Phoretic Mite Discrimination Among Male Burying Beetle (*Nicrophorus investigator*) Hosts

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ABSTRACT *Nicrophorus* beetles reproduce by burying small vertebrate carcasses underground in a brood chamber. All stages of the phoretic mite *Poecilochirus* (Mesostigmata: Parasitidae) associate closely with *Nicrophorus* beetles by clinging to them for transportation and by reproducing in the beetles' brood chamber. Presumably, the fitness of phoretic mites is affected by the ability of their beetle host to successfully locate and bury a carcass. Previous studies have shown that thermoregulation during flight, competitive ability, burying speed, and burial depth are all positively correlated with adult beetle body size. This study, conducted in the Rocky Mountains of southwestern Colorado, addresses whether deuteronymph mites discriminate among male *Nicrophorus investigator* Zetterstedt (Coleoptera: Silphidae) hosts based on beetle body size, a proxy for beetle condition. We found that the number of phoretic mites on wild-caught male *N. investigator* beetles was positively correlated with beetle body weight and other measures of adult beetle body size. Laboratory trials with pairs of *N. investigator* beetles also demonstrated that deuteronymph mites preferentially associate with larger beetle hosts. A test to determine whether mites select hosts based on nutritional status was inconclusive. These results suggest that deuteronymph mites discriminate among adult male *Nicrophorus* based on body size, which is consistent with a choice that would benefit the mite. The precise mechanism by which mites detect size is not known, but it is most likely chemical.

KEY WORDS *Nicrophorus investigator*, phoretic mites, phoresy, host selection

Phoresy is a behavior in which an organism uses a host, typically of a different species, as a means of transportation. Several species of mites (Mesostigmata: Parasitidae) are phoretic on burying beetles of the genus *Nicrophorus* (Coleoptera: Silphidae). *Nicrophorus* beetles, also known as burying beetles, typically reproduce in pairs by burying a small vertebrate carcass in a brood chamber to provision their offspring (Eggert and Müller 1997, Scott 1998). Mites form close and permanent associations with *Nicrophorus* beetles through phoresy and by reproducing in the brood chamber of their beetle hosts (Schwarz and Müller 1992; Schwarz et al. 1996; Schwarz et al. 1998). Phoretic mites leave the brood chamber with the parent beetles or the beetles' offspring and can transfer between hosts when multiple burying beetles congregate at a carcass or pheromone-emitting male beetle (Springett 1968, Müller and Eggert 1987, Scott 1998, Schwarz and Koulianos 1998).

Phoretic mite densities on *Nicrophorus* beetles vary greatly, but breeding adults typically carry 10–30 mites, and postbreeding adults may carry >100 (Springett 1968, Schwarz and Müller 1992). The relationship between phoretic mites and their hosts ranges from mutualistic to parasitic depending on conditions such as the degree to which mites parasitize beetle eggs and the prevalence of fly eggs which, if not eaten by the mites, produce fly larvae that compete with beetle larvae for carrion (Springett 1968, Wilson and Knollenberg 1987, Beninger 1993, Blackman and Evans 1994).

Small vertebrate carcasses are a rare and ephemeral resource. Phoretic mites have limited mobility and must rely on their burying beetle hosts for access to a carcass, their mutual reproductive habitat. It is no surprise that mites discriminate among beetle species, distinguishing hosts from nonhost species (Springett 1968, Brown and Wilson 1992, Schwarz et al. 1996) given that phoretic mite fitness is directly affected by their ability to select a successful beetle host. Phoretic mites use olfactory cues to differentiate among host species (Springett 1968) and between male and female *Nicrophorus*, preferentially associating with beetles that are reproductively mature (Schwarz and Müller 1992, Schwarz and Koulianos 1998). Studies to date have not examined whether phoretic mites discriminate among adult burying beetles based on other factors such as body size or condition that might indicate a host's ability to successfully reproduce, a host behavior on which the mites' reproductive success ultimately depends.

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Numerous studies have shown that the fitness of *Nicrophorus* beetles is correlated with their body size (Scott 1998, Müller et al. 1990). Large body size is associated with greater probability of overwinter survival (Smith 2002), greater thermoregulatory ability and, by extension, greater flying ability (Merrick and Smith 2004), faster carcass burying speeds (Smith et al. 2000), and deeper burials (Eggert and Sakaluk 2000). Furthermore, larger burying beetles are more successful in defending a carcass from conspecific and congeneric competitors (Otronen 1988, Müller et al. 1990, Trumbo 1990), and they are therefore more likely to rear a brood.

As in most holometabolous insects, linear measures of adult size do not change after the final eclosion from the pupa. Thus, elytra length and pronotum width are considered invariant measures of adult size. In contrast, body condition and nutritional status may vary in adults based on muscle mass and nutritional reserves. Various measures of size may be important predictors of successful reproduction, although adult male *Nicrophorus* seem to use linear measures over mass to assess their opponents (Safryn and Scott 2000). It is not known which, if any, of these measures of size and condition are used by mites to select a promising host.

In this study, we measured the ability of mites (*Poecilochirus carabi* G. & R. Canestrini and *P. subterraneus* Müller) to discriminate between beetles based on both invariant measures of body size (elytra length and pronotum width) and variable measures (body mass, physical condition, and nutritional status) in the field and in the laboratory. Body weight, elytra length, and pronotum width are all highly correlated in *Nicrophorus investigator* (Smith et al. 2000). This study was carried out on male individuals of *N. investigator* (Anderson and Peck 1985), a holarctic burying beetle that inhabits the vicinity of the Rocky Mountain Biological Laboratory (RMBL) at 2,900-m elevation on the western slope of the Rocky Mountains in Gunnison County, CO. The primary reference used to identify phoretic mites was Hyatt (1980).

Materials and Methods

Beetle Collection. Male *N. investigator* beetles were collected during July 2004 from both pitfall traps and caged rodent carcasses placed in montane meadows near the RMBL. Traps consisted of tin coffee cans with metal screen funnel tops, baited with chicken meat (Smith et al. 2000). Traps were buried with rims at soil level and covered with a weighted metal screen (1.5-cm openings) to exclude large scavengers. Caged rodent carcasses (20–30 g) consisted of deer mice (*Peromyscus maniculatus* Wagner) and laboratory mice (*Mus* sp.) placed under metal screens (1.5-cm openings) to exclude large scavengers. Traps and caged rodent carcasses were visited every few days and during each visit wild-caught beetles were collected and kept together in a single holding container for 2 to 5 h before being weighed and divested of their mites.

Mite Distribution among Wild-Caught Beetles. The number of phoretic mites associated with each wild-caught male beetle was used to evaluate mite distribution patterns among field-collected *N. investigator* hosts. Beetles were drawn from the common holding container at random and their mites were removed with a stream of carbon dioxide focused through a pipette tip. The carbon dioxide temporarily incapacitated the mites and the beetle, but all recovered within ≈5 min. All mites from each beetle were counted and separated into two size classes large (*P. carabi*, >1 mm long) and small (≤1 mm long, preliminary identification *P. subterraneus*). Mites were kept in the two size-class groups in separate plastic containers with damp cotton balls and chicken meat. Both groups of mites were cumulative, meaning that new mites gathered throughout the experiment were added to the existing containers. After the mites were removed, the mite-free beetles were measured and placed in separate 5-cm square plastic containers. Body weight (nearest 0.01 g), elytra length (nearest 0.1 mm), and pronotum width (nearest 0.1 mm) were measured for each wild-caught beetle. To prevent desiccation of the beetles, damp cotton balls were placed in the holding containers and replaced regularly.

A Poisson regression was used to analyze the relationship between the body size of wild-caught beetles and the number of phoretic mites found on each beetle. A Poisson regression was selected instead of a linear regression model because as beetle body size increased, the variance in body size also increased. A principal components analysis (PCA) in combination with a Poisson regression on the principle components also was carried out to evaluate the relative contribution of beetle body weight, elytra length, and pronotum width in predicting mite number on wild-caught beetles. The SAS procedures used to perform Poisson regressions and PCA were GENMOD and PRINCOMP, respectively (SAS Institute 1985). The option SCALE = DEVIANCE also was included in the Poisson regression model to correct for over dispersion in the data (SAS Institute 1985). Pseudo-R^2 values for Poisson regressions were calculated as the proportional decrease in the deviance measure of model fit between a model with just a constant term and the model of interest.

Mite Choice Trials between Paired Beetles. Pairwise choice trials ($N = 69$) of captive beetles and mites were conducted to evaluate whether mites discriminated between paired wild-caught male *N. investigator* beetles of different sizes. Immediately preceding the pairwise choice trials, ten *P. carabi* were selected at random from the large size-class mite colony and placed in a cylindrical plastic vial that was ≈8 cm in height and 4 cm in diameter. We used 10 mites because this number was within the range of mites found on wild-caught beetles and the number was large enough to reveal different association patterns between hosts. Two beetles that had been captured on the same day and whose mites had been removed (see wild-caught beetle experiment above) were then selected at ran-

dom and placed in the plastic vial with the ten large mites. The vial was occasionally tapped to keep the mites at the bottom of the vial where they would encounter the beetles. After 5 min, the beetles were separated and a stream of carbon dioxide was used to remove the mites. The number of mites clinging to each beetle was counted, the mites were returned to the colony, and the beetles were returned to their individual plastic holding containers. With the exception of one trial that was discarded from the data set, all 10 mites selected a beetle host by the end of the 5-min trial. After the pairwise choice trials, 37 beetle pairs were randomly selected to participate in a nutritional status trial.

A signed rank test and a Spearman's rank correlation were used to analyze the relationship between beetle body weight and phoretic mite number in the mite choice trials between paired beetles. The SAS procedures used to perform the signed rank test and Spearman's rank correlation were UNIVARIATE and CORR, respectively (SAS Institute 1985).

Mite Choice Trials between Fed and Unfed Beetles. Beetle pairs ($N = 37$) assigned to the nutritional condition experiment were returned to their plastic holding containers after the pairwise choice trials, and one beetle within each pair was selected at random to receive a surplus of chicken meat in its container, whereas the other beetle remained unfed. After 2 or 4 d under these feeding conditions, beetle pairs were tested for mite preference in a second pairwise choice trial using the same protocol as the first pairwise choice trial. To test for an effect of nutritional condition on phoretic mite preference, we calculated the difference in mite number on the fed beetle between the first and second pairwise choice trials and compared this with the change in the relative weight difference for each beetle pair:

$$\text{change in relative weight of a beetle pair} = [(W_{1,\text{fed}} - W_{1,\text{unfed}}) - (W_{2,\text{fed}} - W_{2,\text{unfed}})]$$

where $W_{1,\text{fed}}$ is the weight of the fed beetle at the time of the first pairwise choice trial, and $W_{2,\text{unfed}}$ is the weight of the unfed beetle at the time of the second pairwise choice trial.

A Mann–Whitney U test was used to determine whether the 2- versus 4-d feeding treatments had different effects on the beetles. A signed rank test and a Spearman's rank correlation were used to analyze the relationship between beetle body weight and mite number in the mite choice trials involving feeding treatments. The SAS procedures used to perform the Mann–Whitney U test, the signed rank test, and the Spearman's rank correlation were NPAR1WAY, UNIVARIATE, and CORR, respectively (SAS Institute 1985).

Results

Beetle Collection. In total, 137 male *N. investigator* beetles were collected in the field from 7 to 21 July 2004. We removed and counted a total of 1,047 phoretic mites (612 large, 435 small) from those beetles. The mean number of total mites (large and small combined) found on wild-caught beetles was 7.6 (variance = 17).

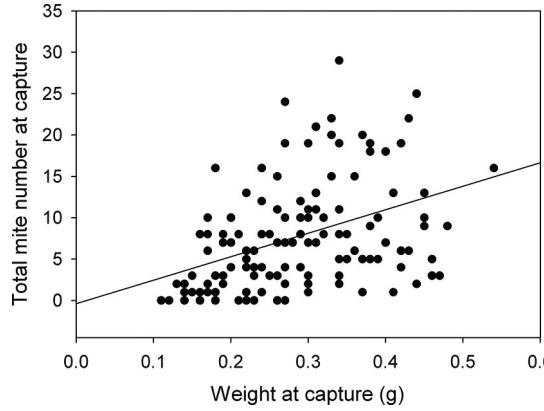

Fig. 1. Relationship between beetle body weight and number of phoretic mites at time of capture. Body weight of male *N. investigator* beetles was positively correlated with number of mites found on those beetles when collected from the field.

Mite Distribution among Wild-Caught Beetles. A Poisson regression (SAS version 9.1, SAS Institute, Cary, NC) showed that the total number of mites on each wild caught beetle was highly correlated with beetle weight ($F = 26.77$; df = 1, 135; $P < 0.0001$; pseudo-$R^2 = 0.17$). For clarity, we also graphed this as a linear regression (Fig. 1). That linear regression was highly significant ($P < 0.0001$, $R^2 = 0.1725$), had a slope of 28.379 with a standard error of 5.349, and an intercept of −0.368 with a standard error of 1.592. Beetle weight, elytra length, and pronotum width were all highly correlated. A principle components analysis was conducted using the beetle weight, elytra length, and pronotum width. The first principal component was highly significant ($F = 19.77$; df = 1, 134; $P < 0.0001$) and explained almost 98% of the variability of mite distribution among wild-caught beetles (Eigenvalue = 2.932). Eigenvectors for the first principal component were more or less equally loaded among body weight, elytra length, and pronotum width (0.576, 0.578, and 0.578, respectively). The second principal component was also significant ($F = 10.02$; df = 1, 134; $P = 0.0019$) and explained ≈1.4% of the variation (Eigenvalue = 0.043). Eigenvectors for the second principal component, interpreted as beetle density or stoutness, were loaded positively on body weight, but negatively on elytra length and pronotum width (0.816, −0.456, and −0.356, respectively).

Mite Choice Trials between Paired Beetles. Phoretic mites also selected larger beetles in the laboratory choice trials (Fig. 2). A signed rank test (SAS version 9.1) for the data from the pairwise choice experiments showed that beetle body weight was a significant predictor of mite number in the pairwise choice experiments ($S = 260.5$, $P = 0.0470$). A Spearman's rank correlation statistic from these data also

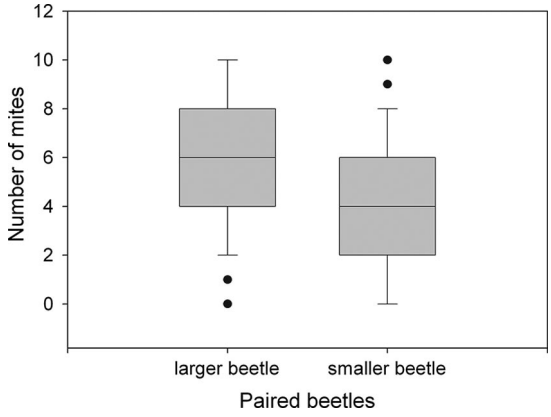

Fig. 2. Box plot of phoretic mite number on larger versus smaller beetles in choice trials with paired beetles. On average, the larger beetle in each beetle pair attracted more mites during choice trials.

showed that beetle weight was correlated with mite preferences ($r = 0.23725$, $P = 0.0497$).

Mite Choice Trials between Fed and Unfed Beetles. A Mann–Whitney *U* test showed that there was no significant difference between beetles subjected to feeding treatments for 2 versus 4 d ($U = 1256.5$; $P = 0.15$). A Mann–Whitney *U* test on the combined data from both 2-d and 4-d treatment groups showed that feeding treatments had a significant effect on beetle weight ($U = 1845.0$, $P < 0.0001$). On average, beetles in the fed treatment group gained 0.049 g (variance = 0.0004), and beetles in the unfed treatment group lost 0.0211 g (variance = 0.0003). Spearman's rank correlation and a signed rank test both showed that mite preferences for beetle hosts in pairwise choice trials were not affected by the feeding treatments ($r = -0.24152$; $P = 0.1498$ and $S = -75$; $P = 0.1808$, respectively).

Discussion

This study shows that phoretic mites (*P. carabi*) associated with male *N. investigator* beetles actively select larger beetles as hosts. This behavior would benefit the mites, as larger beetles are better able to locate and defend a carcass, the common breeding resource for both species. The ability to discriminate based on host quality, indicated by beetle body size in this case, parallels earlier results showing that mites preferentially transfer to sexually mature beetles of intermediate age when beetles congregate at carcasses or pheromone-emitting male beetles (Schwarz and Koulianos 1998). Research with phoretic mites on bumblebees also has shown that mites preferentially associate with the bee castes (young queens) that are most likely to increase their fitness (Huck et al. 1998).

The cues used by mites to select a host based on size are not known, but they are likely to be chemical. The suspected ability of mites to use chemical cues is supported by evidence from previous studies which show that deuteronymphs of *P. carabi* have a chemical-sensing organ on their tarsus, that mites can distinguish between sexes of *Nicrophorus* (Springett 1968, Schwarz and Koulianos 1998), and that male and female *Nicrophorus* differ in their chemical signals (Whitlow 2004). For mites to discriminate among beetles of different size, adult beetle body size would have to be correlated with pheromone quantity or quality, which has been demonstrated for some species. For example, pheromone production in the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is used to attract conspecifics to breeding habitat and has been shown to correlate positively with beetle body size (Pureswaran and Borden 2003). *Nicrophorus* females are able to distinguish, by chemical means, males of different sizes (Beeler et al. 2002) and breeding status (Müller et al. 2003). Recent studies of *Nicrophorus* pheromones (mostly hydrocarbons) indicate that they can be extracted, identified, and their active ingredients removed or placed on "clean" beetles (Whitlow 2004). It would be very interesting to apply these techniques to future studies of mite host selection.

The results from the pairwise trials conducted in the laboratory corroborate the mite distribution patterns observed among wild-caught beetles. The unexplained variation may be due to beetle age and/or reproductive maturity of the beetles, or other uncontrolled factors. The signed rank test for the data from the pairwise choice experiments, which just considers relative ranking order, indicated that mites preferred the larger beetle host. The Spearman rank correlation, which also considers the magnitude of the difference between ranked observations, showed that as the difference in weight between the paired beetles increased, the difference in number of mites increased correspondingly.

In our weight manipulation experiment, the inability of the mites to distinguish between males of different nutritional status is problematic. The experimental design applied feeding treatments (fed versus unfed) for 2 or 4 d and on average the unfed beetles did lose weight compared with the fed beetles. However, this change in weight did not affect mite preference for beetle hosts. Thus, we cannot determine whether the feeding treatments failed to affect beetle condition sufficiently to influence mite behavior or whether weight alone is not the primary indicator of beetle size/condition for mites. The latter explanation would be consistent with Safryn and Scott (2000), who found that linear measures were more important than weight when two male *Nicrophorus* assess each other's size, and the PCA results, in which the first principal component, a combination of weight and linear measures, was the best predictor of mite choice.

Our findings that larger beetles were preferred among wild-caught individuals and in laboratory trials, suggest that mite host selection is linked to beetle physiological fitness. Because the energetic and muscular demands of pheromone production, flight, carcass defense, and burial are likely high, we think that

it would be interesting to further pursue this area of research.

In conclusion, we have shown that the close and permanent association found between *Nicrophorus* and their phoretic mites (*Poecilochirus* spp.) includes opportunities for host selection behaviors. Host selection is known to occur in the burial chamber when mites decide whether to depart with an adult *Nicrophorus* or remain with the larvae (Schwarz and Koulianos 1998). In addition, mites have opportunities to select a host based on sex, size, or condition when *Nicrophorus* aggregate at pheromone-emitting male beetles, feeding sites, and carcasses used for reproduction (Springett 1968, Müller and Eggert 1987, Scott 1998, Schwarz and Koulianos 1998). In this study we have shown that deuteronymph mites discriminate among male *Nicrophorus*, selecting hosts that have the greatest probability of successfully locating, defending, and burying a carcass. This is a beneficial behavior, as it increases the probability that the deuteronymph mite will be transported to a *Nicrophorus* burial chamber where it can mature, mate, and reproduce.

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