

Effects of water mites on the damselfly *Ceriagrion tenellum*

JOSÉ A. ANDRÉS and ADOLFO CORDERO Departamento de Ecología e Biología Animal, Universidade de Vigo, Pontevedra, Spain

Abstract. 1. Water mite parasitism is expected to have an important effect on damselfly survivorship and reproductive success, because mites drain considerable amounts of body fluids from their hosts. This study tests the effect of water mite parasitism in a marked population of the damselfly *Ceriagrion tenellum* during 1995 (individuals marked as mature adults) and 1996 (individuals marked as teneral).

2. Almost all teneral individuals were parasitized (98%) and mites were aggregated strongly on some individuals. Parasite load increased during the season.

3. Parasites had no effect on the probability of recapture of hosts as mature adults. The average daily survival rate of lightly- and heavily-parasitized individuals, estimated with Jolly's stochastic method, did not differ significantly.

4. In 1995 parasites had a significant effect on host mating success. The probability of mating was about 25% lower for heavily-parasitized males than for lightly-parasitized males. Lightly-parasitized males also mated more times than heavily-parasitized males, even if heavily-parasitized males lived longer. In 1996, parasitism did not have an effect on male mating success. In both years mites had no effect on female lifetime mating success.

5. These results indicate that water mite parasitism does not reduce damselfly survivorship, but it could reduce male mating success in some circumstances. Further long-term studies are needed, especially in populations with a lower incidence of parasitism.

Key words. *Ceriagrion tenellum*, damselfly, lifetime mating success, parasites, sexual selection, survivorship, water mites.

Introduction

Water mite parasitism is very common in many populations of damselflies (Robinson, 1983; Åbro, 1990). Water mite larvae form a phoretic association with the last instar larvae of the host and only adult odonates are parasitized when larval mites move to the thorax or abdomen of the newly-emerged adult (Mitchell, 1959; Smith, 1988). Parasites are expected to have an important effect on male lifetime reproductive success (Jaenike, 1988; Read, 1988; Borgia & Collins, 1989).

Water mites might reduce lifetime reproductive success of their damselfly hosts in three different ways. First, they seem to drain considerable amounts of body fluids from the host (Åbro, 1990), which could reduce damselfly survivorship

(Forbes & Baker, 1991; Leung & Forbes, 1997). Robinson (1983) studied the effect of water mites on the demographics of *Ischnura posita* and found that parasites shortened female lifespan significantly. Second, water mites could reduce mating success (Forbes, 1991; Rehfeldt, 1995) without any effect on survival if they change host habitat selection or if they reduce male competitive ability, influencing flight (Rehfeldt, 1995; Reinhardt, 1996). For instance, parasitized males could spend less time at rendezvous sites due to extra energetic requirements, or parasitized males could shift to energetically inexpensive reproductive tactics, with low mating returns (Forbes, 1991). Finally, although in damselflies female mate choice remains controversial [see Waage (1984), Utzeri (1988) and Fincke (1997) for contrasting views], females could prefer to mate with unparasitized or parasite-resistant males (Hamilton & Zuk, 1982), as suggested by Rehfeldt (1995).

There are no long-term studies of the impact of water mite parasitism in natural populations of damselflies. The objective of this study was to determine whether water mites reduce

Correspondence: J. A. Andrés and A. Cordero, Departamento de Ecología e Biología Animal, Universidade de Vigo, EUET Forestal, Campus Universitario, 36005 Pontevedra, Spain. E-mail: jaandres@uvigo.es and acordero@uvigo.es

survival and mating success in a natural population of the damselfly *Ceriatrigon tenellum* (De Villers) (Odonata: Coenagrionidae).

Methods

A population of *C. tenellum* was studied using mark–recapture methods for 35 days in August–September 1995 and 59 days in June–July 1996. The population inhabits a small wetland pool ($\approx 250 \text{ m}^2$) with dense vegetation of *Juncus* and *Potamogeton*, situated at Sigüeiro (A Coruña, NW Spain). The biotope is surrounded by a complex vegetation of grasses, ferns (*Pteridium aquilinum*), *Rubus* and *Salix atrocinerea* bushes. Most markings and observations were made in the pool or near the shoreline, where adults of *C. tenellum* were aggregated. No *C. tenellum* were found in neighbouring grass fields. *Ceriatrigon tenellum* was the commonest damselfly in the wetland, although *Pyrrhosoma nymphula*, *Coenagrion puella*, *Coenagrion mercuriale*, *Ischnura graellsii*, and *Lestes dryas* were also present. The study population was assumed to be isolated because 1522 individuals were marked at a large wetland 3 km away (the closest conspecific population) in July 1995, and none of them was found in the study population.

Field work was carried out by one or two observers for a total of 520 h (an average of 5.5 h per day) between 1 August and 4 September 1995, and between 30 May and 28 July 1996. Days without observations were cold and rainy. On such days *C. tenellum* is not reproductively active (J. A. Andrés, personal observation). In total, 2376 males and 1593 females were marked individually by writing a number on their wings with indelible ink (Staedtler® Pancolour 303f pen), measured (total body length, from head to tip of the abdomen to the nearest 0.1 mm), and their activity (mating, alone, etc.) was registered at each sighting. Each specimen was also examined for water mites (*Arrenurus sp.*), and all mites were counted with the aid of a hand lens. In most cases, individuals recaptured the day after marking had almost exactly the same number of mites as the previous day, so it was assumed that no mites were lost during manipulation. In 1995 most individuals were marked as sexually mature adults. To complete the life history of adults, in 1996 marking was concentrated on teneral individuals (individuals with vitreous wings and not fully coloured, 0–1 days old).

Mated individuals were those recorded either copulating or in tandem at least once during a capture/observation session, because a female held in tandem rarely refuses to copulate.

To test the effect of parasites on teneral (1996 data set), the marked individuals were divided into two quantitative groups. Lightly-parasitized animals carried up to twenty-six mites and heavily-parasitized animals more than twenty-six mites. This division is based on the median of the parasitic load distribution, which is insensitive to outliers and generates two groups of equal size, increasing the power of the variance analyses. The first category includes 2% of unparasitized individuals, because they were so few that they could not be analysed separately.

In the 1995 data set, the marked individuals (all mature)

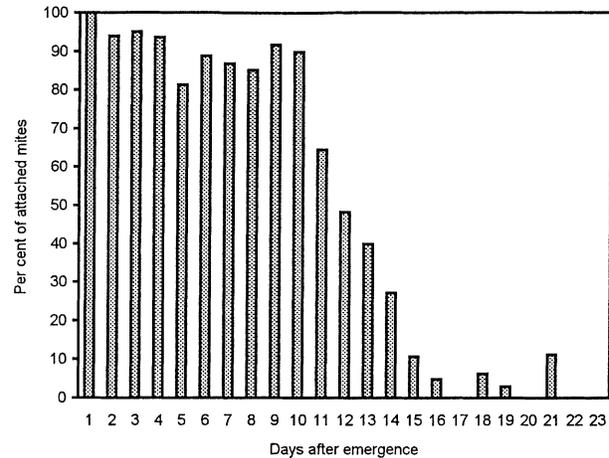


Fig. 1. The frequency distribution of mites as a function of damselfly age. Most mites drop off shortly after the host matures (1 week). Data from fifty-five males marked as teneral in 1996.

were divided into two qualitative categories, parasitized and unparasitized, or into three quantitative groups, based on the number of parasites: without mites, lightly parasitized, and heavily parasitized. As with teneral, the two parasitized groups were divided by the median, which was nine mites for this sample.

Visits are defined as the number of days on which an individual was observed near the water. Data on number of matings, number of parasites and lifespan were transformed as $\sqrt{(x + \frac{1}{2})}$ before being entered into parametric tests. The estimates of survival rate were obtained using POPAN 4 program. Values are presented as mean \pm SE (N). All tests are two-tailed.

Results

Incidence of parasitism in teneral individuals

Water mites parasitizing *C. tenellum* engorge over the pre-reproductive period and the first days of the reproductive period of their host. *Ceriatrigon tenellum* become sexually active 1 week after emergence (J. A. Andrés, personal observation) and parasites begin to drop off around 11 days after emergence (Fig. 1). Almost all teneral individuals were parasitized (98% of males and females). Mites were found attached mainly on the ventral surface of the thorax of host damselflies. Some individuals heavily loaded with parasites had mites in the lateral or dorsal sclerites of the thorax, and in the ventral part of the abdomen, especially in the first abdominal segment. No parasites were found attached at the wings.

In both sexes, the distribution of mites on teneral individuals was non-random (Kolmogorov–Smirnov test against Poisson distribution, males: $z = 12.47$, $n = 1014$, $P < 0.001$; females: $z = 12.81$, $n = 833$, $P < 0.001$). The variance:mean ratio of mite numbers during the 2 months indicated that mite distribution in males (18.67) and females (23.25) was strongly aggregated in some individuals. Values of aggregation were almost constant between weeks of the season and the mean

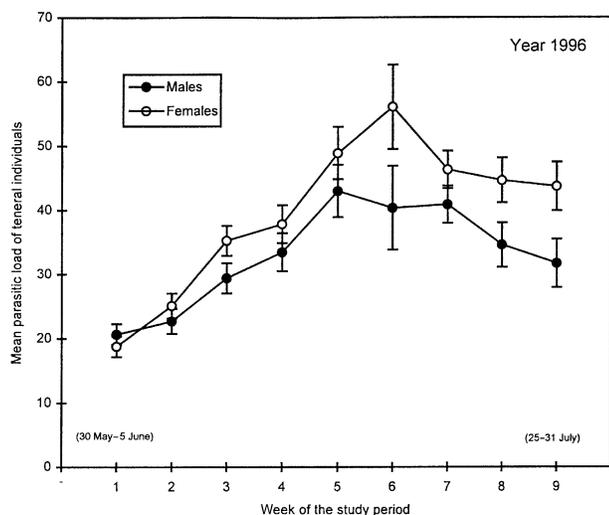


Fig. 2. Variation in mean (\pm SE) parasitic load (attached mites/individual) during the 1996 study period.

aggregation was lower in males (16.45 ± 0.83 , $n = 9$ weeks) than in females (19.97 ± 0.85 , $n = 0.9$; Mann–Whitney, U -test = -2.69 , $P < 0.01$).

The correlation between the number of parasites and date of emergence was positive (males $r = 0.28$, $n = 1014$, $P < 0.001$; females $r = 0.36$, $n = 833$, $P < 0.001$). This was due to the increase in parasitic load during the first 5 weeks of the season (Fig. 2). The mean number of attached mites per individual was 31.4 ± 0.80 (range: 0–120, $n = 1014$) in males and 35.6 ± 1.04 (range: 0–135, $n = 833$) in females. Both means are significantly different (ANCOVA, date of marking covariate: $F_{1,1884} = 195.57$, $P < 0.001$; main effects (sex): $F_{1,1884} = 8.25$, $P < 0.01$). The proportion of parasitized individuals was the same in males (98.1%) and females (98.2%, $\chi^2_1 = 0.005$, NS).

When date of marking was controlled, the parasitic load was not correlated with body size (males: partial $r = 0.03$, $n = 873$, $P = \text{NS}$; females: partial $r = 0.01$, $n = 733$, $P = \text{NS}$).

The effect of parasites on the pre-reproductive period

Because mites engorged during the teneral period, a negative effect of parasites on the probability of recapture of hosts as mature adults was expected. To test this hypothesis, first the parasitic load distribution of teneral individuals that were never recaptured was compared with that of teneral individuals that matured (Fig. 3). Males that reached a mature age were more likely to belong to the less parasitized classes (Kolmogorov–Smirnov test, $Z = 1.664$, $P < 0.01$). In females, differences between distributions were near to significance (Kolmogorov–Smirnov test, $Z = 1.292$, $P = 0.071$). Nevertheless, given that parasitic load increased during the season while the recapture probability decreased, the effect of parasites on the probability of recapture as mature adults could have been due to the greater recapture probability of males marked during the first half of the study (that also had fewer parasites). In fact, the above differences disappear

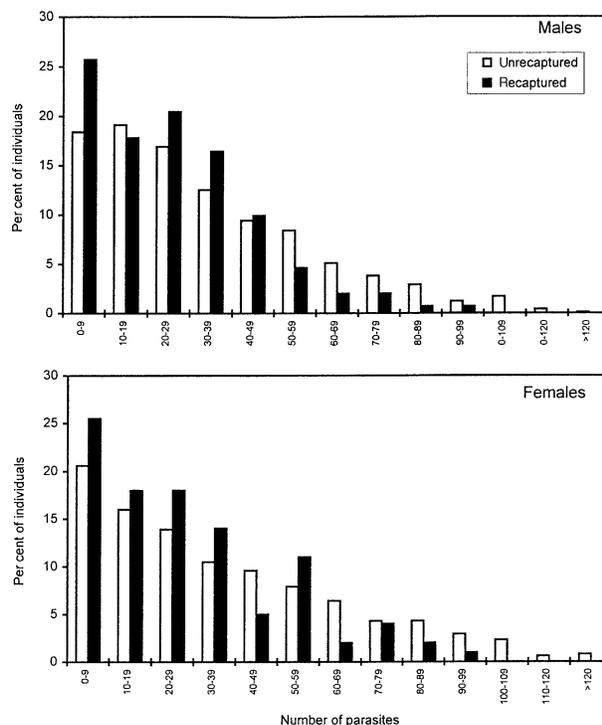


Fig. 3. The frequency distribution of mites in teneral individuals that were recaptured as mature adults or not recaptured. $N = 1014$ males and 833 females marked during 1996.

if the analysis is carried out separately for the first 4 weeks or the last 5 weeks of the sampling period.

Therefore mites seem not to have any effect on survivorship to maturity. Furthermore, lightly-parasitized males had a greater recapture rate (recaptured: 90, unrecaptured: 372) than heavily-parasitized males (recaptured: 62, unrecaptured: 387) ($\chi^2_1 = 5.26$, $P < 0.05$), but this is because lightly-parasitized males were marked earlier (Mann–Whitney U -test = -7.140 , $P < 0.001$). Similar results were found when the analysis was carried out separately for the first 4 weeks or the last 5 weeks of the study period.

In addition, when date of marking was taken into account, no differences were found between the mean number of mites parasitizing individuals never sighted as mature adults (males, 32.7 ± 0.90 , $n = 759$; females, 36.8 ± 1.14 , $n = 659$) and the mean number of parasites in damselflies recaptured as sexually-mature individuals (males, 25.1 ± 1.55 , $n = 152$; females, 28.0 ± 2.60 , $n = 100$; males: ANCOVA, covariate: $F_{1,149} = 65.24$, $P < 0.001$; main effects: $F_{1,149} = 2.16$, $P = \text{NS}$; females: ANCOVA, covariate: $F_{1,97} = 112.34$, $P < 0.001$; main effects: $F_{1,97} = 0.193$, $P = \text{NS}$).

Parasites had no effect on host lifespan. Analysing only recaptured individuals and controlling for the date of marking, heavily-parasitized males lived as long (9.8 ± 0.6 days, $n = 113$) as lightly-parasitized males (11.3 ± 0.6 , $n = 142$; ANCOVA, covariate: $F_{1,252} = 17.146$, $P < 0.001$; main effects: $F_{1,252} = 0.130$, $P = \text{NS}$). The same is true for females: lightly-parasitized females lived 12.4 ± 0.66 days ($n = 77$), whereas

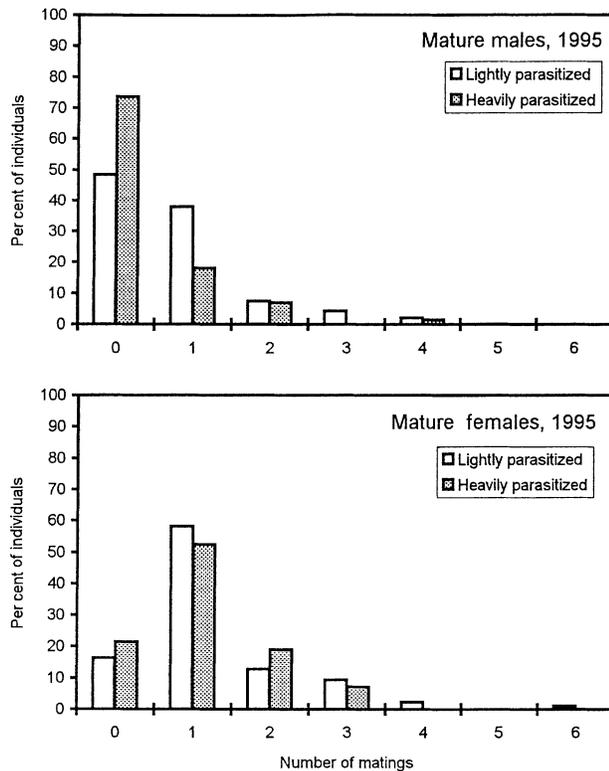


Fig. 4. Frequency distribution of lifetime mating success for individuals marked as mature adults in 1995.

heavily-parasitized females lived 10.8 ± 0.84 days ($n = 77$; ANCOVA, covariate: $F_{1,151} = 8.93$, $P < 0.01$; main effects: $F_{1,151} = 0.368$, $P = \text{NS}$).

The average daily survival rate, estimated with Jolly's stochastic method, does not differ between heavily-parasitized individuals ($\phi_{\text{males}} = 0.796 \pm 0.033$, $\phi_{\text{females}} = 0.774 \pm 0.036$) and those lightly parasitized ($\phi_{\text{males}} = 0.828 \pm 0.027$, $\phi_{\text{females}} = 0.791 \pm 0.031$; Mann-Whitney U : males $P = \text{NS}$, females $P = \text{NS}$).

The effect of parasites on the reproductive period

In 1995, only sexually-mature adults were marked, and because mites drop off when the host matures, unparasitized individuals could be true unparasitized hosts or individuals that lost their parasites before marking. Therefore parasitized individuals are likely to be younger. To avoid this problem, for the 1995 data set statistical analyses are presented excluding the unparasitized category. Furthermore, for both years, in the ANOVA, lifespan was entered as a covariate, which is an indirect measure of their age.

In 1995 parasites had a significant effect on male mating success. The distribution of matings for lightly- and heavily-parasitized males were significantly different (Kolmogorov-Smirnov test, $z = 1.54$, $P < 0.05$; Fig. 4). The mean number of parasites in males marked alone (11.6 ± 0.99 , $n = 113$) or in copula (7.3 ± 1.33 , $n = 54$) was significantly different

(U -test, $z = 8.834$, $P < 0.01$). However, this difference is only marginally significant if the date of marking is introduced as a covariate (ANCOVA, covariate: $F_{1,164} = 11.689$, $P < 0.001$; main effects: $F_{1,164} = 3.834$, $P = 0.052$). Mating was not assortative by parasitic load: excluding unparasitized animals, there was no correlation between the number of mites in copulating males and females ($r_s = -0.089$, $n = 26$, $P = \text{NS}$). The probability of mating was greater in lightly-parasitized males (mated 49, unmated 46) than in heavily-parasitized males (mated 19, unmated 53); $\chi^2_1 = 10.76$, $P < 0.001$.

The above results are robust to age effects because, although heavily-parasitized males lived significantly longer than lightly-parasitized males (ANCOVA, date of marking covariate: $F_{1,68} = 15.328$, $P < 0.001$; main effects: $F_{1,68} = 6.14$, $P < 0.05$), lightly-parasitized males mated more often than heavily-parasitized males (Table 1; ANCOVA, lifespan covariate: $F_{1,67} = 11.055$, $P = 0.001$; date of marking covariate: $F_{1,67} = 19.461$, $P < 0.001$; main effects: $F_{1,67} = 5.632$, $P < 0.05$). In females, no significant differences were found, in number of matings or mature lifespan, between lightly- and heavily-parasitized individuals (Table 2).

In 1996, parasitism did not have an effect on male mating success (only animals that matured are included in the analyses). Mating success of heavily-parasitized males (mated: 24, unmated: 38) was similar to that of lightly-parasitized males (mated: 40, unmated: 48; $\chi^2_1 = 0.67$, $P = \text{NS}$). After controlling for the date of marking, the number of matings did not correlate with the number of mites in parasitized males (partial $r = 0.12$, $n = 124$, $P = \text{NS}$) or females (partial $r = -0.04$, $n = 97$, $P = \text{NS}$). No difference was detected in the mean number of matings between lightly- and heavily-parasitized males (Table 1; ANCOVA, date of marking covariate: $F_{1,146} = 0.577$, $P = \text{NS}$; adult lifespan covariate: $F_{1,146} = 0.667$, $P = \text{NS}$; main effects: $F_{1,146} = 0.489$, $P = \text{NS}$). Similar results were found for females: all but one of fifty-four lightly-parasitized females mated, as did all but four of forty-six heavily-parasitized females ($\chi^2_1 = 2.44$, $P = \text{NS}$).

For the 1996 data set, the effect of water mites on mature lifespan was tested analysing marked tenerals that lived at least one day as mature. No differences in lifespan were found between lightly-parasitized males (Table 1) or females (Table 2) and those heavily-parasitized (males ANCOVA, date of marking covariate: $F_{1,147} = 0.01$, $P = \text{NS}$; main effects: $F_{1,147} = 2.41$, $P = 0.188$; females ANCOVA, covariate: $F_{1,97} = 0.842$, $P = \text{NS}$; main effects: $F_{1,97} = 0.265$, $P = \text{NS}$).

Differences in mating success in 1995 could have been due to a lower number of reproductive visits to the pond by heavily-parasitized males if they spent more time in feeding areas. To test this hypothesis the mean number of reproductive visits of the groups with different parasitic load was compared, after controlling for the date of marking and the mature lifespan of each individual. In both years no difference was found between lightly- and heavily-parasitized males (1995 ANCOVA, lifespan covariate: $F_{1,67} = 44.82$, $P < 0.001$; date of marking covariate: $F_{1,67} = 0.554$, $P = \text{NS}$; main effects: $F_{1,67} = 0.141$, $P = \text{NS}$; 1996 ANCOVA, date of marking covariate: $F_{1,146} = 12.49$, $P < 0.001$; mature lifespan covariate: $F_{1,146} = 0.092$, $P = \text{NS}$;

Table 1. Mean values \pm SE (N) of fitness components in males.

Fitness component	Unparasitized	Lightly parasitized	Heavily parasitized
1995 Mature lifespan	8.84 \pm 0.28 (466)	10.20 \pm 1.07 (45)	15.77 \pm 1.78 (26)
Visits	3.51 \pm 0.10 (466)	3.09 \pm 0.25 (45)	3.69 \pm 0.37 (26)
Number of matings	0.90 \pm 0.04 (466)	1.11 \pm 0.17 (45)	0.73 \pm 0.20 (26)
Matings/visit	0.29 \pm 0.01 (466)	0.36 \pm 0.05 (45)	0.25 \pm 0.07 (26)
1996 Mature lifespan	–	8.77 \pm 0.65 (88)	7.38 \pm 0.68 (62)
Visits	–	2.17 \pm 0.17 (88)	1.85 \pm 0.16 (62)
Number of matings	–	0.42 \pm 0.07 (88)	0.52 \pm 0.06 (62)
Matings/visit	–	0.23 \pm 0.05 (88)	0.17 \pm 0.05 (62)

Table 2. Mean values \pm SE (N) of fitness components in females.

Fitness component	Unparasitized	Lightly parasitized	Heavily parasitized
1995 Mature lifespan	7.87 \pm 0.40 (166)	9.84 \pm 1.14 (32)	9.77 \pm 1.49 (13)
Visits	2.53 \pm 0.68 (166)	2.62 \pm 0.18 (32)	2.46 \pm 0.21 (13)
Number of matings	2.26 \pm 0.07 (166)	2.09 \pm 0.22 (32)	1.92 \pm 0.24 (13)
Matings/visit	0.90 \pm 0.02 (166)	0.76 \pm 0.06 (32)	0.78 \pm 0.08 (13)
1996 Mature lifespan	–	9.39 \pm 0.71 (54)	9.49 \pm 0.68 (46)
Visits	–	1.35 \pm 0.09 (54)	1.45 \pm 0.10 (46)
Number of matings	–	1.27 \pm 0.10 (54)	1.21 \pm 0.10 (46)
Matings/visit	–	0.89 \pm 0.06 (54)	0.82 \pm 0.05 (46)

main effects: $F_{1,146} = 0.756$, $P = \text{NS}$; Table 1). Similar results were found for females (Table 2).

If heavily-parasitized males have greater energetic constraints, a greater mating efficiency (matings:reproductive visit) would be expected in lightly-parasitized males. To analyse this, only males that visited the pond at least twice as sexually-mature adults were taken into account. In 1995 the mating efficiency of lightly-parasitized males was greater than that of heavily-parasitized males (ANCOVA, lifespan covariate: $F_{1,67} = 18.01$, $P < 0.001$; date of marking covariate: $F_{1,67} = 9.85$, $P < 0.001$; main effects: $F_{1,67} = 5.28$, $P < 0.05$). In contrast, no difference was found in mating efficiency for the 1996 data set (Table 1).

Discussion

The damaging effect of water mites varies in different host species, and mite-induced reduction in survival has been reported in several insect groups (see Smith, 1988, for a review). However, no effect of mites on host survival was found in this study. In damselflies, water mite parasitism reduces survival significantly during periods of food deprivation in the laboratory (Forbes & Baker, 1991; Leung & Forbes, 1997), but in the field this effect has only been found in some types of individuals (Robinson, 1983). The lack of effect found in this study could be explained if mites only reduce the survival of damselflies after long periods of rainy and cold weather, during which damselflies cannot feed. During this study, cold periods were rare and short events (the longest period of rainy weather was 3 consecutive days in July 1996). Thus, water mite parasitism probably does not influence

damselfly demographics in populations that rarely have high levels of nutritional stress due to environmental conditions.

Parasites could reduce the lifetime mating success of their host (parasite-mediated sexual selection), with little or no effect on survival. Reduced mating success of parasitized males has been reported previously for *Enallagma ebrium* (Forbes, 1991) and *C. mercuriale* (Rehfeldt, 1995). However, these results were obtained from short-term studies, and are therefore sensitive to age differences between male categories. Young individuals have more parasites, and their lower mating probability is likely to be due to their age and not to parasites. This study is the first to analyse the effect of water mite parasitism on lifetime mating success in a damselfly. In 1995, heavily-parasitized males had a lower mating probability than lightly-parasitized males, whereas female lifetime mating success was independent of the parasitic load. Surprisingly, in 1996, differences in lifetime mating success were not detected between parasitism categories. These contrasting results can be explained in several ways. First, parasitism categories were defined on the basis of the mite distribution, which could change between years. It is possible that parasites reduce mating success of their host only if their number is greater than a minimum threshold. This threshold might change between years if different environmental conditions affect host condition. Unfortunately there are no data on mite numbers on general individuals for the 1995 data set. It is also possible that parasites reduced male lifetime mating success in 1996, but it was not possible to detect this effect due to the low recapture rate of mature individuals in that year, which increased variances and decreased the power of the statistical tests. The contrasting results stress the necessity of repeating observations in different years, and/or different populations.

Two different models of parasite-mediated sexual selection could account for reduced lifetime mating success of parasitized males: females discriminated against males, avoiding mates with parasitized individuals due to indirect (*good genes*) benefits, or parasitized males were less competitive in intrasexual searching for mates. Rehfeldt (1995) found that *C. mercuriale* females used refusal display against infested males. Since the majority of parasitized individuals are young, females could in fact be avoiding harassment by immature males. In the present study almost all teneral males were parasitized and, although Anderson (1988) suggests that the aggregated distribution of parasites indicates the occurrence of heterogeneity in genetic factors underlying resistance, this might also be explained by an aggregated spatial distribution of mites in the water (Mitchell, 1959). A highly-aggregated spatial distribution of larval water mites in places where damselfly larvae wait to emerge determines that only very few individuals are able to escape parasitism.

On the other hand, in natural ponds with a high density of predators (at this site *Triturus boscai*, *Rana perezi*, *Dytiscus marginalis*, and others were very common), the increased activity of larvae to avoid parasitism may result in a substantially higher mortality due to predation (Baker & Smith, 1997), so there may be strong natural selection pressures that favour individuals not exhibiting behavioural defences against water mites. Furthermore, female damselflies usually cooperate in copulation when they are seized in tandem by a male, unless they have no eggs to lay. This fact led Utzeri (1988) and Cordero (1990) to postulate that males could sometimes force copulation by insistent and prolonged tandem (but see Fincke, 1997). Thus, during the observation period, females only refused to copulate in the late afternoon when they had already oviposited. The reduced lifetime mating success of parasitized males in 1995 therefore was probably due to a direct effect of parasites on male probability of mating and not to female choice.

The mating system of *C. tenellum* is scramble competition polygamy. In this mating system, selection should act primarily on traits that increase male ability to find receptive females (Conrad & Pritchard, 1992). Results presented here indicate that, at least in 1995, heavily-parasitized males had lower mating efficiency (Table 1) than lightly-parasitized males. This fact could be associated with a parasitic diminution of male flight ability and searching efficiency. Although no parasites were found attached to the wings, the stylostoma of parasites attached to the ventral or lateral face of the thorax could be introduced within flight musculature (Smith, 1983), where it can produce cellular and tissue damage (Åbro, 1982, 1984). This could lead to a reduction of the host flight capacity. Parasitized males could make more restricted flights, mainly to catch prey, which probably means a lower probability of finding receptive females. Most females were discovered already in tandem, indicating that they were found by males immediately they appeared at the water. Water mite parasitism seems to reduce flight distances in *C. mercuriale* (Rehfeldt, 1995) and *Nehalennia speciosa* (Reinhardt, 1996). A decrease in male sexual motivation due to parasitism seems unlikely and, at least in *E. ebrium*, parasitized males were as sexually motivated as unparasitized males (Forbes, 1991). The likely explanation

is that parasitized males opted for mating tactics that are energetically inexpensive (Forbes, 1991).

To conclude, these results indicate that water mite parasitism does not reduce damselfly survivorship, but could reduce male lifetime mating success in some circumstances. More long-term studies are needed, especially in populations with a lower incidence of parasitism, before the effect of this kind of parasite on damselflies can be generalized.

Acknowledgements

We thank Dr C. Utzeri for his comments, and A. Cordoba-Aguilar for hours of discussions and field assistance. Two anonymous referees provided helpful comments on the manuscript.

References

- Åbro, A. (1982) The effects of parasitic water mite larvae (*Arrenurus* spp.) on zygopteran imagoes (Odonata). *Journal of Invertebrate Pathology*, **39**, 373–381.
- Åbro, A. (1984) The initial stylostome formation by parasitic larvae of the water mite genus *Arrenurus* on zygopteran imagines. *Acarologia*, **25**, 33–46.
- Åbro, A. (1990) The impact of parasites in adult populations of Zygoptera. *Odonatologica*, **19**, 223–233.
- Anderson, R.M. (1988) The population biology and genetics of resistance to infection. *Genetics of Resistance to Bacterial and Parasitic Infection* (ed. by D. M. Wakelin and J. M. Blackwell), pp. 79–85. Taylor and Francis, New York.
- Baker, R.L. & Smith, B.P. (1997) Conflict between antipredator and antiparasite behaviour in larval damselflies. *Oecologia*, **109**, 622–628.
- Borgia, G. & Collins, K. (1989) Female choice for parasite-free male satin bowerbirds and the evolution of bright male plumage. *Behavioural Ecology and Sociobiology*, **25**, 445–454.
- Conrad, K.F. & Pritchard, G. (1992) An ecological classification of odonate mating systems: the relative influence of natural, inter- and intra-sexual selection on males. *Biological Journal of the Linnean Society*, **45**, 255–269.
- Cordero, A. (1990) The adaptive significance of the prolonged copulations of the damselfly, *Ischnura graellsii* (Odonata: Coenagrionidae). *Animal Behaviour*, **40**, 43–48.
- Fincke, O.M. (1997) Conflict resolution in the Odonata: implications for understanding female mating patterns and female choice. *Biological Journal of the Linnean Society*, **60**, 201–220.
- Forbes, M.R.L. (1991) Ectoparasites and mating success of male *Enallagma ebrium* damselflies (Odonata, Coenagrionidae). *Oikos*, **60**, 336–342.
- Forbes, M.R.L. & Baker, R.L. (1991) Condition and fecundity of the damselfly, *Enallagma ebrium* (Hagen) – the importance of ectoparasites. *Oecologia*, **86**, 335–341.
- Hamilton, W.D. & Zuk, M. (1982) Heritable true fitness and bright birds: a role for parasites? *Science*, **218**, 384–386.
- Jaenike, J. (1988) Parasitism and male mating success in *Drosophila testacea*. *American Naturalist*, **131**, 774–780.
- Leung, B. & Forbes, M.R.L. (1997) Fluctuating asymmetry in relation to quality and fitness in the damselfly, *Enallagma ebrium* (Hagen). *Oecologia*, **110**, 472–477.

- Mitchell, R. (1959) Life histories and larval behaviour of Arrenurid larval water mites parasitizing Odonata. *Journal of New York Entomological Society*, **1**, 1–12.
- Read, A.F. (1988) Sexual selection and the role of parasites. *Trends in Ecology and Evolution*, **3**, 97–102.
- Rehfeldt, G.E. (1995) Natürliche Feinde, Parasiten und Fortpflanzung von Libellen. *Odonatological Monographs 1*, pp. 1–173. Aqua & Terra, Wolfenbüttel, Germany.
- Reinhardt, K. (1996) Negative effects of *Arrenurus* water mites on the flight distances of the damselfly *Nehalennia speciosa* (Odonata: Coenagrionidae). *Aquatic Insects*, **4**, 233–240.
- Robinson, J.V. (1983) Effects of water mite parasitism on the demographics of an adult population of *Ischnura posita* (Hagen) (Odonata: Coenagrionidae). *American Midland Naturalist*, **109**, 169–174.
- Smith, B.P. (1983) The potential of mites as biological control agents of mosquitoes. *Research Needs for Development of Biological Control of Pests by Mites* (ed. by M. A. Hoy, L. Cunnigam and L. Knutson), pp. 79–85. University of California, Berkeley, California.
- Smith, B.P. (1988) Host–parasite interaction and impact of larval water mites on insects. *Annual Review of Entomology*, **33**, 487–507.
- Utzeri, C. (1988) Female ‘refusal display’ versus male ‘threat display’ in Zygoptera: is it a case of intraspecific imitation? *Odonatologica*, **17**, 45–54.
- Waage, J.K. (1984) Sperm competition and the evolution of odonate mating systems. *Sperm Competition and the Evolution of Animal Mating Systems* (ed. by R. L. Smith), pp. 251–290. Academic Press, Orlando, Florida.

Accepted 20 December 1997