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Response of terrestrial isopods, *Armadillidium vulgare* and *Porcellio laevis* (Isopoda: Oniscidea) to the ant *Tetramorium caespitum*: morphology, behavior and reproductive success

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Summary

Little is known about the effects of predatory stress on reproduction in terrestrial isopods (Crustacea: Oniscidea). We studied direct and indirect influences of predatory ants *Tetramorium caespitum* (Hymenoptera: Formicidae) on the behavior and reproduction of two terrestrial isopods, *Armadillidium vulgare* and *Porcellio laevis*. *A. vulgare* females were more cryptic than *P. laevis* females in both the presence and absence of ants, but in both species control animals were more cryptic than experimental animals exposed to ants. This likely resulted from increased movement in the presence of ants. Both species also avoided ventilated enclosures containing ants, but control animals not previously exposed to ants remained significantly further away. *P. laevis* also remained significantly further from ants than *A. vulgare*, suggesting that *P. laevis* more actively avoids potential predators. This is consistent with morphological differences between the two species: *A. vulgare* can roll into a sealed ball whereas the morphology of *P. laevis* permits swift locomotion. Furthermore, mortality rates of *P. laevis* were greater than *A. vulgare* when both were directly exposed to ants in the laboratory, and *P. laevis* suffered significantly more attacks than *A. vulgare* under experimental conditions. However, the length of the brooding period in *A. vulgare* was shorter in ant-exposed females than in controls, whereas experimental and control *P. laevis* females showed no such difference. This could be an adaptive trade-off for *A. vulgare* because in the late brooding period the distended marsupium can prevent rolling into a closed ball for protection. The results of this study underscore the relationships between morphology, behavior, and reproductive success.

Key words: *Armadillidium vulgare*, *Porecellio laevis*, isopod, woodlouse, reproduction

Introduction

Predatory stress can impact prey reproduction by interrupting or suppressing the reproductive cycle, decreasing the number of offspring produced, and/or reducing overall reproductive fitness and success (Lima and Dill, 1990; Malakoff, 1997; Durant, 2000; Toussaint et al., 2000; Adamec, 2001). Prey animals may respond with reactive or anticipatory deflective behaviors (Cooper, 1998), passive behaviors to avoid being attacked, and active defense mechanisms that are

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morphological, physiological, behavioral, or life-historical (Kavaliers and Choleris, 2001). Animals that adopt avoidance and anti-predator behaviors may thereby increase reproductive success (Durant, 2000). Predation risk can thus influence decisions about mating, reproduction, and number of offspring (Kats and Dill, 1998; Fox and Csezak, 2000; Mappes et al., 1997; Kavaliers and Choleris, 2001; Scheuerlein et al., 2001), and cues associated with this risk may be direct (i.e., an encounter with the predator itself) or indirect (Grostal and Dicke, 1999). For instance, some moths (*Ostrinia nubilalis* and *Pseudaletia unipuncta*) modify mating behavior when exposed to recordings of bat echolocation calls (Acharya and McNeil, 1998). In another study, the wolf spider *Pardosa milvina* altered foraging habits, avoided laying eggs on areas exposed to predators, and produced lighter egg sacs and fewer eggs in the presence of direct and indirect predator cues (Persons et al., 2002).

In the present study we examine predatory stress and reproductive biology of two terrestrial isopods (Crustacea: Oniscidea), *Armadillidium vulgare* and *Porecellio laevis*. Females brood eggs and young immatures in a ventral marsupium (Surbida and Wright, 2001; Kight et al., 2000; Kight and Ozga, 2002). Because larger females develop larger marsupia, body size is positively associated with fecundity (Lawlor, 1976; Kight et al., 2001). Gravid females can regulate pH of the marsupial fluid and control osmolality, thereby protecting the young from potential physiological stresses such as dehydration (Surbida and Wright, 2001). Embryos develop within the brood pouch for approximately 25–26 days in temperate conditions (Sutton, 1972; Lawlor, 1976). As the fluids within the pouch disappear, young mancas emerge from the marsupium over 2–4 days (Surbida and Wright, 2001) or as much as 7 days (Lawlor, 1976).

It is possible that differences in the morphology of *A. vulgare* and *P. laevis* might reflect differences in their responses to predation risk. Although both species have well-developed eyes, overlapping armored plates, seven pairs of legs, and three tagma (head, pereon, and pleon) (Abzhanov and Kaufman, 1999; 2000), *A. vulgare* can flex into a sealed ball, whereas *P. laevis* cannot. *A. vulgare* exhibits this defensive behavior when disturbed, whereas *P. laevis* must flee and seek cover, although it may also exhibit a “death feint” (Sutton, 1972; Hal and Beal, 1982). The legs of *P. laevis* are held laterally and are adapted for swift locomotion, whereas those of *A. vulgare* are held directly beneath the body (Sutton, 1972).

Natural selection for antipredatory behavior and morphology has likely been strong because terrestrial isopods have many predators. Arthropods such as ants (Deslippe et al., 1995), spiders (Barmeyer, 1975; Nyffeler and Benz, 1981; Pollard et al., 1995), centipedes, harvestmen, and beetles (Sutton, 1972) are common predators. Vertebrate predators include frogs (Lehman, 1978), toads (Sutton, 1972; Linzey et al., 1998), salamanders (Whitaker et al., 1986), owls, kites, hedgehogs, and pygmy shrews (Sutton, 1972; Grainger and Farley, 1978; Kawaji and Shiraishi, 1980). Oniscids are also parasitized by other arthropods such as blowflies (Sutton, 1972).

Although there are several published accounts of predation on terrestrial isopods, we are aware of no studies that have experimentally examined the effects of predatory stress. Here we examined the impact of cues and/or the chronic presence of the ant *Tetramorium caespitum* on the behavior and reproductive success of *A. vulgare* and *P. laevis*. We predicted that differences in morphology would be associated with differences in behavioral and reproductive responses to ant harassment and/or indirect cues associated with the presence of ants.

Materials and Methods

For all experiments, *T. caespitum* (Hymenoptera: Formicidae: Myrmicinae) was selected as the predator because it was usually collected in the same locations as isopods in Essex and Sussex counties, New Jersey, USA, and because this species readily attacked isopods in the laboratory. Large numbers of *T. caespitum* were efficiently captured with baited traps. *T. caespitum* employ two recruiting tactics during foraging (Beekman et al., 2001). Upon discovering food, ants deposit pheromone attractants that attract other foragers and result in the formation of a pheromone trail. Because ants rely on direct and indirect cues for foraging, it is possible that prey species, such as terrestrial isopods, could use these cues for detection. In all experiments, *T. caespitum* were starved for 24 h prior to exposure to isopods.

Only female isopods were used in experiments. Male genitalia are characterized by two pairs of gills modified for sperm transfer on the ventral pleon, while females exhibit no external genitalia, but during reproduction retain a ventral marsupial pouch (Sutton, 1972). Prior to all experiments, specimens were maintained in environmental chambers at 21 °C and a 15L:9D light/dark photocycle in ventilated plastic enclosures containing moist cellulose sponge and fed carrots *ad libitum*. Data were analyzed following Siegel and Castellan (1988) with $\alpha = 0.05$.

Experiment I: Concealment behavior in response to ant exposure

This experiment compared how *A. vulgare* and *P. laevis* respond to the presence of ants when concealing shelter was available. Experiments were conducted in 15×15×5 cm plastic enclosures containing similar arrangements of gravel, twigs and leaves. Each experimental enclosure housed five *A. vulgare* females, five *P. laevis* females, and 20 *T. caespitum*, whereas control enclosures did not contain ants. Six replicate enclosures were observed simultaneously for 6 h; experimental groups on September 15, 2002, and control groups on October 1, 2002. Each isopod was individually labeled on the dorsal cuticle with white fingernail polish. A total of 60 *A. vulgare* and 59 *P. laevis* were observed (*A. vulgare*: experimental N = 30, control N = 30; *P. laevis*: experimental N = 30, control N = 29). Following a 45-min acclimation period, the ants were introduced and the position of isopods recorded as having 100, 75, 50, 25, or 0% of their body exposed. The position of each individual was then measured every 30 min.

Experiment II: Positional response to indirect cues from ants

This experiment examined positional behavior in response to indirect cues from ants. A 31×24×5 cm experimental enclosure was divided lengthwise into four lanes of equal dimensions (31×6×5 cm). A Petri dish (6.0 cm diameter) containing 20 *T. caespitum* was placed at one end of each lane. Each Petri dish lid had a 3-cm hole covered by nylon plankton netting, permitting any volatiles from ants to vent into the larger enclosure, presumably forming a concentration gradient relative to the source. Lanes were covered with transparent plastic after introduction of isopods.

Two conspecific females were placed into each lane equidistant from the Petri dish and the opposite end of the lane. One female had been directly exposed to *T. caespitum* for 15 min prior to the experiment, whereas the other female was never exposed to ants in the laboratory. The position of each isopod was video recorded for 15 min and the location of each specimen noted every 3 min. Thirty naïve and thirty ant-experienced individuals were tested for each isopod species.

Experiment III: Reproductive success under ant exposure

This experiment examined the effects of chronic direct and indirect cues from *T. caespitum* on the brooding period and fecundity of *A. vulgare* and *P. laevis*. Isopods were collected from Essex and Sussex counties, NJ, during May and June 2003. *T. caespitum* were collected from Essex County, NJ, from May to August 2003. Females were examined daily for the onset of brooding, as determined by the enlargement and yellow coloration of the marsupium. Each brooding female was then isolated in a 15×15×5 cm enclosure that contained only a moist sponge and fed carrots *ad libitum*.

Brooding females were divided into experimental and control same-species groups with similar estimated body size distributions (length and width of each specimen were measured at the end of the experiment to minimize handling stress). The enclosures of experimental females (*A. vulgare*, N = 34; *P. laevis*, N = 35) also contained a ventilated Petri dish containing 10 *T. caespitum* as described in the previous experiment. Dead ants were replaced until mancas emerged. Control brooding females (*A. vulgare*, N = 33; *P. laevis*, N = 26) were placed in similar enclosures but with no ants in the Petri dish. Experimental females were also transferred to a Petri dish and directly exposed to 10 ants for 15 min every 48 h, whereas control females were transferred to Petri dishes without ants for the same period. Manca were counted and removed each day they emerged from the marsupium until no more immatures emerged. Sample size for the *P. laevis* experimental group was ultimately larger than the control group because individuals were added to the experimental group following high mortality attrition.

Experiment IV: Do ants attack both species?

This experiment examined whether ants attack one isopod species more than the other. Non-brooding females of each species were placed together in 9×9×3 plastic container along with 20 *T. caespitum*. Interactions between ants and isopods were video recorded for 10 min and the number of attacks on each subject noted. Thirty independent replicates were run for a total of 30 *A.vulgare* females and 30 *P. laevis* females.

Results

Experiment I: Concealment behavior in response to ant exposure

A. vulgare controls were significantly more concealed than conspecifics exposed to ants (Fig. 1, Wilcoxon Mann Whitney Test, control $U = 144.0$, experimental $U = 0.0$, $P < 0.0001$). This was also the case in *P. laevis* (control $U = 144.0$, experimental $U = 0.0$, $P < 0.0001$). *A. vulgare* was significantly more concealed than *P. laevis* in both experimental groups

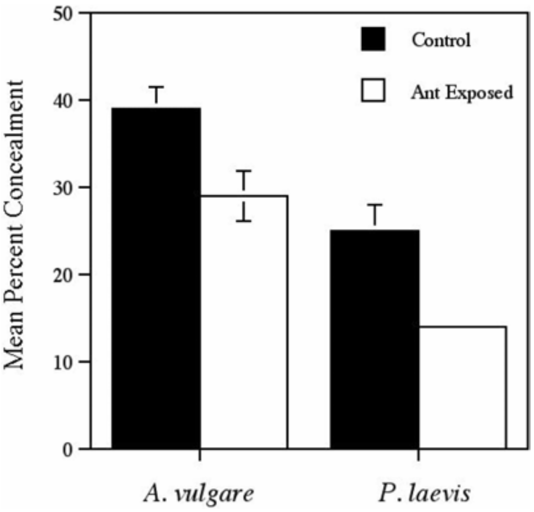

Fig. 1. Mean percent concealment of *Armadillidium vulgare* and *Porcellio laevis* under control conditions (black bars) and when directly exposed to ants (white bars). Vertical error bars represent standard error on the mean.

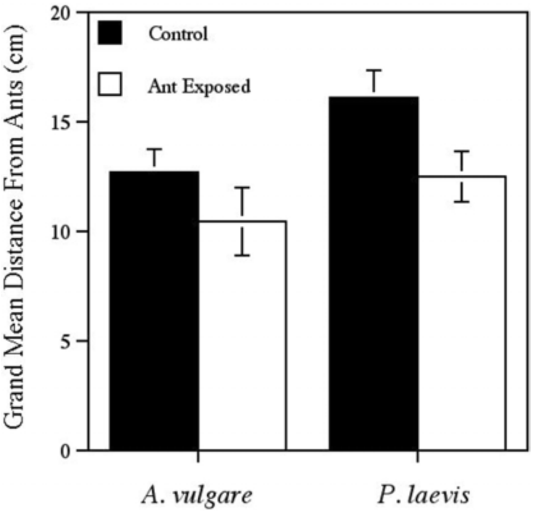

Fig. 2. Grand mean distance from ants (cm) calculated from individual mean distance of *Armadillidium vulgare* and *Porcellio laevis* under control conditions (black bars) and when previously exposed to ants (white bars). Vertical error bars represent standard error on the grand mean.

(Wilcoxon-Mann-Whitney, *A. vulgare*: U = 144.0, *P. laevis*: U = 0.0, P <0.0001) and control groups (*A. vulgare*: U = 142.0, *P. laevis*: U = 2.0, P <0.0001).

Experiment II: Positional response to indirect cues from ants

Individual mean distance from ants was calculated from each set of six observations. Control groups of both isopod species were positioned significantly further away from ants than conspecifics that were previously exposed to ants (Fig. 2, Wilcoxon 2-sample Test, *A. vulgare*: W = 775, P = 0.03917; *P. laevis*: W = 778.5, P = 0.04436). There were, however, no differences between treatment groups of either species in the minimum distance recorded (Wilcoxon 2-Sample Test, *A. vulgare*: W = 795, P = 0.07727; *P. laevis*: W = 889.5, P = 0.7117). Hence individuals tended to explore the range of the enclosure but maintained overall differences in average distance from the ants. *P. laevis* controls were significantly further from ants than *A. vulgare* controls (Wilcoxon 2-sample Test, W = 779, P = 0.04594). There were, however, no significant differences between *A. vulgare* and *P. laevis* that were previously exposed to ants (Wilcoxon 2-sample Test, W = 815.5, P = 0.1433).

Experiment III: Reproductive success under ant exposure

Some subjects were omitted from reproductive statistical analysis based on the following criteria: (a) extreme brood period outliers (first and fourth modified boxplot quartiles) for which initial date of brooding was most likely incorrectly assigned, (b) females that aborted brooding, (c) females that died before immatures emerged, and (d) females with <1 offspring. These omissions render data analysis more conservative (the null hypothesis is more difficult to reject), but more reliable. All criteria were evenly applied across treatment groups, and adjusted sample sizes were: experimental *A. vulgare,* N = 19; control *A. vulgare,* N = 24; experimental *P. laevis,* N = 13; control *P. laevis*, N = 14.

A. vulgare females exposed to ants had significantly shorter brooding periods (time between first observation of gravid state to first observation of released manca) than controls (Fig. 3, Wilcoxon Mann Whitney Test: exposed U = 119, control U = 337, P = 0.0080), but no difference was found between experimental (U = 90) and control *P. laevis* females (U = 92, P = 0.9806).

The dimensions of within-species treatment groups were not significantly different in length (Wilcoxon 2-sample Test: *A. vulgare* W = 422, P = 0.9124; *P. laevis* W = 199.5, P = 0.5963) or width (*A. vulgare* W = 414, P = 0.9318; *P. laevis* W = 201.5, P = 0.5340). Hence, any effects on fecundity should not be due to differences in body size (and size of the marsupium). However, no significant differences in fecundity (number of mancas to emerge from the marsupium) were observed betweeen experimental and control groups of either species (Fig. 4, Wilcoxon-Mann-Whitney Test, *A. vulgare* control U = 235.5, *A. vulgare* exposed U = 220.5, P = 0.8641; *P. laevis* control U = 104.5, *P. laevis* exposed U = 77.5, P = 0.5281).

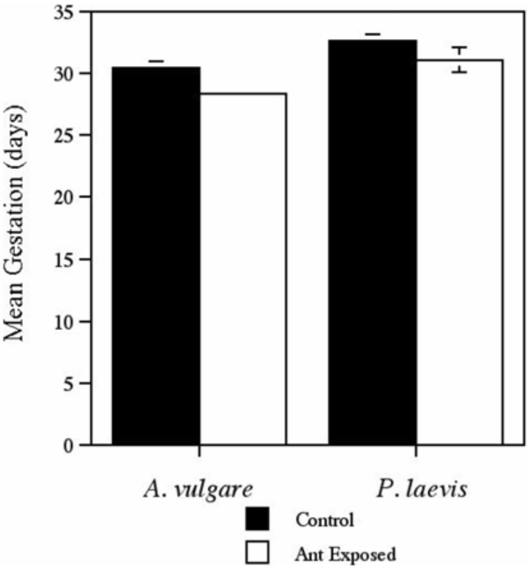

Fig. 3. Mean gestation (days) of *Armadillidium vulgare* and *Porcellio laevis* under control conditions (black bars) and when directly exposed to ants (white bars). Vertical error bars represent standard error on the mean.

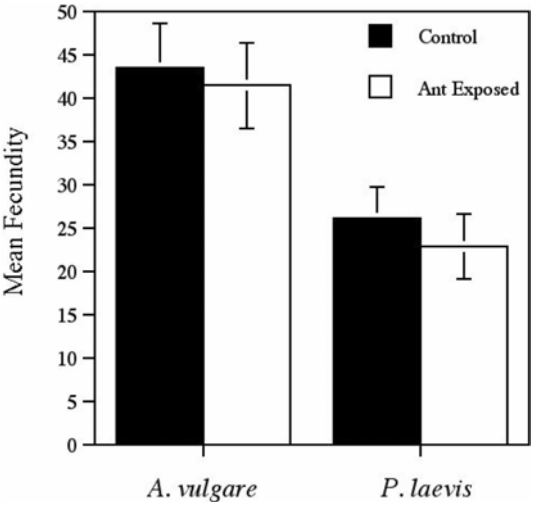

Fig. 4. Mean fecundity (i.e., number of live mancas) of *Armadillidium vulgare* and *Porcellio laevis* under control conditions (black bars) and when directly exposed to ants (white bars). Vertical error bars represent standard error on the mean.

There were no significant differences between *A. vulgare* control and experimental females in mortality (Fig. 5,Yate's Corrected Chi-Square, $\chi^2 = 1.86$, $P = 0.1724$), but *P. laevis* experimental females suffered significantly higher mortality than conspecific controls (Fig. 5, Yate's Corrected Chi-Square, $\chi^2 = 5.75$, $P = 0.0.0164$).

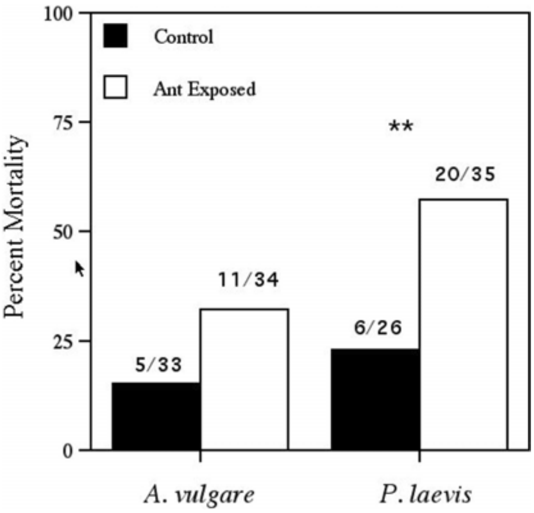

Fig. 5. Percent mortality of *Armadillidium vulgare* and *Porcellio laevis* under control conditions (black bars) and when directly exposed to ants (white bars). Asterisks refer to significance at = 0.01.

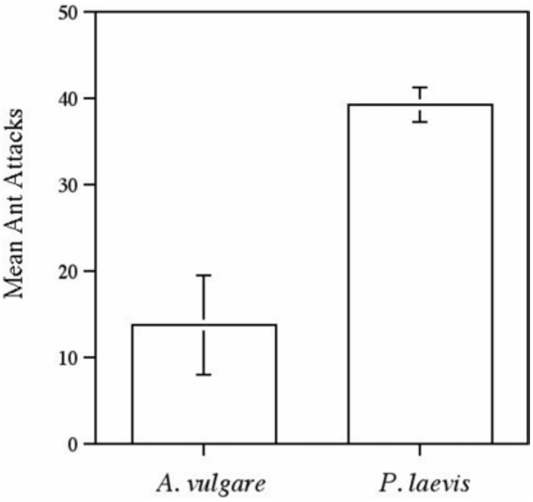

Fig. 6. Mean ant attacks on *Armadillidium vulgare* and *Porcellio laevis*. Vertical error bars represent standard error on the mean.

Experiment IV: Do ants attack both species?

P. laevis were attacked by ants significantly more often than *A. vulgare* (Fig. 6, Wilcoxon 2-sample Test, $W = 629$, $P < 0.0001$). Correspondingly, *A. vulgare* were marginally more likely to be attacked when the body was extended and not rolled into a ball (Wilcoxon Matched Pairs Signed-Ranks Test, extended $W^+ = 287$, rolled $W^- = 119$, $P = 0.05725$). This should be viewed conservatively, however, because the total amount of time subjects spent in each posture was not recorded.

Discussion

This study demonstrates that terrestrial isopods respond behaviorally and reproductively to direct and indirect cues from ants. This was reflected in immediate defensive (ball-rolling) and aversive behavior (fleeing, and/or avoidance of point source cues) in the presence of ants. *A. vulgare* females also significantly reduced the brooding period by an average of 2 days when chronically exposed to ants. Both isopod species were collected in habitats where *T. caespitum* was common, and this species of ant heavily attacked isopods in captivity, particularly *P. laevis*. Although Sutton (1972) cautioned against the assumption that predators in laboratory conditions feed on oniscids in natural conditions, *A. vulgare and P. laevis* do appear to detect and avoid *T. caespitum*.

Contrary to expectation, we found that both species were less cryptic (in terms of overhead visibility) in the presence of ants. Although there was a 2-week interval between control and experimental observations, our general observations were that crypsis was affected by frequent movements of isopods when ants were present. This seemed to occur mostly after harassment, whereas undisturbed isopods often remained for long periods of time at a single location. Increased movement undoubtedly increased the likelihood a subject would be visible during observations. We also found that *A. vulgare* remained more concealed than *P. laevis*, whether or not they were in the presence of ants. This is consistent with our observations during collection that *A. vulgare* was more reclusive than *P. laevis*. *A. vulgare* were generally discovered rolled in balls under soil or rocks, and only occasionally visually detected from above. While this general reclusive behavior need not necessarily result from direct interactions with predators, it may result in effective predator-avoidance. Ball rolling was, however, an active response when ants attacked *A. vulgare* in the laboratory. *P. laevis* were much less reclusive when collected, and were often mobile and exposed, or fleeing when cover was overturned.

We predicted that reproduction in *P. laevis* would be negatively affected by ant exposure in the laboratory because mobile avoidance and escape tactics offered limited success in enclosed spaces. Other forms of chronic stress, such as forced bouts of locomotion, have been shown to result in lower fecundity and shorter brooding periods in *P. laevis* (Kight and Nevo, 2004). However, in the present study there were no significant differences in brooding duration or fecundity between *P. laevis* controls and those exposed to ants. It seems unlikely, though, that *P. laevis* would encounter predators under natural conditions in enclosed spaces from which there is no escape. The ability of *P. laevis* to flee quickly, even when encumbered with eggs, is presumably adaptive for predator avoidance.

A less anticipated result was that ant-exposed *A. vulgare* reduced the length of the brooding period by an average of two days. This could be a reflection of morphological constraints. The marsupium of *A. vulgare* becomes so distended near the end of the brooding period that females are often unable to roll completely into a ball. This could render late-gestation *A. vulgare* females more vulnerable to ant harassment, and in the present study rolled females were less likely to be attacked than distended females (although females in the fifth experiment were not brooding). Reduced brooding was most likely the result of early offspring release rather than accelerated development due to constant thermal conditions in the study. Because *A. vulgare* can breed sequentially for several years (Lawlor, 1976), early release of immatures may be a short-term cost with longer-term benefits. Porcellionids can also breed over several years (Warburg, 1995), but though *P. laevis* did not exhibit a trade-off in response to ant harassment, it has been observed to do so under other kinds of stress (Kight and Nevo, 2004).

If isopods can detect and discriminate a concentration gradient of ant volatile compounds, *A. vulgare* and *P. laevis* were expected to position themselves distant to the source. This occurred, but was most pronounced in isopods that had no previous direct experience with ants. It could be that prior ant exposure results in habituation; however, this seems unlikely because the subjects had only been exposed once before the experiment. A second explanation could be that control isopods exhibited a novelty effect — a stronger response to a new stimulus. A mutually inclusive hypothesis is that the relative stress experienced by controls and ant-exposed subjects was asymmetrical. For previously exposed isopods, a shift from direct to indirect cues represents a decrease in stress, while for controls a shift from no cues to indirect cues would be an increase in stress. Of the two isopod species, *P. laevis* controls were on average positioned significantly further away from the ants. This could reflect a strategy in *P. laevis* that relies more on locomotion than defense.

Because terrestrial isopods are presumably important prey items for a diverse assemblage of predators, the differences in adaptive behavioral responses of different species, here *A. vulgare* and *P. laevis*, may be associated with their morphological differences in mechanisms of defense. The results of the present study support the hypothesis that defensive morphology can influence behavior and reproductive success in terrestrial isopods.

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