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# Assortative pairing with respect to parasite load in the beetle *Timarcha maritima* (Chrysomelidae)

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## Key words:

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chrysomelidae;  
*Gregarina munieri*;  
parasitism;  
sexual selection;  
*Timarcha maritima*.

## Abstract

Because of their effects on host reproductive behaviour, parasites are theoretically expected to create sometimes assortative mating among hosts, with heavily parasitized individuals pairing together and lightly parasitized ones pairing among themselves. We investigated the influence of protozoan gut parasites on the pairing pattern of the chrysomelid beetle *Timarcha maritima*. In the field, fecundity was negatively correlated with the parasite load of females, unpaired males were significantly more heavily infected than paired ones and, among pairs, males and females were matched for parasite load. Mate choice experiments in the laboratory showed that males have some ability to avoid heavily infected partners when given the choice between two females. Male competitiveness, measured as their mobility, was also negatively correlated with parasite load. These results indicate that parasite-related assortative pairing in this beetle could result from parasitized females being less fecund and parasitized males less competitive.

## Introduction

Alterations of host attractiveness and/or host competitiveness by parasitic infections are commonly reported in various host taxa and generally lead to a negative relationship between parasite load and mating success (Read, 1988; Borgia & Collis, 1989; Milinski & Bakker, 1990; Zuk, 1992). In addition, because of depleted energy reserves or reduced survival, parasitized hosts may also invest less time and energy in discriminating among mates (Poulin, 1994; Simmons, 1994; McLennan & Shires, 1995; Poulin & Vickery, 1996). Given that in natural populations both sexes are often parasitized, a combination of several effects is expected to promote assortative mating with respect to infection (Møller, 1991). For instance, when both males and females are choosy and attempt to avoid mating with infected individuals, there should be assortative mating with respect to parasite load (Møller, 1991, 1994). Similarly,

when males are choosy and parasites reduce both female fecundity and male competitiveness, vigorous males with few or no parasites should gain access to more fecund females with no or few parasites, leaving more heavily parasitized males to mate with the more heavily parasitized and less fecund females (Thomas *et al.*, 1996). Despite theoretical expectations for parasite-related assortative mating, this phenomenon is practically ignored (Møller, 1991; Thomas *et al.*, 1996).

During the breeding season, males of the wingless beetle *Timarcha maritima* (Chrysomelidae) defend neither resources nor access to groups of females, but instead compete indirectly by searching for receptive partners (scramble competition polygyny, Chevin, 1992). Their efficiency in acquiring mates depends primarily on their encounter rate with females when moving on the substrate. Males take an active role in initiating copulation, trying to mount the female shortly after the first contact or after a brief sexual pursuit. Like many invertebrates, both males and females of this beetle are naturally parasitized by protozoan gut parasites (*Gregarina munieri*, Schneider 1876, Class Sporozoa) (F.T., unpublished observations). Hosts become infected by ingesting spores that later develop in trophozoites, a

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feeding stage living attached to the intestine for a period of several days to weeks (Zuk, 1987a). Gregarines usually alter host nutrition because they act as a physiological barrier between the midgut cells and digested food (Harry, 1970; 1987b; Zuk, 1987a). Given that gregarine infections often result in a simultaneous reduction of host viability and fecundity (Abro, 1971; 1987b, 1988; Zuk, 1987a; Simmons, 1993), we evaluated the empirical evidence for a direct influence of *Gregarina muniere* upon the pattern of pairing in the beetle *T. maritima*. We observed beetles in the field and conducted a series of experiments in controlled conditions to identify the process by which parasite-related assortative pairing may occur in this insect.

## Materials and methods

### Field study

All beetles were collected during March 1996 in the Dune de Paracou (Sables d'Olonne, Vendée, France). We sampled a wide section of dune actively searching by visual detection for beetles in pairs ( $n = 182$  pairs). We also collected an additional sample of unpaired individuals ( $n = 186$ , i.e. 100 males and 86 females). All insects were preserved in alcohol (70%). In the laboratory, individuals were sexed, measured (elytron length) and dissected in order to estimate their gregarine load. Because the number of trophozoites per individual was generally high, we estimated the parasite load as follows: entire gut contents were placed in a Petri dish with alcohol (70%) and manually stirred for 15 s during which time distribution of trophozoites became homogeneous in the Petri dish. By placing a grid ( $5 \times 5$ -mm squares) under the Petri dish, we estimated parasite load as the mean number of trophozoites per square (estimated from five squares under a dissecting microscope 400 $\times$ ) and then multiplied by the total number of squares. The measurement error in trophozoite estimates based on single squares (i.e. proportion of within-individual variation to total variation, Merilä & Björklund, 1995) was 3.8%. The fecundity could be estimated through counting the number of yolky eggs contained in the abdomen of females.

Analyses of nonrandom pairing using standard statistical procedures requires that different pairs form independently (Johnson & Marzluff, 1990). Given that once two individuals form a pair, the pairing opportunities for other individuals are reduced, we used randomization techniques to analyse patterns of assortative pairing. Thus, we estimated the significance of both size- and parasite-related assortative pairing by considering the observed sets of pairs as one of many but equally possible outcomes that could have arisen by chance. We then formed 20 000 possible outcomes by pairing the male and female size (and then parasite load) at random (randomizing the order of the female values) and, for

each iteration, we calculated the regression coefficient between the two sets of values. Comparing the observed regression coefficient with the randomization distribution indicates the probability that it is significantly different from zero (Manly, 1991). Randomization analyses were performed using RT 2.0 (B. Manly, University of Otago, New Zealand).

### Mate choice experiment

These beetles ( $n = 204$ , 68 paired males and 136 paired females) were collected in March 1997 (Dune de Paracou). Before being tested, individuals were isolated for 1 h in small opaque plastic cups (diameter: 6 cm, height: 7 cm) containing 1 cm of natural sediment and food (*Gallium arenarium*). Mate choice experiments were conducted in similar cups. One male and two females were placed in each cup. Subjects were assembled in such a way that no individual was present with its former partner. We examined 68 cups and once the male had mounted a female, individuals were preserved in alcohol and later measured and dissected with the same methodology as before to determine their parasite load. To analyse mate choice, we used a General Linear Model with a Binomial Error distribution using GLIM software (NAG, 1986), with stepwise backward deletions of nonsignificant terms to test the choice of the male (0 = male has chosen the more heavily infected female, 1 = male has chosen the more lightly infected female). The ratio of the female parasitic loads ( $R$ , i.e. the parasite load of the more heavily infected female divided by the parasite load of the more lightly infected female), the parasitic load of the male ( $PLM$ ) and the absolute size difference between the two females ( $DSF$ ) were used as explanatory variables. By this analysis, influence of female size and male parasite load on choice is also assessed. In order to control for unequal relative difference between female parasite loads when analysing variation in  $R$ , we also introduced in the model the total parasitic load ( $TPL$ , sum of parasitic load of the two females).

### Male competitiveness

A sample of 120 males was collected during March 1997 in the Dune of Paracou with the same method as before. Males were isolated for 15 min in opaque plastic cups (diameter: 6 cm, height: 7 cm) containing 1 cm of natural sediment before being tested. We measured mobility as the total horizontal distance a male moved during 3 min in an experimental corridor (70 cm  $\times$  20 cm) containing natural sediment. Temperature remained constant during the experiment (15 °C). All males were then preserved in alcohol, measured by length, dissected and their parasite load determined.

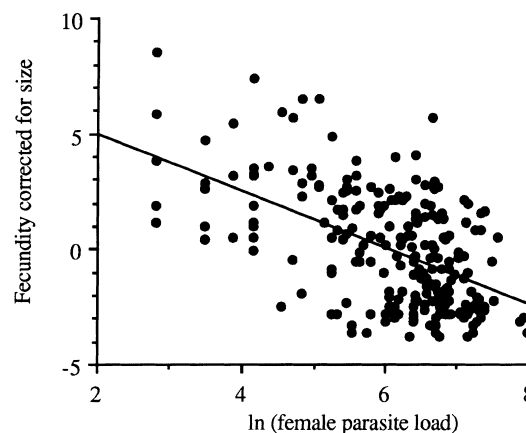
## Results

In the field, prevalence of infection was almost 100% (Table 1). The mean parasite load was significantly higher in males than in females in both paired (Table 1, Wilcoxon signed-ranks test;  $z = -2.50$ ,  $P = 0.01$ ) and unpaired individuals (Table 1, Mann-Whitney test;  $z = -2.60$ ,  $P = 0.009$ ). Unpaired males were more heavily infected than paired males (Table 1, Mann-Whitney test;  $z = -3.3$ ,  $P = 0.0009$ ), whereas no significant difference was observed between the mean parasite load of paired and unpaired females (Table 1, Mann-Whitney test;  $z = -0.58$ ,  $P = 0.56$ ). Unpaired individuals were slightly but significantly larger than paired ones (Table 1, unpaired  $t$ -test, males:  $t = -4.9$ , d.f. = 280,  $P = 0.0001$ ; females:  $t = -2.2$ , d.f. = 266,  $P = 0.03$ ).

Fecundity could be estimated on 233 females from the field collection. There was no significant difference between the number of eggs of paired ( $2.8 \pm 2.6$ ,  $n = 163$ ) and unpaired females ( $3.1 \pm 2.6$ ,  $n = 70$ ) (two-sample  $t$ -test;  $t = -0.70$ ,  $P = 0.48$ ). Fecundity was positively related to elytron size of female but negatively correlated with parasite load (Fig. 1, multiple regression on log-transformed data,  $r^2 = 0.28$ ,  $n = 233$ ,  $P < 0.0001$ ). The multiple regression equation is: fecundity =  $-0.003$  (SE = 0.0003)  $\times$  parasite load + 0.748 (SE = 0.31)  $\times$  elytron length (mm) – 1.245. Thus, at equal size, the fecundity of infected females is reduced.

Among the 182 pairs, size assortative pairing was not significant (randomized regression on log-transformed data,  $r = 0.04$ ,  $n = 182$ ,  $P = 0.63$ ). However, males and females were significantly positively matched for parasite load (Fig. 2, randomised regression on log-transformed data,  $r = 0.50$ ,  $n = 182$ ,  $P < 0.0001$ ), indicating that gregarines have a major role in pair formation in this beetle.

Among the 68 cups analysed for the mate choice experiment, there was no significant effect of the male's parasite load on its choice and males did not tend to select the larger female (Table 2). However, when substantial variation existed between the parasite load of the two females tested, males significantly preferred the least parasitized female (Table 2). Male mobility in the experi-

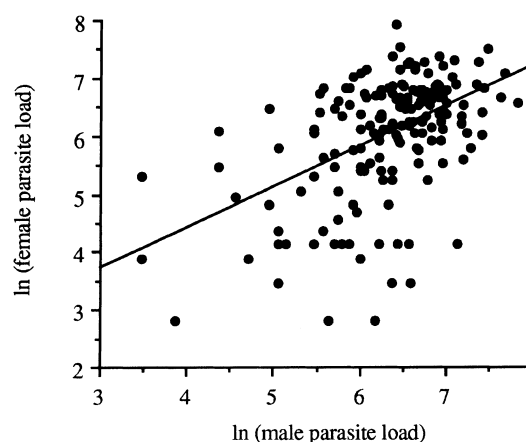


**Fig. 1** Relationship between fecundity corrected for size and female parasite load (linear regression,  $y = -0.003x + 1.647$ , SE = 0.0003).

mental corridor was not related to elytron length ( $r = 0.08$ ,  $n = 120$ ,  $P = 0.35$ ). However, there was a strong and negative correlation between mobility and parasite load (linear regression on log-transformed parasite load data; Fig. 3,  $r = -0.91$ ,  $n = 120$ ,  $P = 0.0001$ ).

## Discussion

During the two years of the study, and as observed one year before (F. Thomas, unpublished data), gregarines appeared quite common in prevalence and in intensity in this population of beetles. For numerous hosts, it seemed obvious that gregarines could alter host nutrition because the midgut was completely occluded by a large number of trophozoites. Whether interindividual variation in parasite loads results from varying degrees of genetic susceptibility or other phenomena cannot be determined from these data. Similarly, the fact that males are more



**Fig. 2** Assortative pairing with respect to parasite load (linear regression,  $y = 0.704x + 1.609$ , SE = 0.09).

**Table 1** Prevalence (proportion of infected individuals), mean intensity (mean parasite load of infected individuals) of infection by *Gregarina munieri* and size (elytron length) in paired and unpaired males and females of *T. maritima* in the field.

	Paired		Unpaired	
	males	females	males	females
Sample size	182	182	100	86
Prevalence	100%	100%	100%	98.8%
Intensity $\pm$ SD	687 $\pm$ 417	613 $\pm$ 435	827 $\pm$ 389	688 $\pm$ 565
Size (mm)	6.6 $\pm$ 0.4	7.7 $\pm$ 0.5	6.8 $\pm$ 0.3	7.8 $\pm$ 0.4

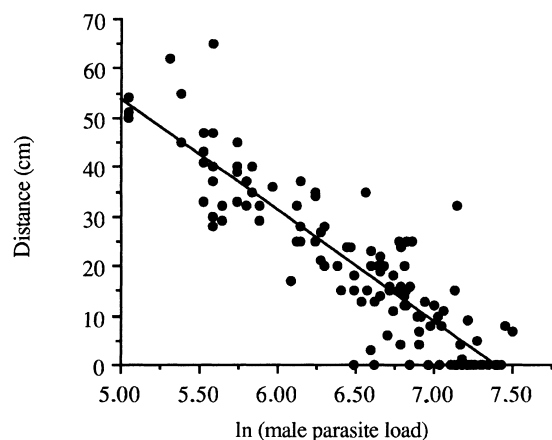
**Table 2** Male choice in relation to several explanatory variables. (General linear model analysis with a binomial error distribution, *R*: parasite load of the more heavily infected female divided by the parasite load of the more lightly infected female; *PLM*: parasitic load of the male; *DSF*: absolute size difference between the two females; *TPL*: sum of parasitic load of the two females; Interaction terms were not significant.)

Variables	$\chi^2$	d.f.	P
<i>R</i>	7.14	1	0.007
<i>TPL</i>	2.35	1	0.12
<i>PLM</i>	0.16	1	0.69
<i>DSF</i>	0.32	1	0.57

heavily infected than females remains unexplained but has already been observed in gryllids infected by gregarines (Zuk, 1987a; Simmons & Zuk, 1992; but see Simmons, 1994, for the opposite pattern).

The decreased fecundity of *T. maritima* infected with gregarines is reported here for the first time and is clearly intensity dependent. Reduction of host fecundity following gregarine infection has already been reported for instance in the bush cricket *Requena verticalis* (Simmons, 1993, 1994). In many insect species, the availability of food has direct effects on the number of eggs produced (Gillot, 1995). Because gregarine trophozoites absorb food before it can be used by the host, heavily infected females have probably less resources and energy to invest in the synthesis of the yolk components than uninfected ones. It could also be possible that females of low quality would be both less fecund and more susceptible to infection compared with other females. Experimental manipulation of parasite loads would be necessary to address this point.

Although large females of *T. maritima* produce more eggs than smaller ones, males did not show a tendency to select the larger female over the smaller one during the



**Fig. 3** Relationship between male mobility and parasite load (linear regression,  $y = -23.123x + 170.196$ ,  $SE = 0.989$ ).

mate choice experiment. In addition, we found no evidence that males and females tend to be matched for size in our large pair collection. These results contrast with studies on other beetles where size assortative pairing was reported to be positive and significant (McCauley & Wade, 1978; McLain & Boromisa, 1987; Crespi, 1989; Brown, 1993; but see Kasuya, 1985, and Dickinson, 1992). The fact that unpaired individuals are slightly larger than paired ones remains difficult to explain without further field and experimental investigations on the relationships between operational sex ratio, body size and reproductive success in this beetle.

The most striking pattern of pairing in this beetle remains, however, the positive assortative pairing with respect to the parasite load. Parasite-related assortative pairing is poorly documented and exact causes of this phenomenon are not well understood. According to Møller (1994), assortment by parasite intensities of the tropical fowl mite *Ornithonyssus bursa* in the barn swallow could be a direct consequence of mutual mate choice based on tail length, a secondary sexual character closely associated with parasite load. In the amphipod *Gammarus insensibilis* infected by the trematode *Microphallus papillorobustus*, parasite-related assortative pairing results from two main phenomena. Because *M. papillorobustus* induces a strong photophilic behaviour in its host, a spatial segregation between infected and uninfected individuals exists in nature (Thomas *et al.*, 1995, 1996). In addition, infected females are less attractive (lower fecundity) and infected males are less competitive (Thomas *et al.*, 1996).

In the case of *T. maritima*, several hypotheses can be proposed to explain parasite-related assortative pairing. A temporal covariation could generate the pairing pattern observed if uninfected individuals of both sexes are ready to mate earlier than infected individuals and if the pairing durations are long relative to the breeding period. Gregarines are frequently reported to delay physiological processes in their hosts (Harry, 1970; Zuk, 1987a). Heavily infected individuals, after the overwintering period, could be ready to mate later than more lightly infected ones. Although this explanation cannot account for the laboratory experiments, further field information on pairing duration in *T. maritima* and on the pattern of post-wintering emergence in relationship with parasite load would be necessary to evaluate this hypothesis. Alternatively, the positive relationship between the parasite load of males and females in pairs can indicate that gregarines have a major role in pair formation in *T. maritima*. Evidence for male avoidance of infected females is not common (but see Edwards & Barnard, 1987; Rosenqvist & Johansson, 1995; Thomas *et al.*, 1996). However, given that infected females are less fecund than uninfected ones, selection should presumably favour males who can detect and avoid heavily infected females. Although we have no evidence that males exert true choice in this beetle, males at the

laboratory tended to pair with the least infected partner when substantial variation existed between female infections. We cannot, however, exclude the hypothesis that this result comes from the least infected female being more successful in competitive mate searching than the other female. It would also be necessary to determine if assortative pairing really corresponds to assortative mating in this species. Contrary to other studies (e.g. Poulin, 1994; Simmons, 1994), we did not find reduction in male selectivity with increasing levels of infection. However, heavily infected males were less vigorous than lightly infected ones. The idea that male competitiveness is negatively affected by the parasite load is consistent with (i) the higher mean intensity observed in the field for unpaired males compared with paired ones and (ii) the strong negative relationship between the parasite load and mobility. Given that in the scramble competition of *T. maritima*, male efficiency in acquiring mates depends primarily on encounter rates, it seems likely that mating opportunities are reduced by infection. A similar effect of the infection on female mobility could contribute to the observed pattern of pairing in the field. These results thus give some support to the hypothesis that parasites can create assortative mating among hosts. The pattern of pairing observed for *T. maritima* is likely to result, at least partially, from heavily infected females being less attractive and heavily infected males being less competitive. Further investigations are needed to understand the proximal factors allowing males to discriminate heavily and lightly infected females.

Most of the discussion and tests of parasite-mediated sexual selection have assumed that the ability of the choosing sex to select or to encounter mates was unaffected by parasites. Since it seems clear that the opposite may be true, assortative mating with respect to parasite load could be common in many systems. There is a clear need to improve our understanding of the evolutionary consequences of such phenomena.

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