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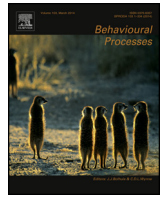
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Do Predator Cues Influence Turn
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Scott Kight, *Montclair State University*



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Do predator cues influence turn alternation behavior in terrestrial isopods *Porcellio laevis* Latreille and *Armadillidium vulgare* Latreille?

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ABSTRACT

Terrestrial isopods (Crustacea: Oniscidea) make more alternating maze turns in response to negative stimuli, a navigational behavior that corrects divergence from a straight line. The present study investigates this behavioral pattern in two species, *Porcellio laevis* Latreille and *Armadillidium vulgare* Latreille, in response to short-term vs. long-term exposure to indirect cues from predatory ants. Neither isopod species increased the number of alternating turns in response to short-term indirect exposure to ants, but both species made significantly more alternating turns following continuous indirect exposure to ants for a period of one-week. These results are surprising given differences in behavioral and morphological predator defenses between these species (the Armadillidiidae curl into defensive postures when attacked, whereas the Porcellionidae flee). The marked similarity in alternating turn behavior of the two families suggests evolutionary conservation of antipredator navigation mechanisms.

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1. Introduction

Diverse organisms alternate between left and right turns at consecutive directional branches, including humans (Pate and Bell, 1971), rodents (Dember and Richman, 1989), arthropods (Grosslight and Harrison, 1961), unicellular organisms (Lepley and Rice, 1952), and even human sperm (Brugger et al., 2002). Changing the direction of consecutive turns appears to be a strategy for efficiently moving through a complex environment because alternating turns correct divergence from a straight line (Hughes, 1967, 1978). For example, in the terrestrial isopod *Armadillidium vulgare*, individuals that make alternating turns optimize foraging success for higher quality food items (Tuck and Hassall, 2004).

Alternating turn behavior has been particularly well studied in the Oniscidea, isopod detritivores common to many terrestrial ecosystems (Hughes, 1967, 1978, 1985, 1987, 1989, 1992). Terrestrial isopods use alternating turns to navigate efficiently when escaping negative or potentially harmful conditions. For example, Hughes (1967) found that individuals kept in a bright, dry environment before testing made more alternating turns in a multiple T maze, and also ran faster than those kept in the cool, moist environmental conditions favored by terrestrial isopods. Food deprivation (Hughes, 1978), excessive substratum disturbance (Houghtaling

and Kight, 2006), and exposure to predators (Hughes, 1967, 1978; Carbines et al., 1992) are also associated with increased alternating turns. Female isopods also tend to make more alternating turns when brooding eggs and manca (Kight, unpublished data). Hence turn alternations may be an indicator of stress in terrestrial isopods.

The relationship between stress and turn alternation, however, could potentially be affected by acclimation or habituation to environmental conditions during prolonged exposure. Terrestrial isopods are known to exhibit different behavioral and physiological responses to short-term vs. chronic sources of stress. For example, both *A. vulgare* (Refinetti, 1984) and *Porcellio laevis* (Nair et al., 1989) acclimate quickly to increases in ambient temperature. Both species also reduce negative chemotaxis after long-term exposure to cues from predatory ants (Castillo and Kight, 2005). Chronic substrate disturbance is also associated with reduced alternating turns in *P. laevis*, although it is unclear whether this is due to acclimation, developmental plasticity, or evolutionary adaptation in populations inhabiting areas characterized by high disturbance (Houghtaling and Kight, 2006).

A decrease in turn alternation behavior might therefore be expected when individuals acclimate to negative stimuli. In the present study, we examine the relationship between short-term and long-term predator cues and alternating turn behavior in *P. laevis* and *A. vulgare*. Oniscids are subject to predation from diverse animals, including ants (Deslippe et al., 1995), spiders (Barmeyer, 1975; Nyffleler and Benz, 1981; Pollard et al., 1995), frogs (Lehman, 1978), toads (Linzey et al., 1998), salamanders (Whitaker et al.,

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1986), birds (Kawaji and Shiraishi, 1980), and mammals (Grainger and Farley, 1978).

This wide array of predators could be associated with evolutionary divergence in the Oniscidea. Morphological differences between the Armadillidiidae and Porcellionidae, for example, are associated with antipredator behavior; *A. vulgare* generally flexes the body into a “ball” position when exposed to predators, whereas *P. laevis* cannot do so and must flee, seek cover, or exhibit a “death feint” (Sutton, 1972; Hal and Beal, 1982). If porcellionid nervous systems are adapted for running escape, *P. laevis* should make more alternating turn corrections than *A. vulgare* in response to predator cues, especially during the initial exposure to a novel stimulus. However, if isopods habituate to predator cues, as suggested by Castillo and Kight (2005), both species might reduce turn alternations following prolonged exposure to predator cues.

2. Materials and methods

We acquired living specimens of *P. laevis* and *A. vulgare*, in addition to the ant *Tetramorium caespitum* (Hymenoptera: Formicidae) from Carolina Biological Supply (<http://www.carolina.com>) in February 2012. The animals were collected near Burlington, NC, USA (personal communication). To control for possible behavioral differences between sexes, only females were used as experimental subjects. We housed subjects in same-species groups of approximately 50 isopods in 12 cm × 9 cm × 7 cm ventilated plastic enclosures containing moist cellulose sponges and food (carrots) provided *ad libitum*.

We created four treatment groups by placing separate enclosures of each isopod species in a larger plastic container (30 cm × 27 cm × 11 cm) that either contained only the isopod enclosures, or the isopod enclosures in addition to a 12 cm × 9 cm × 7 cm ventilated plastic enclosure containing approximately 200 ants. We maintained subjects under these conditions for a period of one week prior to behavioral observation and data collection. Hence one treatment group of each isopod species was presumably exposed to chronic but indirect volatile ant cues, whereas the other two groups served as unexposed controls. *T. caespitum* actively preys upon both isopod species and direct (attacks) as well as indirect (presumably olfactory, see Pasteels et al., 1986; Beekman et al., 2001) ant cues are known to influence antipredator and reproductive behavior in *P. laevis* and *A. vulgare* (Castillo and Kight, 2005).

To measure alternating turn behavior, we used a Plexiglass multiple T-maze with a 40 mm × 10 mm × 10 mm entrance alley leading to a forced right turn (Fig. 1, modified from Hughes, 1967). After the entrance alley there is another 40 mm alley leading to

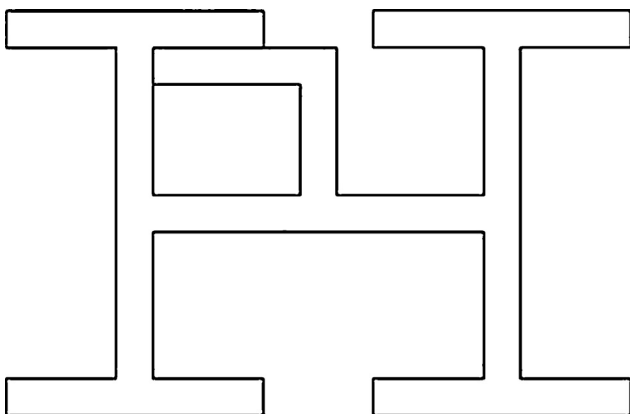


Fig. 1. Multiple T-maze modified from Hughes (1967). Each turn leads to a 40(l) × 10(w) × 10(h) mm alley.

a T-junction, where test subjects were forced to make the first of three turn decisions. The alley between each subsequent T-junction was 40 mm. Each subject could therefore make zero, one, two, or three alternating turns.

To begin each trial, we used entomological forceps to place an isopod within the entrance of the maze and observed its behavior until it reached one of eight possible ending points (Fig. 1). In the few instances that a subject did not clearly move from one turn to the next (e.g. reversing or retreating from a T-junction), it was repositioned at the beginning of the maze and the trial was restarted. Between trials, the maze was rinsed thoroughly with a 95% ethyl alcohol solution to remove potential conspecific cues left by the previous subject. In some experimental trials (described below), 20 ants were placed in the maze for 5 min and then removed immediately before the isopod was placed in the maze. In those trials, the maze was presumed to contain ant olfactory cues.

We tested independent groups of 30 individuals of each isopod species (for a total of 240 individuals) under the following conditions:

1. Control. Subjects were never exposed to ants (−/−).
2. Pre-maze exposure. Subjects were housed with ants for one week but not exposed to ant cues in the maze (+/−).
3. Maze exposure. Subjects were not housed with ants but exposed to ant cues in the maze (−/+).
4. Pre-maze and maze exposure. Subjects were housed with ants for one week and also exposed to ant cues in the maze (+/+).

3. Results

To determine whether patterns of turn alternation were consistent with what might be expected by chance, we calculated the expected probabilities for each outcome as follows: 0 alternations ($0.125 = 0.5^3$ for not alternating on any turn), 1 alternation ($0.375 = 3(0.5^3)$ for alternating once on either the 1st, 2nd or 3rd turn), 2 alternations ($0.375 = 3(0.5^3)$ for alternating twice on either the 1st and 2nd, 2nd and 3rd, or 1st and 3rd turns), or 3 alternations ($0.125 = 0.5^3$ for alternating on every turn). In both *P. laevis* and *A. vulgare*, the experimental treatment of maze-only ant exposure did not significantly differ from chance (Figs. 2 and 3; Chi-Square Goodness of Fit, d.f. = 3; *A. vulgare*, $X^2 = 5.02$, $p = 0.1703$; *P. laevis*, $X^2 = 3.42$, $p = 0.3313$). The *A. vulgare* control group also did not differ from chance when the Bonferroni correction was applied ($\alpha = 0.0085$, $X^2 = 8.76$, $p = 0.0327$). All other treatments, however, resulted in turn alternation patterns that significantly differed from chance expectations ($p < 0.0001$).

Pairwise comparisons for each treatment (Wilcoxon Two Sample Test with Bonferroni correction) revealed no significant

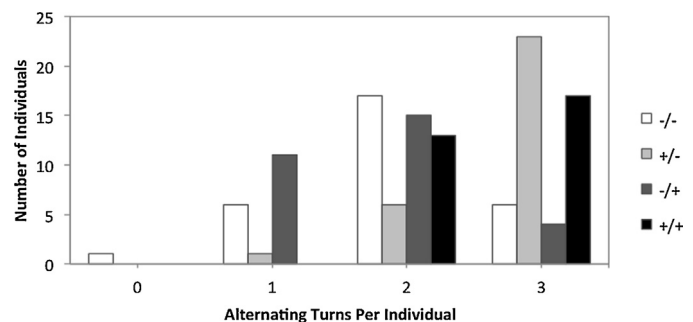


Fig. 2. Number of individuals exhibiting different numbers of turn alternations in *Armadillidium vulgare* never exposed to ants (−/−, $\bar{X} = 1.93$), housed with ants but not exposed to ant cues in the maze (+/−, $\bar{X} = 2.73$), not housed with ants but exposed to ant cues in the maze (−/+, $\bar{X} = 1.77$), and housed with and exposed to ant cues in the maze (+/+, $\bar{X} = 2.57$) during maze trials.

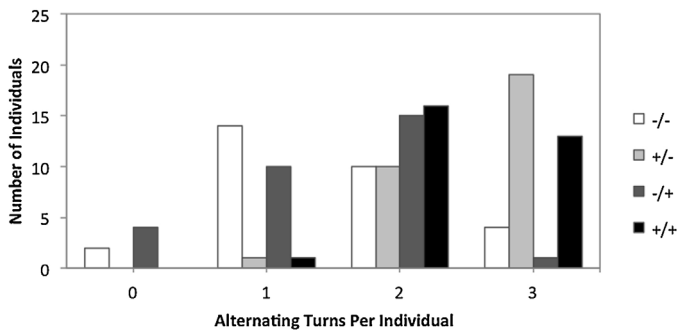


Fig. 3. Number of individuals exhibiting different numbers of turn alternations in *Porcellio laevis* never exposed to ants (-/-, $\bar{X} = 1.53$), housed with ants but not exposed to ant cues in the maze (+/-, $\bar{X} = 2.60$), not housed with ants but exposed to ant cues in the maze (-/+, $\bar{X} = 1.43$), and housed with and exposed to ant cues in the maze (+/+, $\bar{X} = 2.40$) during maze trials.

differences between *P. laevis* and *A. vulgare* in turn alternations for any treatment. There were, however, significant within-species differences between treatment groups (Figs. 2 and 3).

In *A. vulgare* (Fig. 2), analysis of variance indicated significant differences among experimental groups (ANOVA, $F(3, 116) = 17.42$, $p < 0.001$) in the number of alternating maze turns. *Post hoc* analysis with Bonferroni correction (Fig. 2, $p < 0.0085$) demonstrated that *A. vulgare* housed with ants prior to testing (+/- and ++) made significantly more turn alternations than those not housed with ants prior to testing (-/- and -/+). There were, however, no differences between *A. vulgare* exposed to ant cues in the maze (-/+ and ++) and those not exposed to ant cues in the maze (-/- and +/).

Likewise, in *P. laevis* (Fig. 3), analysis of variance indicated significant differences among groups (ANOVA, $F(3, 116) = 22.23$, $p < 0.001$) in the number of alternating maze turns. As with *A. vulgare*, *post hoc* analysis with Bonferroni correction revealed that *P. laevis* housed with ants prior to testing (+/- and ++) made significantly more turn alternations than those not housed with ants prior to testing (-/- and -/+). There were, however, no differences between *P. laevis* exposed to ant cues in the maze (-/+ and ++) and those not exposed to ant cues in the maze (-/- and +/).

4. Discussion

Upon detecting a predator, a prey animal can respond in diverse ways, from anticipatory to reactive behaviors (Cooper, 1998), passive behavior that minimizes the risk of attack, to an array of morphological, physiological, or life-historical defense mechanisms (Kavaliers and Choleris, 2001). Predation risk has evolutionary consequences for prey populations because predation can impact mating, reproduction, and number of offspring (Kats and Dill, 1998; Mappes et al., 1997).

Cues that predict predation risk may be indirect (Grostal and Dicke, 1999). For example, squirrels use patches differently when the environment has been experimentally altered with cues that are indirectly associated with predation risk (Thorson et al., 1998). Likewise, oldfield mice, *Peromyscus polionotus*, respond to indirect cues for predation risk by altering foraging behavior (Orrock et al., 2004). Indirect cues from predators can provide considerable contextual information. For example, juvenile field crickets avoid indirect cues from cricket-fed spiders but not from spiders that have not preyed upon crickets (Kortet and Hedrick, 2004).

The present study found that increases in turn alternation in *P. laevis* and *A. vulgare* are associated with chronic exposure to indirect predator cues, but that short-term recent exposure seems to have no effect. In fact, patterns of turn alternation when isopods were only briefly exposed to ant cues in the maze did not differ from chance expectation. These results are surprising in light

of earlier work that found isopods (*P. laevis* and *A. vulgare*) with previous exposure to predatory ants showed less aversive behavior in response to cues from *T. caespitum* (Castillo and Kight, 2005). Castillo and Kight (2005) found that when terrestrial isopods were placed in an arena containing indirect cues from ants (live ants behind a perforated barrier), individuals that had never been exposed to ants positioned themselves more distantly from the ants than those with previous experience with ant cues. The authors speculated that the previously exposed isopods had either habituated to ant cues, or that the unexposed isopods exhibited a novelty effect.

The results of the present study, however, had a seemingly opposite outcome. If we suppose that turn alternation is a form of aversive behavior, then isopods with previous ant experience showed no evidence of habituation, nor did isopods lacking previous ant experience exhibit a novelty effect upon encountering ant cues only in the maze. The present results, however, are consistent with an earlier study in which *P. laevis* exhibited an increase in turn alternation after prolonged pretest exposure to bright light (Hughes, 1967). In addition to a general photophobia in isopods, Hughes also suggested that the light source had created a drier, more adverse environment.

It may be that differences in positional behavior (Castillo and Kight, 2005) and turn alternation behavior in the present study are simply an artifact of differences in the design of the test arenas employed in the two studies. Castillo and Kight used an apparatus that forced isopods to move in a straight line relative to the source of predator cues. In that study, isopods were also housed in the arena for the entire study period. Hence positional behavior was measured after subjects had sufficient time to discover that there was no avenue of escape. In the present study, however, isopods were given a novel environment (the maze) to explore for escape opportunities *de novo* – an activity for which those isopods previously exposed to ant cues were perhaps more motivated.

In the present study, an alternative explanation for low turn alternations in isopods not exposed to chronic ant cues could be that they exhibited thigmotaxis, or wall-following behavior. If these subjects maintained unbroken contact with a wall while exploring the maze, this would increase the incidence of similar consecutive turn directions. We did not systematically record data on thigmotactic tendencies, but our anecdotal observations suggest that this was not the case. We did not observe any particular tendency for isopods in any treatment group to maintain contact with the walls of the maze, and individuals making three consecutive turns in the same direction were rare in all treatment groups.

Interestingly, and in contrast, Carbines et al. (1992) found an increase in *P. laevis* turn alternation when isopods were briefly exposed to a predatory spider (*Dysdera crocata*, Araneae: Dysderidae) prior to exploring the maze. In that study, however, the predator interacted directly with the experimental subject: trials commenced after a tethered spider made physical contact with the isopod. In comparison with the results of the present study, in which short-term exposure to ant cues in the maze did not result in increased turn alternation, it is difficult to determine whether isopods make more alternations in response to spiders than to ants, or if direct interaction with a predator is required to stimulate the effect.

Ramey et al. (2009) recently compared spontaneous alternation behavior in two species of crab, a native blue crab (*Callinectes sapidus*) and invasive green crab (*Carcinus maenas*) in North America. The invasive *C. maenas* exhibited significantly greater alternations than the native *C. sapidus*, suggesting that the behavior might improve foraging efficiency and contribute to the ecological competitive advantage the green crab presently has over the blue crab in North America. In a subsequent study (Balci et al., 2014), the authors demonstrated higher spontaneous alternation

in *C. maenas* than a second North American native species (fiddler crab, *Uca pugnax*). When tested in the presence of a predator, the invasive *C. maenas* reduced alternation performance, although the effect was not statistically significant. The authors speculated that low alternation behavior in *C. sapidus* might be due to high levels of risk-sensitivity. It is therefore possible that exposing the invasive *C. maenas* to a predator increased risk-sensitivity and consequently reduced turn alternations.

In the present study, however, there was a strikingly similar response of the two species to the experimental treatments (Figs. 2 and 3). We predicted that differences in antipredator behavior between the Armadillidiidae and the Porcellionidae would be associated with predator-mediated differences in turn alternation behavior in *A. vulgare* and *P. laevis*. That the two species did not differ from one another suggests that there might be evolutionary conservation in the neural architecture associated with navigation. Perhaps the neural mechanisms underlying isopod turn alternation are generic because the behavior is used in diverse environmental contexts (foraging, Tuck and Hassall, 2004; temperature and humidity, Hughes, 1967; disturbance, Houghtaling and Kight, 2006; predators, Carbines et al., 1992). Such diversity in the function of turn alternation could constrain evolutionary divergence of its use as an antipredator strategy in the two lineages.

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