

Phototaxis in the Terrestrial Isopod: A Mechanism for Investigating Invertebrate Learning and Memory

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Recommended Citation

Buzzelli, Christopher; Kent, Jessica; Pawlak, Chelsea; and Kaut, Kevin P. () "Phototaxis in the Terrestrial Isopod: A Mechanism for Investigating Invertebrate Learning and Memory," *Journal of Neuropsychology and Behavioral Processes*: Vol. 1, Article 1.

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Cover Page Footnote

Dr. Kevin P. Kaut (kpk@uakron.edu) is the corresponding author for this work. Research was conducted by Christopher Buzzelli with follow-up studies contributed by Jessica Kent and Chelsea Pawlak. All research sponsored by The Department of Psychology at the University of Akron.

Phototaxis in the Terrestrial Isopod: A Mechanism for Investigating Invertebrate Learning and Memory

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Abstract

Isopods readily explore new environments and typically prefer contexts with lower levels of illumination (i.e., negative phototaxis). In the first of two behavioral experiments reported here, the ability of isopods to discriminate between light and dark nesting regions was confirmed, although evidence suggests an initial 'instinctive' draw toward a darker context. Extending these findings to experiment 2, isopods were trained against their negatively phototactic tendency and had to exit a darkened start chamber in order to locate nesting material in a brighter chamber. Within-session improvements in latency to enter the nesting region were noted across training trials, coupled with evidence of somewhat better memory for the light-dark discrimination on probe tests taken immediately after training relative to probe tests taken over retention delays of 1-2 days, 5 days, and 12 days. Results are discussed within a Tinbergian ethological framework, and offer points of future integration of information processing perspectives with instinctive perspectives of behavior using an evolutionarily 'old' yet readily available species.

Key Words: Isopod, invertebrate, learning, memory, spatial navigation

**Journal of
Neuropsychology
and Behavioral
Processes:**

Volume 1

**Inaugural Edition:
Mentored Research**



Introduction

Considerable work in the comparative literature, both historically and in recent years, has documented the rather remarkable learning and memory capabilities of invertebrates. Within the broader context of invertebrate behavioral research, a more specific literature has explored the unique navigational skills of various species within their respective ecological niches. Such research, for example, has characterized the sensory cues used by ants (Narendra, Si, Sulikowski & Cheng, 2007), cockroaches (Mizunami, Weibrecht & Strausfeld, 1998), honeybees (Menzel & Giurfa, 2006), crabs (Dimant & Maldonado, 1992; Tomsic, de Astrada, Sztarker, & Maldonado, 2009) and crickets (Wessnitzer, Mangun, & Webb, 2008) to guide exploratory behavior. Indeed, such research has

demonstrated that select species are quite adept at using odors (e.g., moths, Kanzaki, 1996), visual signals and landmarks (e.g., honeybees, ants, crickets), light gradients (slugs), and even magnetic fields (marine isopods, Ugolini & Pezzani, 1995) as sources of information with which to guide search patterns. More recently, research with the African dung beetle has identified yet another unique stimulus—i.e., celestial light patterns—as an environmental feature that guides species navigation and survival (Dacke, Baird, Byrne, Scholtz, & Warrant, 2013). Moreover, the dung beetle work has stimulated further interest in the relationship between sensory and motor capabilities of invertebrates as they solve problems inherent in their ecological context.

From an evolutionary perspective, it is intriguing to consider not only the sensory and motor adaptations of invertebrates, but also the nature of memory mechanisms (i.e., hidden units)

as evolved biological components capable of storing information and later biasing, or otherwise altering sensory-motor organization and planning. Mechanisms of memory, including the identification of short-term (STM), intermediate-term (ITM), and long-term memory components (LTM), are well noted within the invertebrate literature (Bardou, Leprince, Chichery, Vaudry, & Agin, 2010; Maleszka, Helliwell, & Kucharski, 2000; Ye, Ye, & Wang, 2008). Identifying the observable manifestations of such memory characteristics, including STM and LTM is of scientific interest, inasmuch as this yields comparative models with which to further investigate the nature of memory. In addition, such research often provides a framework for studying the physiological basis of memory itself.

Amidst the many questions to consider regarding the sensory physiology and biochemical nature of invertebrate information processing, it remains of particular interest to ask how invertebrates learn about their environment, and what, if any strategies are employed to succeed in locating desired materials. Moreover, given the geological record of invertebrates in general, many having an ancestral history dating back hundreds of millions of years (e.g., Schram, 1970), invertebrates offer a modern day window into the earliest developmental origins of information processing systems. In this regard, it is of value to expand our investigations into invertebrate behavior and physiology, while extending avenues of research into somewhat lesser known niches in the animal kingdom.

An invertebrate of particular interest, and one that has received noticeably less attention than more commonly studied insects such as bees (Menzel & Giurfa, 2006), ants (Narendra et al., 2007), and worms or molluscs (Hopefield & Gelperin, 1989; Kasai, Watanabe, Kirino, & Matsuo, 2006; see also Kersten & Kaut, 2011) is the terrestrial crustacean—more specifically, the isopod. Commonly referred to as a ‘sowbug’, ‘pillbug’, ‘woodlice’, or ‘rolly polly’, the isopod is believed to have emerged approximately 300 million years ago (Schram, 1970), diverging from a marine ancestor, and adapting to diverse environmental conditions. The isopods of interest to the present work (e.g., *Armadillidium vulgare*, *Oniscus asellas*, *Porcellio scaber*) typically feed on decaying organic material and nest among materials within the upper soil regions (see Zidar, Hribar, Zizek, & Strus, 2012). Commonly found in areas of forestation, these isopods appear somewhat sedentary—at least during daylight

hours—although they readily navigate within local environments, and are quite mobile for purposes of spatial navigation research (Stottlemeyer & Kaut, 2011).

Isopod mobility, particularly their tendency toward environmental exploration and scavenging, has been of recent interest. At one level, this work has explored the unique sensory abilities of isopods, reflecting their sensitivity to stimuli such as light (Hassall, Zimmer, & Loureiro, 2005; Sutton, 1972 cited in Hughes, 1992), tactile cues (Moriyama & Takeda, 2007), environmental temperature (Schuler, Cooper, Storm, Sears, & Angilletta, 2011) and even chemical traces (Zidar et al., 2012). Additionally, and of particular relevance here, this work has provided behavioral evidence of the integrative abilities of the isopod nervous system, inasmuch as these organisms alter their behavior to move away from light (i.e., negative phototaxis), re-orient movement patterns when antenna sensitivity is compromised (Moriyama & Takeda, 2007), and avoid environmental toxins present in soil (e.g., pyrethrins, Zidar et al., 2012).

Amidst the growing understanding of sensory and motor abilities of the terrestrial isopod, Hassall, Zimmer and Loureiro (2005) previously identified a number of additional questions and potentially new directions for research involving this species. In particular, numerous behavioral issues remain to be investigated, including mechanisms of learning as they relate to migratory behavioral adaptations. For example, questions remain regarding the environmental cues used by isopods to locate sites for safety, food, and nesting. The adaptive ability of desert isopods (*Hemilepistus*) to orient by visual landmarks and return to a shelter site has been well established; however, questions remain regarding the ability of other terrestrial species to navigate similarly (Hassall et al., 2005). Adaptive behavior among invertebrates, not unlike many higher order species, is a function of ethologically relevant ‘key stimuli’ that trigger or otherwise activate programmed patterns of behavior (Petri, 1996). The present work seeks to characterize the sensory-motor integration skills used by isopods to navigate within an artificially contrived environment. Predicated on previous

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reports from this lab and elsewhere (Hughes, 1992; Stottlemeyer & Kaut, 2011), the current study is designed to replicate the pattern of negative phototaxis reported in the isopod, yet extend this finding by examining the process of acquisition for a light-dark discrimination task. A principal goal here is to better define how isopods use environmental cues to locate shelter (i.e., nesting material) while additionally considering the influence of memory—or characteristics of forgetting—that might impact navigational success in this species.

General Method

Overview

Isopods readily explore novel environments, and nest in materials associated with shelter (e.g., tree bark, decaying leaves). In the following experiments, isopods were trained to use brightness cues to locate nesting material. The pattern of negative phototaxis was specifically investigated, and behavioral evidence of acquisition across training trials and post-training retention was examined.

Materials

In Experiment 1 isopod phototaxis was explored through the use of a rectangular maze (31 cm L x 22 cm W) constructed of white and black opaque Plexiglas (see Figure 1A). A partition divided the north end of the chamber into two 'nesting' compartments (dimensions), one of which was constructed of black Plexiglas flooring and walls (i.e., darkened quadrant). Located in the corner of each nesting compartment was a cylindrical shelter/nesting region matching the quadrant color and containing two apertures through which isopods could enter to find nesting materials (e.g., decaying vegetation and organic material).

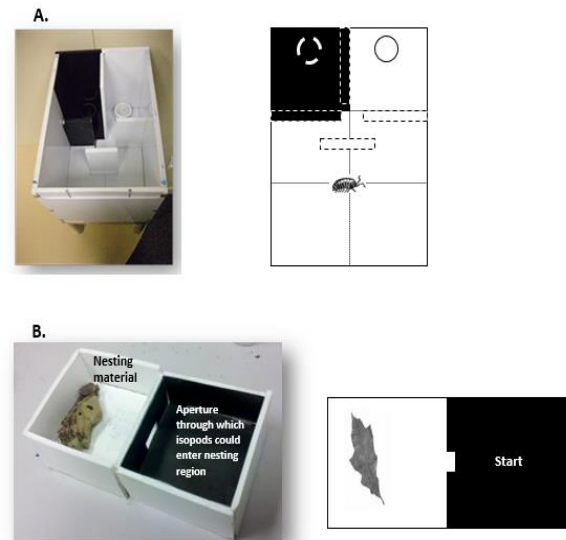
In Experiment 2 isopod nest finding was further examined through the use of a two compartment apparatus made of white foam board and black construction paper (22 cm L x 11 cm W, see Figure 1B); nesting materials were located on the brighter (light reflective) side of the apparatus. Isopods were trained to locate the nesting material through an aperture in the dividing partition, and behavioral patterns of acquisition and retention were investigated.

Subjects

Terrestrial isopods obtained from a local forestation region in Northeast Ohio were collected. Isopods are plentiful, easily obtainable,

and readily maintained in a typical terrarium containing dirt, vegetation, and other materials from the site of isopod collection. Room temperature (73° F) and moisture levels were monitored to insure isopod longevity in captivity.

Figure 1



Experimental Apparatus. 1A. Overview of navigation apparatus used in Experiment 1 (Left). Four walls (partitions) indicated by dashed outlines in the accompanying schematic (Right) were used to separate the dark and light chambers containing nesting regions (circles) in the first 10 days of Experiment 1. During the subsequent 5 days (i.e., Reversal days), the partitions were removed and the nesting sector was switched (e.g., light to dark, or dark to light). 1B. Two-choice chamber used in Experiment 2. Isopods were started in center of darkened half and could enter nesting side through an aperture in the partition. Nesting materials (e.g., dried leaves) were present in the light side of the apparatus.

Experiment 1

The ability of isopods to use intra-maze reflective light cues and locate a nesting region was examined. Nesting materials hidden within cylindrical shelter sites were associated with either the light or dark maze quadrant. Negative phototaxis was anticipated to facilitate nest-finding in the darkened maze quadrant and compromise performance when the nesting cylinder was located in the light quadrant.

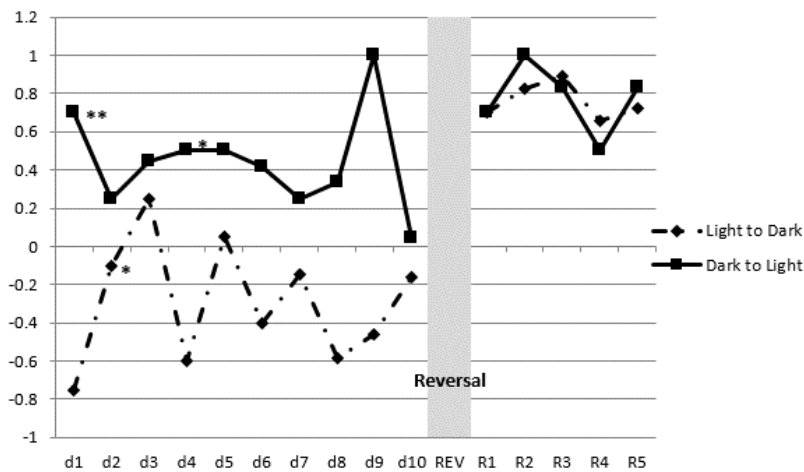
Procedures

Four groups of isopods (total $n = 20$; 5 isopods per group) were each trained on two versions of the nest-finding task in the rectangular maze (Figure 1A). The first version (i.e., nest located in the light vs dark quadrant) involved 10 days of training, and the second version, which involved a reversal of nesting quadrant (i.e., order of versions light \rightarrow dark, dark \rightarrow light counterbalanced across groups) was conducted over five days. During the second version, the dividing partition between nesting quadrants was removed along with the three other walls/barriers, thus creating an open maze with no obstructions.

Results and Discussion

The mean nesting quadrant preference scores for each group of isopods (Light vs Dark nesting groups) on maze Version 1 and 2 are illustrated in Figure 2. Quadrant preference scores (i.e., 'quadrant' here refers to one of the 6 divisions of the maze) were calculated at the end of each 5 minute segment according to the formula $(x - y) \div (x + y)$, where 'x' was the number of isopods located within the nesting quadrant (i.e., in quadrant or cylinder) and 'y' represented the number of isopods outside the target quadrant. For Version 1, a separate 2 (group) \times 4 (minute 5, 10, 15, 20) repeated measures ANOVA was conducted for each of the 10 training days. Figure 2 reflects the consistently enhanced

Figure 2



Nesting Region Preference scores. Preference index scores for the nesting region in the first 10 days of training (d1-d10). The Dark region was preferred by isopods in both groups, reflected by an improved preference index profile for isopods trained to locate the nest in the darker region. During the reversal sessions (R1-R5), barriers were removed and nest-finding was comparable between groups regardless of light or dark location.

On each training day, isopods were placed as a group in the southern portion of the maze to begin a 30 minute nest-finding trial. The shelter cylinder within the nesting quadrant contained apertures permitting access to nesting material, whereas the cylinder in the non-nesting quadrant had no such apertures (thus providing no access). At the end of each 5 minute segment isopod location was observed, and the number of isopods located in the nesting quadrant or within the nesting cylinder was recorded. At the conclusion of the 30 minute nest-finding trial, isopods located outside of the shelter cylinder were gradually probed to enter the cylinder.

performance for groups searching for the Dark nesting quadrant, with statistically significant main effects for group noted on day 1, $F(1, 2) = 168.20, p = .006$, day 2, $F(1, 2) = 49.00, p = .02$, and day 4, $F(1, 2) = 30.250, p = .032$, and approaching significance again on day 8, $F(1, 2) = 11.659, p = .076$. Based on the results of maze Version 1, it would appear that isopods discriminate between different intra-maze luminance levels, although negative phototaxis strongly influences this performance. As noted in Table 1, isopods were commonly found in the darkened quadrant (i.e., individual isopod location was recorded each minute across all 10 training days), with the percentage of isopods located in the correct nesting quadrant much enhanced for those in the Darkened condition (Mean = 49.39%, SD = 4.47) compared to those in the Light quadrant condition (Mean = 15.26%, SD = 3.3), $t(1.841) = 8.688, p = .017$. In support of negative phototaxis, it is noteworthy that even the isopods in the Light quadrant condition were strongly drawn toward the 'non-nesting' darkened quadrant (Mean = 33.92%, SD = .94), whereas isopods in the Dark quadrant condition were seldom found in the light nesting quadrant (Mean = 9.39%, SD = 1.25), $t(1.856) = 22.159, p = .003$. Overall, there was no difference between the Dark or Light nesting quadrant groups in the percentage of isopods found in the remaining four quadrants.

In maze Version 2, the nesting quadrant was reversed within groups and the barriers separating nesting regions were removed.

preferred in this species (i.e., ‘moist/humid, dark, and cooler locations’; Anselme, 2013 reporting on the work of Sutton, 1972), they nevertheless demonstrate the ability to associate light

Table 1

Percentage of Isopods Located in Each of the Six Maze Regions at One-Minute Intervals Across All Ten Training Days

| | Location of Nest | |
|--------------------------|------------------|---------------|
| | Light Quadrant | Dark Quadrant |
| Nesting Quadrant (1) | 15.26 (3.3) | 49.39 (4.47)* |
| Non-Nesting Quadrant (2) | 33.92 (0.94) | 9.39 (1.25)** |
| Quadrant 3 | 13.16 (0.93) | 12.11 (0.00) |
| Quadrant 4 | 13.73 (4.33) | 12.09 (2.62) |
| Quadrant 5 | 12.62 (2.06) | 7.52 (0.26) |
| Quadrant 6 | 11.30 (0.83) | 9.47 (0.36) |

Note: The above data reflects the percentage of isopods located in each of the maze quadrants at each minute of daily training—averaged across all 10 training days of Maze Version 1. Note: For those trained with the nest in the Light Quadrant, 33.92% of isopod location was recorded in the ‘non-nesting’ or darkened quadrant, whereas only 15.26% of the time isopods were located in the correct (Light) quadrant.

* $p < .05$
 ** $p < .01$

conditions with nesting material, and forage accordingly. In Experiment 2, we used a light-dark discrimination task, but specifically located nesting materials on the light half of the chamber—working against their negative phototactic tendency.

Procedure

Isopods (total $n = 15$) were placed individually in the center of the dark half of the chamber illustrated in Figure 1B. Each isopod received a series of 10 trials (i.e., approximately 3 minute intertrial interval), and the latency to enter the light side of the chamber and total amount of time in the light and dark halves was recorded for each trial. At the conclusion of each trial, isopods remained in the nesting material for an additional minute (sometimes guided back into the

Unobstructed access to the nesting regions appeared to facilitate performance in both groups. A separate 2 (group) x 4 (minute 5, 10, 15, 20) repeated measures ANOVA for each of the five days of reversal training failed to identify a significant difference between groups (p -values > .25). As reflected in Figure 2 (see reversal trials), mean preference index scores were uniformly above chance (i.e., 0.00), with both groups now performing comparably. Given this pattern, we can assume a good level of discrimination learning—even among isopods switched from the dark nesting quadrant in Version 1 to the light quadrant in Version 2. Indeed, it is suspected that in maze Version 1 isopods were typically drawn into the darker quadrant, and spent more time there (e.g., even groups with Light quadrant nests) due to reduced locomotion in the darkened space, or confined search activity within the walls limiting their escape from the darkened quadrant.

Experiment 2

Isopods demonstrate a proclivity toward negative phototaxis (see Sutton, 1972—as cited in Hughes, 1992), a finding supported in Experiment 1. Although darker environmental conditions are

nesting material).

For purposes of memory testing, isopods were assigned to one of four memory probe test delays: an immediate probe (i.e., one minute after a single session of 10 trials), and one of three long-term delays of either 1-2 days, 5 days, or 12 days. Only those isopods trained over three sessions (typically one 10-trial session per day) were assigned to a long-term probe condition. All probe tests were conducted without nesting material, consisting of two successive 2-minute trials. The first probe trial was started in the center of the apparatus dark half, with the second probe started from the center of the light half (i.e., former nesting region).

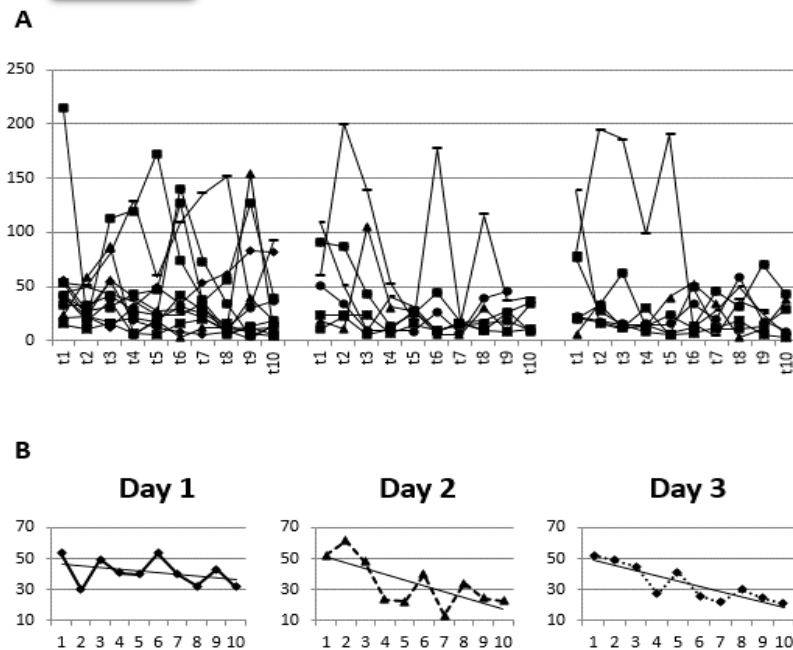
Results and Discussion

The latency of individual isopods to enter the nesting half of the chamber on each trial across training days is represented in Figure 3A, with overall mean latencies per trial illustrated in the separate panels in Figure 3B. Obviously, there is some variability in individual performance across trials (see 3A), although the general trend across isopods was to escape the dark chamber

and enter the light nesting half within 60 seconds (see 3B).

short of statistical significance, $t(5) = 1.077, p = .330$.

Figure 3



Latencies to locate nesting compartment in Experiment 2. 3A. Latency scores (in seconds) for all isopods across across the three training sessions (i.e., 10 trials per session, t1-t10). 3B. Mean latencies per trial for each training session (referred to as 'Day'). Note, for one isopod, sessions 2 and 3 occurred sequentially on Day 2.

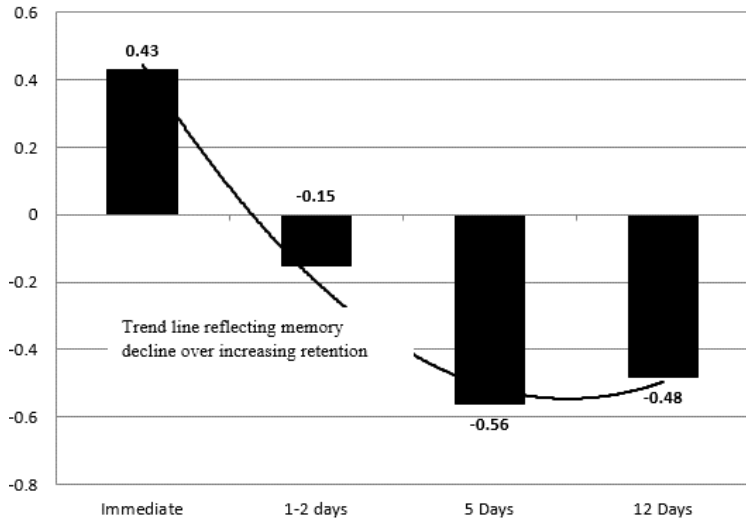
Two trends in this data are noteworthy with regard to learning and memory, and suggest areas for further investigation. First, there is evidence to suggest improved escape performance for isopods within each of the three training sessions—referred hereafter as 'days'. For example, the Day 1 linear trend toward improved escape latency between trial 1 ($M = 53.25, SD = 52.33$) and trial 10 ($M = 31.5, SD = 28.75$) suggests learning across trials, although not reaching statistical significance, $t(11) = 1.303, p = .219$. A quantitatively more marked within-session improvement was noted for the second session of training, with Day 2 escape latency for trial 10 ($M = 22.83, SD = 14.96$) better than the latency at trial 1 ($M = 52.33, SD = 40.96$), yet again failing to reach statistical significance, $t(5) = 1.711, p = .148$. On the third training session, a similar pattern of within-session improvement was noted, with Day 3 trial 10 performance ($M = 21.17, SD = 17.30$) quantitatively faster than the latency observed on the first trial ($M = 47.33, SD = 50.84$), but falling

These data suggest a benefit of massed practice *within* a given training session (see also Tomsic et al., 2009), and reflect the potential for this species to learn a rather novel discrimination task and benefit from experience accrued across trials. The second trend in this data, and of potentially greater interest, is the rather consistent pattern of 'forgetting' or performance decline between the end of one training session (i.e., trial 10) and the first trial of a subsequent session (see Figure 3B). Although the current statistical findings preclude more definitive statements regarding this pattern, it is noteworthy that isopods typically showed much slower (and rather uniform) escape latencies on the first trial of a new training session (i.e., averaged across Days 2 and 3, $M = 54.49, SD = 44.05$) relative to the last trial of the previous training session (i.e., averaged across Days 1 and 2, $M = 27.06, SD = 22.31$), suggesting an interesting pattern of retention failure *between* training sessions.

A more specific examination of temporal patterns of memory change involved the planned memory probe tests (i.e., Immediate, 1-2 days, 5 days, 12 days). On each probe trial, the amount of time spent in the dark and light halves of the experimental chamber was recorded and then converted into a preference index according to the formula $(x - y) \div (x + y)$, where 'x' was the amount of time spent in the nesting (light) half of the chamber, and 'y' was the amount of time spent in the dark half. As noted in Figure 4, preference index scores were numerically best at the Immediate retention probe ($M = .43, SD = .18$), with a noticeable decline at intervals of 1-2 days ($M = -.15, SD = .54$), 5 days ($M = -.62, SD = .39$), and 12 days ($M = -.48, SD = .35$), although a one-way ANOVA did not identify a significant difference among the retention intervals, $F(3, 4) = 2.894, p = .166$ (eta squared for memory probe \times group = .685). Nevertheless, it is noteworthy that immediate retention at the conclusion of ten training trials was superior to performance at the

longer term intervals, with memory scores generally worsening at these longer delays.

Figure 4



Probe test preference index scores at immediate and long-term delays. Positive preference index scores indicate greater preference for the nesting compartment. Note: Isopods in the Immediate testing condition (n = 2) received 10 training trials on Day 1 followed immediately by the retention probe tests. Isopods undergoing long-term retention probes (n = 2 per group), all received 3 sessions of training (i.e., 10 trials per session) followed by the respective retention probes.

General Discussion

Isopod behavior, most notably their active exploration of the environment, provides a unique opportunity to investigate learning and memory in this invertebrate species. Isopods readily adapt to novel environments, utilizing a variety of cues—particularly visual and tactile stimuli (e.g., Anselme, 2013; Hughes, 1992; Stottlemeyer & Kaut, 2011) to explore their surroundings. Given the instinctive nature of isopod behaviors, evident in their rather predictable locomotor activities and patterned responses to certain stimuli (i.e., ‘key stimuli’, such as light, edges, nesting material), the data reported here lends itself to interpretation within the ethological framework originally proposed by Tinbergen (as cited in Petri, 1996; see also Tinbergen, 2005). This hierarchical framework (see Figure 5) provides the structure for conceptually (and experimentally) addressing the relationship between instinctive influences and

information processing mechanisms impacting adaptive behavior.

The use of sensory cues to guide search strategies as part of an adaptive navigation system is an essential component in invertebrate survival behavior (Menzel & Guirfa, 2006). When placed in a novel experimental environment, such as the ones used here, isopods typically engage in appetitive search behaviors, characteristically showing thigmotactic behavior upon making contact with perimeter edges (refer to Figure 5). Antennae-guided locomotion appears to be a principal search routine in this species (see also Moriyama & Takeda, 2007). As noted in Experiment 1, isopods are also negatively phototactic, showing a preference for darker environments (i.e., approach behavior), a finding rather consistent with their tendency to nest among decaying materials and vegetative groundcover away from direct sunlight (Anselme, 2013). An ostensibly protective disposition that serves species survival within its environmental niche, this behavioral tendency can be modified through experience. Indeed, when barriers to exploration were removed, isopods initially trained to locate

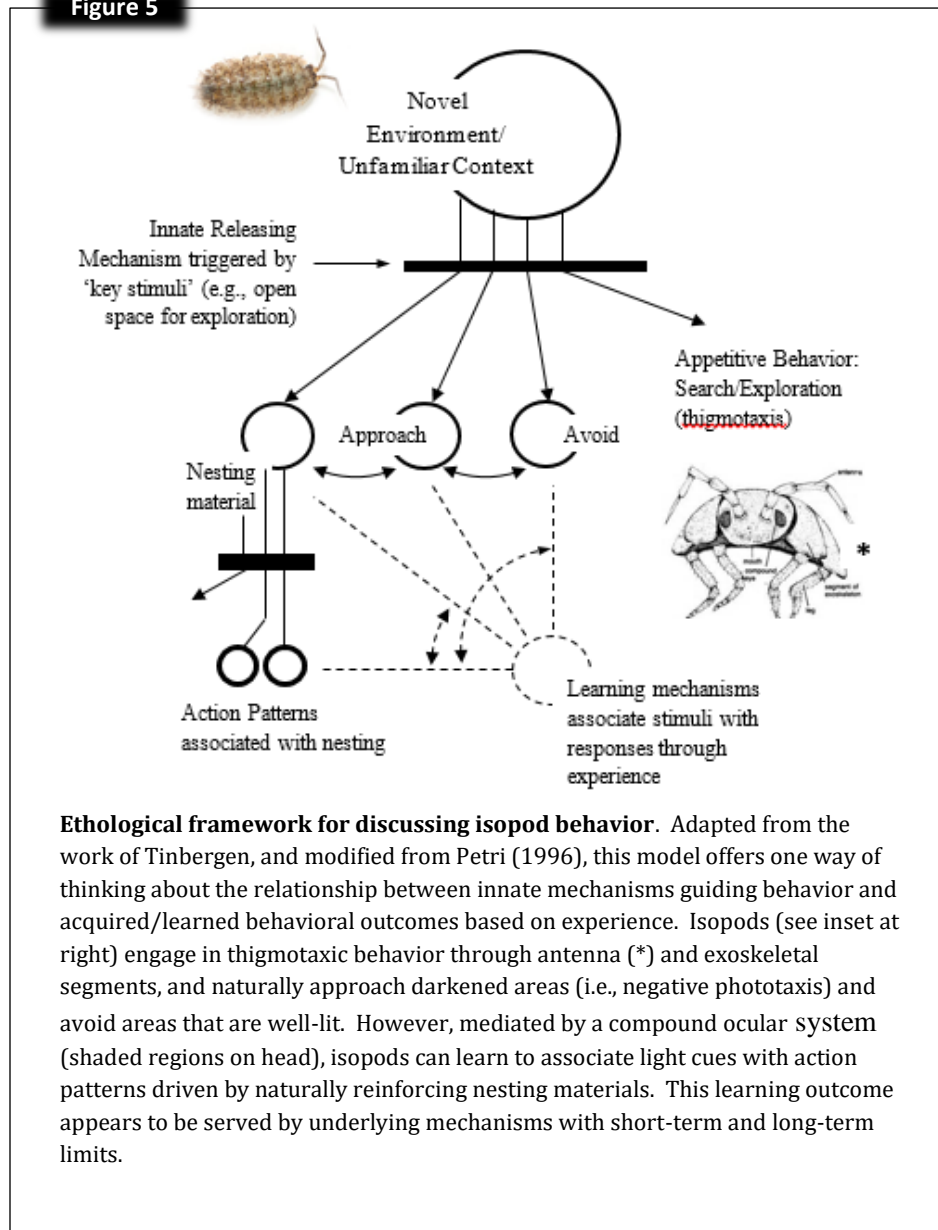
nesting material within the dark ‘quadrant’ (refer to Figure 2, pre-reversal) readily learned to associate the light quadrant with a new nesting location (see also Figure 2, post-reversal). Essentially, isopods learn to discriminate among brightness cues (Hughes, 1992), and associate innate ‘avoidance cues’ (i.e., key stimulus of light) with natural reinforcers even when working against their negative phototactic tendency.

In both of the experiments conducted here, exploratory behavior typically continued until reaching a nesting location, although periodic stopping/freezing, ‘cornering behavior’ (i.e., positioned ‘head’ first into a corner), or attempts at wall climbing were occasionally noted (cf. Anselme, 2013). Nevertheless, isopods rarely navigated away from nesting material once making contact. Customarily, the behavioral repertoire of these isopods was to enter the nesting material, take up position away from surface exposure, and eliminate/reduce movement. The nesting material used here (dried leaves, acorn husks, desiccated bark) ostensibly

served as an important key stimulus triggering the action patterns associated with nesting behavior.

corroborate other reports of massed practice effects in invertebrates (e.g., crabs, Tomsic et al., 2009), although this finding requires further

Figure 5



The reinforcement value of nesting material was of particular importance in Experiment 2, intended here as a means of identifying acquisition patterns within sessions in addition to assessing retention over various long-term intervals. The quantitative decrease in latency to reach the 'desirable' nesting chamber across the 10 trials within sessions (refer to Figure 3B) suggests a short-term or intermediate memory system operating across repeated trials and short intertrial intervals. These findings

investigation to better distinguish a memory-related interpretation from a purely activity-based, exploration-mediated account of within-session changes. Anselme (2013) argues that changes in intra-session performance—for example, habituation to repeated stimulus presentations—are best explained by an organism's adaptation to the environment, although learning and memory processes certainly influence adaptation (see his discussion, p. 58). It is our contention that much like the decreases in latency observed across repeated trials in certain rodent learning paradigms (e.g., water maze, Kaut & Bunsey, 2001; 2005), the negatively sloped trendlines within sessions (again, refer to Figure 3B) offer an intriguing starting point for future investigations of the behavioral and even physiological processes involved in short-term or intermediate term memory among

invertebrates (e.g., Ye et al., 2008). Indeed, the findings in Experiment 2 provide an initial perspective on long-term memory retention (and forgetting) in the isopod—further supporting Anselme's contention that elementary cognitive processes are present in woodlice (isopods). Given the ubiquitous nature of memory as an adaptive mechanism across a great diversity of species (see Alcock, 2009), the suggestion of immediate memory preservation relative to long-term memory decline (24-hour, 5-day, 12-day) is

of particular interest. Indeed, the quantitative evidence of a near monotonic decline in preference index scores across retention delays is a fortuitous finding in this species, thus encouraging subsequent plans to investigate the parameters and possible mechanisms associated with different memory components in this phylogenetically 'old' species (see Figure 5).

Variations on the navigation tasks used here and elsewhere (e.g., with ants, see Narendra et al., 2007) can be a useful way to further integrate ethological research with information processing perspectives among invertebrates. These 'simpler' organisms offer important advantages in terms of availability, housing, experimental methods/apparatus, and cost (see also Stottlemeyer & Kaut, 2011). Moreover, the isopod can be of value in further exploring species-environment interactions (Zidar et al., 2012) through a consideration of behavioral ecology questions (see Hassell et al., 2005) in the context of ethologically guided evolutionary framework (Tinbergen, 2005).

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