Effects of *Macrocheles* mites on longevity of males of the dimorphic dung beetle *Onthophagus binodis*

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**Abstract**

In this study we tested the nature of the phoretic relationship between the cosmopolitan mite *Macrocheles merdarius* and the dimorphic dung beetle *Onthophagus binodis*. We observed and experimentally manipulated the number of mites on individual beetles and tested how mite infestation affects male longevity. There was a significant effect of mites on male longevity: males in our mites-added treatment died on average 15 days earlier than males in our mites-removed treatment. Interestingly, the number of mites on males was significantly repeatable suggesting that individuals may differ in their susceptibility to infestation. Major males had more mites on them than minor males, and the proportion of mites on minor males was negatively density dependent.

**Key words:** longevity, mites, *Macrocheles*, dung beetle, *Onthophagus binodis*, alternative reproductive strategies

**INTRODUCTION**

Ectoparasites have often been shown to have profound effects on host life-history parameters and fitness (Smith, 1988; Lehmann, 1993). In general, parasites may have a negative effect on host reproductive success (Moller, 1990b; Forbes & Baker, 1991; Hurst et al., 1995; Polak & Markow, 1995; Polak, 1996), reduce body mass or condition (Moller, 1990b; Forbes & Baker, 1991; Polak, 1996, 1998), or reduce life span (Moller, 1990b; Forbes & Baker, 1991; Polak, 1996; Polak & Starmer, 1998).

Beetles, and especially dung beetles, frequently carry dense populations of mites (e.g. Hyatt, 1959; Springett, 1968; Hanski & Cambefort, 1991; Tomkins et al., in press). Mites are generally considered to associate with beetles phoretically (Ridsdill-Smith & Hall, 1984; Hanski & Cambefort, 1991), assuming only a passive role while attached to their host. Attachment is viewed merely as a means of facilitating mite dispersal from deteriorating dung pads to fresher habitats (Hanski & Cambefort, 1991). However, because mites can occur in vast numbers on beetles they may conceivably present a significant pathology for beetles, but so far there are no studies examining the mite-beetle association in any detail. Polak (1996) examined the association between *Drosophila nigrospiracula* and the phoretic mite *Macrocheles subbadius*. In the *Drosophila*--*Macrocheles* association, mites are transported between rotting cacti by their hosts. However, Polak (1996, 1998) found that mites ingested host haemolymph and reduced host condition, reproductive output and longevity, indicating that the association was in fact facultatively parasitic.

*Onthophagus binodis* is a dung beetle species recently introduced from Africa and now widespread in south-western Australia (Ridsdill-Smith, 1986). Adults bury dung and make brood masses in the soil, in which the offspring completes its development (Ridsdill Smith, Hall & Craig, 1982; Cook, 1988). *Onthophagus binodis* is commonly found at densities in excess of 100 beetles/dung pad (Ridsdill Smith et al., 1982), and dung pads also support a rich fauna of mites, as well as other beetles (Ridsdill-Smith & Hall, 1984). In particular, *O. binodis* is frequently found to be densely populated by the cosmopolitan macrochelid mite, *Macrocheles merdarius*.

Typical of most onthophagines, male *O. binodis* are dimorphic for the size of the horn found on the pronotum (Cook, 1987; Simmons, Tomkins & Hunt, 1999; Kotiaho & Tomkins, in press); large (major) males possess horns while small (minor) males do not. Male dimorphisms are associated with a variety of behavioural differences that collectively characterize an alternative reproductive strategy (Cook, 1990; Emlen, 1997; Hunt & Simmons, 1998; Simmons et al., 1999). Examination of the costs and benefits associated with
alternative mating tactics are rare (Alcock, 1996), although such measures are critical to our understanding of the evolutionary maintenance of male dimorphisms (Gross, 1996).

The distribution of *M. merdarius* across the male morphs of *O. binodis* was examined in an attempt to establish whether major and minor males differ in their susceptibility to infestation. The effects of *M. merdarius* infestation on adult male longevity were then examined experimentally.

**METHODS**

Beetles used in this study were offspring of parents collected from a population in Walpole, southern Western Australia, in January 1998. Adults were maintained and offspring reared under laboratory conditions of 28 °C and 14 : 10 h light : dark photoperiod. Infestations of *M. merdarius* were initiated from dung collected from a dairy farm in Serpentine, 67 km south of Perth. We have occasionally observed some individuals of other species of mites in our laboratory populations, but the numbers are insignificant in comparison to *M. merdarius*.

**Level of infestation**

Eight populations of beetles were established, each consisting of 28 minor and 22 major males. The ratio of minor to major males was chosen to reflect that of natural populations with morphs recognized on the basis of pronotum width; males > 5.80 mm were categorized as major males (see Simmons et al., 1999). Five of the populations were provided with 50 female beetles. Mean (±SE) pronotum width of majors, minors and females in our experiment were 6.18 ± 0.02, 5.35 ± 0.03 and 5.75 ± 0.04 mm, respectively, and all were significantly different from each other (*F*\(_{2,296} = 178.39, \ P < 0.001*; Tukey MD > 40, \ P < 0.001 for all comparisons). Each population was housed in a 15 l bucket two-thirds filled with sand and topped with 1 or 2 litres (1 litre/50 individuals) of cow dung. Dung and sand were changed every week. The number of mites on individual beetles was counted under a binocular microscope from 10 randomly sampled males of each morph from each population. Mites were counted up to 100 individuals, after which the excess number of mites was estimated with increments of 50 mites. After counting, mites were gently brushed off with a toothbrush from every individual of each of the populations. Mites were counted and removed on a weekly basis until the frequency of 1 of the male morphs in the population fell below 10 individuals. Although the environment of each population was changed each week, data from the same populations between weeks are not strictly independent and our data were treated accordingly.

**Effect of mites on male longevity**

The number of major males emerging from our laboratory culture was not sufficient to include both morphs in our longevity experiment. At emergence, the pronotum width of minor males was measured and males were randomly allocated to 1 of 2 treatment groups. Male size did not differ significantly between treatment groups (*F*\(_{1,98} = 0.00, \ P = 0.981*).

To determine the effect of mites on longevity of the minor males, we experimentally reduced or increased the numbers of mites. Numbers were reduced by gently brushing mites off with a toothbrush, and increased by pouring mites onto the beetles in the other treatment. This procedure was repeated at weekly intervals. To ascertain that the manipulation was effective, the number of mites on each male was counted on 3 occasions, with an interval of 4 weeks between each count. Mites were counted as described above.

Beetles were housed individually in 7 × 7 × 5 cm containers two-thirds filled with sand and topped with 20 ml of dung. The dung was changed each week and the sand was changed every 2 weeks. Survival of the males was recorded weekly. We had 50 males in each treatment.

**RESULTS**

**Levels of infestation**

Major males had significantly more mites on them than minor males (paired *t*-test on the mean number of mites per week on the two morphs within a population, *t*\(_{7} = 6.51, \ P = 0.000*; mean number (±SE of mites on minor and major morphs was 35.4 ± 2.09 and 57.1 ± 4.53, respectively). The repeatability of mite counts across sampling events was examined for each of our eight populations. The total number of mites counted on both major and minor males combined was not significantly repeatable across our sampling events (*F*\(_{7,37} = 1.11, \ P = 0.380*); each sampling event was characterized by a different intensity of infestation. The proportion of all mites counted on minor males was not repeatable either (*F*\(_{7,37} = 0.90, \ P = 0.515*). Thus, mite counts between samples were not related and, given that each count was derived from an independent environment (sand and dung were changed between counts and all beetles cleaned), we treat our samples as independent in order to examine the influence of mite density on infestation. As the total number of mites in the population at the time of sampling increased, the number of mites on both minor and major males increased. However, as mite population density increased above 46.5 mites/beetle, the numbers found on minors reached an asymptote while the numbers found on majors and females continued to rise (Fig. 1). Thus, the proportion of mites on minor males was negatively density dependent. The number of mites on females followed the pattern observed for major males (Fig. 1).
Effect of mites on male longevity

During each of the three mite counts, there were significantly more mites on males in the mites-added treatment than in the mites-reduced treatment (Mann–Whitney; first $Z_1 = 3.69$, $P < 0.001$; second $Z_1 = 6.05$, $P < 0.001$; third $U_{18,7} = 117$, $P < 0.001$). The mean number of mites on males in mites-added and mites-reduced treatments were 63.1 ± 6.5 and 12.2 ± 1.7 mites/male, respectively. Thus, the treatment had the desired effect on mite numbers, while the numbers were within the range observed in our unmanipulated laboratory populations.

The addition of mites had a detrimental effect on the longevity of minor males. The mean longevity of minor males in the mites-added treatment was 66.8 ± 4.1 days and in the mites-reduced treatment 82.2 ± 5.9 days; survival curves differed significantly between treatments (Kaplan–Meier log rank test $\chi^2_1 = 9.06$, $P = 0.003$; Fig. 2). Interestingly, in the mites-reduced treatment, the numbers of mites in successive counts were significantly repeatable ($r = 0.27$, lower and upper 95% confidence intervals being 0.07 and 0.53, respectively; $F_{38,57} = 1.94$, $P = 0.011$). Repeatabilities for the mites-added treatment were not calculated because any repeatability could have resulted from the possible cumulative effects of adding mites. Male size, measured as pronotum width, was never correlated with mite load in either treatment (mean of three counts: mites removed $r_{47} = 0.12$, $P = 0.427$; mites-added $r_{46} = 0.05$, $P = 0.765$).

**DISCUSSION**

Infestation by *M. merdarius* decreased the longevity of minor male *O. binodis* by an average of 15.4 days. Given that the mean adult longevity is only 9.9 weeks (Ridsdill Smith *et al*., 1982), a reduction of 20% in the adult male reproductive life span is likely to represent a significant evolutionary cost for males. Polak (1996) found a 50% reduction in longevity of *Drosophila nigrospiracula* infested with *M. subbadius*, and Hurst *et al*. (1995) found a 10% reduction in coccinellid beetles *Adelia bipunctata* infested with *Coccipolipus hippodamiae* (the latter was not significant perhaps because of the low sample size and lack of statistical power). In both of these examples, mites also had a significant impact on reproductive success; mite-infested male *D. nigrospiracula* were less likely to be found copulating (Polak & Markow, 1995) and female *A. bipunctata* had a reduced lifetime reproductive success (Hurst *et al*., 1995). However, *M. merdarius* is not likely to be parasitic on *O. binodis* and the causes for the observed negative effects of mites on the longevity of their beetle hosts need further experimentation.

Minor males almost always had fewer mites on them than major males. There are two possible explanations for this result. The difference may simply reflect major males having larger bodies; the probability of randomly encountering a mite in the environment is likely to be greater for individuals with large bodies compared to individuals with small bodies. However, size-dependent encounter rates alone are insufficient to explain the density-dependent skew in the proportion of mites on the two morphs. If body size is indeed responsible for the difference in infestation seen between morphs, the maximum load of 45–50 mites per beetle (see Fig. 1) may then represent the maximum carrying capacity for beetles the size of minors.

Fig. 1. Mean number of mites per beetle in each population plotted against mean number of mites per morph in each population. Minors: quadratic regression, $r^2 = 0.75$, $F_{42} = 61.84$, $P << 0.001$; $b_1 = 1.34 ± 0.239$, $t = 5.62$, $P << 0.001$, $b_2 = -0.009 ± 0.002$, $t = -3.49$, $P = 0.001$. Majors, linear regression, $r^2 = 0.93$, $F_{1,43} = 570.94$, $P << 0.001$; $b = 1.47 ± 0.061$, $t = 23.89$, $P << 0.001$. Females, linear regression, $r^2 = 0.89$, $F_{1,11} = 86.87$, $P << 0.001$; $b = 1.18 ± 0.13$, $t = 9.32$, $P << 0.001$.

Fig. 2. Cumulative survival probability of male morphs in the two mite treatments.
There are two observations that are inconsistent with the random encounter scenario for the morph-dependent infestation levels observed in our artificial populations. First, in our manipulations of mite loads, male body size was not associated with mite load in either treatment. We might not expect an association in our mite-removed treatment because mite densities were below the carrying capacity for minors observed in the artificial populations. However, the mites-added treatment had an average infestation level 26% higher than the observed carrying capacity of c. 50 mites/minor. If body size had a significant impact on mite loads, we should have expected smaller minors to have a lower carrying capacity than larger minors, and thus an association between body size and mite load. Second, infestation rates on females were the same as those on major males, even though females were intermediate in body size between the two morphs.

What other factors could account for the greater susceptibility to mite infestation of major males? Beetles become infested with mites when moving through and feeding on dung. The alternative mating tactics adopted by major and minor males may result in a greater exposure of majors to mite infestation. Major males guard the entrance to tunnels in which females breed. Moreover, they assist females in burying dung by bringing dung from the pad down the tunnel and into the brood chamber (Cook, 1988, 1990; see also Hunt & Simmons, 1998). Thus, both major males and females are constantly handling and processing dung. In contrast, minor males dig side tunnels beneath the dung surface and attempt to intercept breeding tunnels in order to sneak copulations (Emlen, 1997). Minor males therefore have a lower exposure to dung than do major males and females. It has been shown with several species of *Macrocheles* mites that surface extracts of their beetle hosts are enough to elicit strong positive responses, suggesting that mites may be actively seeking their beetle hosts (Krantz, 1998). As major males and females of *O. binodis* spend more time in contact with dung than minor males, mites actively seeking for a host are more likely to encounter them. Furthermore, in an earlier study on the dispersal of *Onthophagus taurus* we found that major males disperse from deteriorating dung pads significantly earlier than minor males (Hunt, Kotiaho & Tomkins, 1999). If the dispersal pattern is similar in *O. binodis*, it may make major males more attractive to mites that are ready to disperse and thus contribute to the differences in mite infestations observed in our study.

Interestingly, the variation in mite numbers was significantly lower within individuals than between individuals in the treatment group where mites were removed each week. This suggests that males may also differ in their susceptibility to mite infestation. Differential susceptibility could result if some males are more efficient in grooming themselves and thus reducing the number of mites. Alternatively, there may be genetic differences between males in their susceptibility to mites. In fact, there is evidence from several different organisms that susceptibility to parasites, including ectoparasitic mites, can have a genetic basis (Lively, 1989; Möller, 1990a; Carton & Nappi, 1991; Young et al., 1995; Boulinier et al., 1997). However, although suggestive, more experimental data are required before we can conclude that genetic variance in susceptibility to mites exists in *O. binodis*.

In conclusion, we have experimentally demonstrated that phoretic mites have a significant effect on the longevity of their host and that major males suffer a greater level of infestation than do minor males. Our data thus illustrate a differential fitness cost associated with the adoption of alternative mating tactics that may be an important consideration in understanding the evolutionary maintenance of alternative mating strategies in natural populations of onthophagine dung beetles.

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