the pond more times (1.8 ± 0.07 times versus 1.4 ± 0.03 , $U=5.67$, $p < 0.001$). The correlation between male LMS and mature lifespan was positive (Spearman $r_s=0.25$, $n=962$, $p < 0.001$). Figure 2 shows that mating efficiency (calculated as number of matings divided by number of visits to the pond) was similar for males with short or long mature lifespan, indicating that the ability to obtain matings does not change with age, at least during the first two weeks of life.

Mated males were smaller than unmated ones (29.2 ± 0.1 (204) mm versus 29.4 ± 0.1 (602); $t=2.07$, $p=0.039$). However, the correlation between body length and mating success was not significant ($r_s=-0.06$, $n=806$, $p=0.083$). Since there has been a positive correlation between male mating success and mature lifespan and a negative correlation between male mating success and date of marking ($r_s=-0.10$, $n=962$, $p=0.002$), it is necessary to control these two variables. The partial correlation between body size and the number of copulations is still not significant when longevity and date of marking are controlled for (partial $r=-0.06$, $N=802$, $p=0.090$).

The average mating success of males in 2-mm classes of size was similar whichever measure was used: total number of copulations (Figure 3, ANOVA, $F=0.97$, $P=0.423$); daily mating rate (Fig. 4; copulations/mature lifespan, $F=0.33$, $p=0.861$),

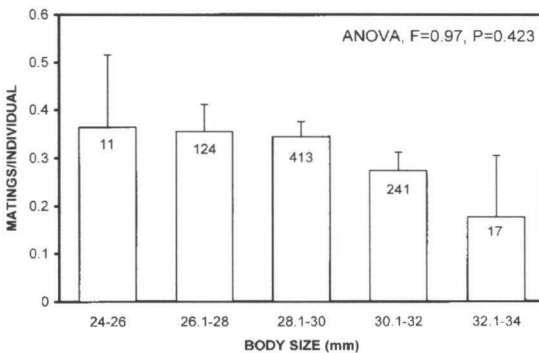


Fig. 3. The average lifetime mating success (+SE) for males of different size. Numbers are sample size.

mating efficiency (Fig. 5; copulations/observations, $F=0.65$, $p=0.631$).

Mating was not assortative by size, but there was a tendency for larger males to mate with smaller females (correlation male-female in mating pairs, $r=-0.14$, $n=186$ pairs, $p=0.055$).

Some males were consistently more successful than others: only 13% (47/356) of mature males marked alone

were subsequently observed in mating, but 20% (55/276) of males marked in copula remated ($\chi^2=5.20$, $p=0.023$). This fact was not due to an effect of longevity, because both groups of males had similar mature lifespan ($U=0.35$, $p=0.729$), but males marked in copula were smaller than males marked alone (29.2 ± 0.1 (135) versus 29.5 ± 0.1 (346), $F=3.92$, $p=0.048$).

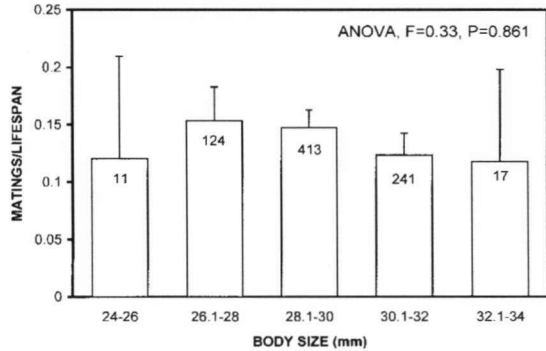


Fig. 4. The daily mating rate (+SE) of males of different size. Numbers are sample size.

DISCUSSION

Ischnura elegans clearly mate more than once per lifetime. Our results contrast with PARR & PALMER's (1971) results, and we think that this is because Parr and Palmer's study was extensive (several ponds studied during the same period), and therefore their sampling effort was too low for detecting most copulations at any single population. A second factor to explain the high proportion of individuals that were never seen to mate is the occurrence of successful tandem and copulation away from the water (VAN NOORDWIJK, 1978), an unusual behaviour that also occurs in *I. graellsii* (CORDERO, 1995). In fact, even though we did not sample every day, male and female *I. elegans* had a similar mating success as *I. graellsii* (CORDERO, 1995). We therefore conclude that this species is not monogamous. The same conclusion was reached by COOPER et al. (1996), who observed several matings per female in a laboratory study, and found by genetic markers that 6 out

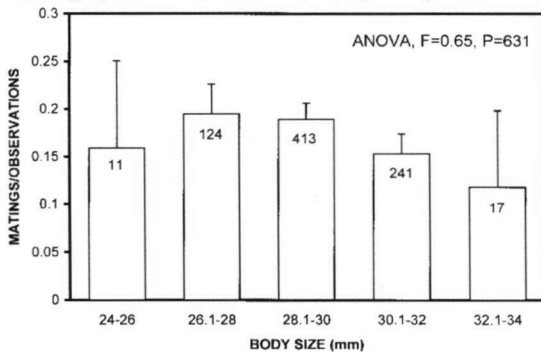


Fig. 5. The average mating efficiency (+SE) of males of different size. Numbers are sample size.

of 9 field females that laid eggs in the laboratory had mated with at least two males.

The main correlate of male LMS was mature lifespan. This has been observed in several other coenagrionids (FINCKE, 1982; BANKS & THOMPSON, 1985; CORDERO, 1995). Mating is a rare event in *I. elegans* and clearly the longer the

period a male is able to survive, the greater are his chances of mating. However, this fact does not mean that mated males are a random sample of the population. It is interesting that males marked in copula were more likely to obtain a new copulation than males marked alone. In a high density population of *I. graellsii*, CORDERO (1995) found the same effect, but in a low density population males marked in copula were less likely to obtain subsequently a copulation than males marked alone. The higher probability of remating by males marked in copula suggests that some males could be able to learn how to find females and therefore achieve greater LMS. If that were the case, this learning seems only possible in relatively dense populations, perhaps because in low density populations the encounter rate between individuals is too low to allow learning.

We found a surprising effect of body size on male LMS: small males had an advantage in mating, a result previously detected in mosquitoes (McLACHLAN & ALLEN, 1987). Nevertheless, the somewhat low correlation between mating success and body size in our sample does not allow us to conclude that small body size per se was advantageous to achieve copulations. Until now, body size has been found to affect male mating success only in territorial damselflies (FINCKE, 1992), where large size can confer some advantages in territorial disputes (but see GRIBBIN & THOMPSON, 1991 for a contrasting result in *Pyrrhosoma nymphula*). We have not identified the phenotypic characters that distinguish successful males from the rest of male population, but our data suggest that mating is not random in male *I. elegans*. HARVEY & WALSH (1993) found that males with more symmetrical wings enjoyed higher lifetime mating success in *Coenagrion puella*, and CORDOBA AGUILAR (1995) found a similar result in short-term mating success in males of *I. denticollis*. If large males were more asymmetric in our population of *I. elegans*, this could explain the mating advantage of small males, as McLACHLAN & CANT (1995) found for male midges. This factor should be taken into account in future work with *I. elegans*.

ACKNOWLEDGEMENTS

Funds M.U.R.S.T. 40% and 60%, and C.N.R. to CU. AC was supported by a travel grant from "Xunta de Galicia".

REFERENCES

- BANKS, M.J. & D.J. THOMPSON, 1985. Lifetime mating success in the damselfly *Coenagrion puella*. *Anim. Behav.* 33: 1175-1183.
- COOPER, G., P.W.H. HOLLAND & P.L. MILLER, 1996. Captive breeding of *Ischnura elegans* (Vander Linden): observations on longevity, copulation and oviposition (Zygoptera: Coenagrionidae). *Odonatologica* 25(3): 261-273.
- CORDERO, A., 1994. The effect of sex and age on survivorship of adult damselflies in the laboratory (Zygoptera: Coenagrionidae). *Odonatologica* 23(1): 1-12.

- CORDERO, A., 1995. Correlates of male mating success in two natural populations of the damselfly *Ischnura graellsii* (Odonata: Coenagrionidae). *Ecol. Ent.* 20: 213-222.
- CORDOBA AGUILAR, A., 1995. Fluctuating asymmetry in paired and unpaired damselfly males *Ischnura denticollis* (Burmeister) (Odonata: Coenagrionidae). *J. Ethol.* 13(1): 129-132.
- FINCKE, O.M., 1982. Lifetime mating success in a natural population of the damselfly, *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae). *Behav. Ecol. Sociobiol.* 10: 293-302.
- FINCKE, O.M., 1987. Female monogamy in the damselfly *Ischnura verticalis* Say (Zygoptera: Coenagrionidae). *Odonatologica* 16(2): 129-143.
- FINCKE, O.M., 1992. Consequences of larval ecology for territoriality and reproductive success of a neotropical damselfly. *Ecology* 73(2): 449-462.
- GRIBBIN, S.D. & D.J. THOMPSON, 1991. The effects of size and residency on territorial disputes and short-term mating success in the damselfly *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae). *Anim. Behav.* 41: 689-695.
- HARVEY, I.F. & K.J. WALSH, 1993. Fluctuating asymmetry and lifetime mating success are correlated in males of the damselfly *Coenagrion puella* (Odonata: Coenagrionidae). *Ecol. Ent.* 18: 198-202.
- McLACHLAN, A. & M. CANT, 1995. Small males are more symmetrical: Mating success in the midge *Chironomus plumosus* L. (Diptera: Chironomidae). *Anim. Behav.* 50: 841-846.
- McLACHLAN, A.J. & D.F. ALLEN, 1987. Male mating success in Diptera: advantages of small size. *Oikos* 48: 11-14.
- MILLER, P.L., 1987. An examination of the prolonged copulations of *Ischnura elegans* (Vander Linden) (Zygoptera: Coenagrionidae). *Odonatologica* 16(1): 37-56.
- PARR, M.J. & M. PALMER, 1971. The sex ratios, mating frequencies and mating expectancies of three coenagriids (Odonata: Zygoptera) in Northern England. *Ent. scand.* 2: 191-204.
- ROBINSON, J.V., 1983. Effects of water mite parasitism on the demographics of an adult population of *Ischnura posita* (Hagen) (Odonata: Coenagrionidae). *Am. Midl. Nat.* 109(1): 169-174.
- ROBINSON, J.V. & R. ALLGEYER, 1996. Covariation in life-history traits, demographics and behaviour in ischnuran damselflies: the evolution of monandry. *Biol. J. Linn. Soc.* 58(1): 85-98.
- ROWE, R.J., 1978. *Ischnura aurora* (Brauer), a dragonfly with unusual mating behaviour (Zygoptera: Coenagrionidae). *Odonatologica* 7(4): 375-383.
- VAN NOORDWIJK, M., 1978. A mark-recapture study of coexisting zygopteran populations. *Odonatologica* 7(4): 353-374.