A Test of Temporal Variation in Risk and Food Stimuli on Behavioral Tradeoffs in the Rusty Crayfish, *Orconectes rusticus*: Risk Allocation and Stimulus Degradation

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Abstract

The effects of temporal variation in exposure to predation risk on behavioral tradeoffs were tested in the rusty crayfish, *Orconectes rusticus*. Based on the risk allocation hypothesis, we predicted that increasing the frequency of encounter with predation risk would yield increasing responses to a food stimulus in the presence of both a risk stimulus and a food stimulus. Crayfish were exposed to risk every 12 h, every 6 h, or left undisturbed for 24 h prior to testing. The risk stimuli used were a plain water control, snapping turtle (*Chelydra serpentina*) cue, and conspecific alarm cue. After 24 h of conditioning, the crayfish were exposed to a combination of risk cue and food cue. The behavioral responses of the crayfish were recorded for 5 min immediately following the introduction of the cues and again for 5 min, 1 h after stimulus exposure. The crayfish were observed at the two times to determine how their responses to the combination of risk and food cues changed over time. The responses of the crayfish were significantly influenced by stimulus treatment, time, and the interaction of time and stimulus treatment. Further analysis indicated that responses to the stimulus treatments changed differently over time. Immediately after exposure, the crayfish were more active in the control and snapping turtle treatments than in the conspecific alarm treatment. The high levels of activity initially observed in the control and snapping turtle treatments waned over time, such that the behaviors recorded 1 h after exposure were not significantly affected by stimulus treatment. Neither frequency nor the interactions of frequency with stimulus and/or time significantly affected crayfish behavior. The results of this study did not support the risk allocation model and contrast with results from similar work on the virile crayfish, *Orconectes virilis*.

Introduction

The conflicting demands of resource acquisition and predation avoidance often require behavioral tradeoffs by prey animals. That is, the animal may pursue a resource stimulus in spite of the presence of a risk stimulus, forego pursuit of the resource in favor of an antipredator response, or exhibit a response intermediate between the responses elicited by either stimulus when encountered on its own. The particular tradeoff made can be influenced by a number of intrinsic and extrinsic factors, such as hunger (Horat & Semlitsch 1994; Hazlett 2003) and resource availability (Hazlett & Rittschof 2000; Martín et al. 2003). Temporal variation in encounters with risk is a potentially important influence on behavioral tradeoffs that has received much recent attention (Lima & Bednekoff 1999; Rohr et al. 2003; Bednekoff & Lima

2004). Temporal variation includes both differences in the recent history of a prey animal with risk stimuli and changes in the intensity of a risk stimulus during a given encounter.

The role that the recent history of encounters with predation risk plays in behavioral tradeoffs was addressed by Lima & Bednekoff (1999). They modeled the influence that variation in the time spent in the presence of predation risk should have on foraging behavior. Their model, the risk allocation hypothesis (RAH), predicted that a prey animal would attempt to satisfy its metabolic needs by foraging during periods of safety, but as the time spent in the presence of risk increased, the animal would be forced to allocate increasing amounts of time to pursuit of food resources during periods of risk exposure. Such a strategy would help to explain why animals are often observed to cease or greatly reduce foraging behaviors in the presence of risk stimuli (Chivers & Smith 1998; Kats & Dill 1998). Experimental designs frequently isolate the test animals for an extended period of time in a risk-free environment, after which the subject is exposed to a single 'pulse' of risk, along with a food stimulus (Sih et al. 2000). The recent history with risk in such a design is that periods of safety are lengthy and periods of risk are relatively brief. Assuming that the prey animal has some sense of the safety-to-risk ratio, a strong antipredator response during brief exposure to risk is predicted by the risk allocation model (Lima & Bednekoff 1999).

The RAH has been tested in several systems, but the influence that prior experience with risk has on behavioral tradeoffs is far from resolved. Snails increased foraging in the presence of risk as exposure to risk increased, but they did not exhibit a corresponding increase in foraging during periods of safety (Hamilton & Heithaus 2001). In another study, snails increased foraging during periods of safety as exposure to risk increased, but they did not respond to pulses of risk (Sih & McCarthy 2002). A test with tadpoles revealed no support for the predictions of the RAH (Van Buskirk et al. 2002). Likewise, no support for the RAH was found in a field test with voles (Sundell et al. 2004). In a test of risk allocation with the virile crayfish (*Orconectes virilis*), we found that a recent history of encounters with risk, either snapping turtle cue or conspecific alarm cue, caused the crayfish to pursue a food cue in the presence of predation risk to the exclusion of much antipredator behavior (Pecor & Hazlett 2003). This result contrasted with the findings of Hazlett (1999), who tested the responses of *O. virilis* to a food cue in the presence of control, snapping turtle, or conspecific alarm cues in a study that did not consider risk allocation.

In addition to recent history with risk, a change in the intensity of a risk cue over time could be an important factor to consider in assessing the tradeoff between resource acquisition and predation avoidance. Rohr et al. (2003) proposed that disregard for differential degradation rates between resource and risk cues could lead to a misestimation of the responses to multiple stimuli. If the risk cue degrades in the environment faster than the resource cue or vice versa, then recording only the initial response to a combination of resource and risk cues paints an incomplete picture of the tradeoff.

We report here tests of the following hypotheses: (1) Increasing the time spent in the presence of predation risk yields increases in the time spent in pursuit of food resources when both risk and food stimuli are encountered by prey animals. (2) The effect that increasing risk exposure has on behavioral tradeoffs depends on the origin of the risk stimulus. In some systems, the responses to predator stimuli and conspecific alarm stimuli suggest that alarm stimulus is a more dangerous cue (e.g. Hazlett 1999). We predicted that a more dangerous stimulus would require more exposure before the tradeoff is made in favor of increased pursuit of a resource stimulus over an antipredator response. (3) Recording only the behaviors exhibited immediately following stimulus exposure produces an incomplete assessment of the behavioral tradeoff.

We tested these hypotheses using rusty crayfish (*Orconectes rusticus*) and snapping turtles (*Chelydra serpentina*) as a model system. No study equivalent to Hazlett's (1999) work with the virile crayfish exists for the rusty crayfish, but we expected that snapping turtle would elicit an antipredator response, intermediate between the responses elicited by a control and conspecific alarm cue. In a study with rusty crayfish from a commercial supplier, Hazlett & Schoolmaster (1998) found that the crayfish exhibited mild antipredator responses to snapping turtle cue once it had been paired with conspecific alarm cue. Although associative learning was needed in that study, we expected the snapping turtle cue to elicit a mild predation risk response without association in the laboratory in the present study. The crayfish we used were collected from a body of water with snapping turtles, and we assumed that they had the opportunity to make the association between a turtle cue and predation risk.

The rusty crayfish-snapping turtle system allowed a comparison to be made between native and

invasive animals. We previously tested the RAH in the virile crayfish using both snapping turtle and conspecific alarm stimuli (Pecor & Hazlett 2003). The virile crayfish used in that study and the rusty crayfish used in the present study were all collected in Michigan, where the virile crayfish is native and the rusty crayfish is a recent invader (Hobbs & Jass 1988). Previous work has determined that, relative to native species, introduced crayfish respond to a wider range of risk cues (Hazlett 2000), retain associations between paired cues longer (Hazlett et al. 2002), and are less motivated by hunger to forage in the presence of predation risk (Hazlett 2003). Contrasting the responses of these two species adds to our understanding of the use of chemical signals by native and introduced crayfishes.

Methods

Collection and Maintenance of Animals

Crayfish, *O. rusticus*, were collected from the Maple Bay area of Burt Lake in Cheboygan County, MI, USA (45°29′N, 84°41′W). Following capture, individuals were maintained in a flow-through holding tank at the University of Michigan Biological Station (UMBS) in Pellston, MI, USA. The water feeding the tank was pumped from Douglas Lake, which is adjacent to UMBS. Crayfish were provided AquaMax™ fish chow daily and offered this food a minimum of three times before they were considered for inclusion in the experiment. Only male crayfish, both Form I and II (Payne 1996), were used in tests and in the preparation of alarm cue, and only males with all sensory appendages intact were used as test subjects. The crayfish used in the study had a mean carapace length of 4.6 ± 0.03 cm. Two snapping turtles, *C. serpentina*, of medium size (carapace length = 20 and 28 cm) were used as predator models. One was collected from Maple Bay, and the other was collected from the Maple River (Emmet County, MI, USA), which empties into Maple Bay. The turtles were kept separately in large aquaria within the laboratory and offered sardines weekly. All protocols for the turtles were approved by the University of Michigan committee on the use and care of animals as part of application no. 8102.

Experimental Design

To test for the existence of risk allocation, a factorial ANOVA design (Zar 1999) was used, with three frequencies of risk exposure and three risk stimuli. The risk exposure schemes were designated as follows. The control treatment was a lack of exposure to a risk stimulus during the 24 h period prior to observation. Low-frequency was exposure to a risk stimulus every 12 h during the 24 h period preceding observation, and high-frequency was exposure to every 6 h during that period. The risk stimuli used were control cue, snapping turtle cue, and conspecific alarm cue. Control cue was Douglas Lake water. Turtle cue was produced by allowing a snapping turtle to condition a 57 l aquarium filled with a volume of Douglas Lake water in liters equal to 1.25 times the length of the carapace of the shell (e.g. a turtle with a carapace length of 24 cm would be placed in 30 l of water). The turtle was moved to the conditioning tank 48 h before the final water sample was needed. The turtle was starved for at least 5 d before the cue was to be generated in order to allow all gut contents to pass (Parmenter 1981). Conspecific alarm cue was prepared by macerating a single crayfish in a volume of Douglas Lake water in milliliters equal to 20 times the mass of the crayfish in grams, e.g. a 15 g crayfish would be macerated in 300 ml of water (Pecor & Hazlett 2003). The resulting solution was filtered, and the filtrate was used as the alarm cue. Ten replicates of each risk-by-frequency treatment were conducted (n = 90). Observations were made between 9:00 and 12:00 hours, and trials were conducted during July and August 2004.

Experimental Protocol

Crayfish to be tested were placed singly in 38 l aquaria. The relatively static environment of an aquarium was chosen, because the crayfish were collected from a relatively static body of water. Brown paper was wrapped around three sides of each aquarium to visually isolate the crayfish from one another. Each aquarium was outfitted with half of a clay pot for use as a shelter and, an air stone and was filled with 12 l of Douglas Lake water. Crayfish were allowed 19 h to acclimate to the experimental aquaria. Acclimation was followed by a 24-h conditioning period. Animals in the low- and high-frequency treatments were exposed to 20 ml of a stimulus solution at 12- and 6-h intervals, respectively, during the conditioning period. Cues were introduced via a syringe and pipette (Pecor & Hazlett 2003). In the control treatment, crayfish were not disturbed during the conditioning period. After 43 h in the test aquaria, the crayfish in all treatments were exposed to 40 ml of a stimulus solution. The control solution was 20 ml of Douglas Lake water plus 20 ml of food

cue. The food cue was prepared by combining 6 g of ground fish chow with 245 ml of Douglas Lake water. The solution was stirred and allowed to set for 5 min before filtration. The filtrate was used as the food cue. The turtle solution was a pairing of 20 ml of turtle cue and 20 ml of food cue. The alarm solution was a pairing of 20 ml of conspecific alarm cue and 20 ml of food cue. For each solution, the two cues were injected sequentially using 20 ml syringes, and the non-food cue was injected first. The cues were allowed 30 s to diffuse throughout the aquarium before the start of observation (Hazlett 1999). Crayfish were observed for 5 min following the final stimulus introduction and for an additional 5 min after 1 h. The observation at 1 h post-exposure allowed for an assessment of whether responses to the stimuli changed over time. A change could result from the decay of chemical cues and/or sensory acclimation of the test animals. Our experiment did not permit discrimination between these two phenomena, rather, it was designed to assess the validity of the assertion that responses can vary depending upon the time of observation following risk exposure.

Behavioral Responses and Data Analysis

A suite of behaviors in response to chemical stimulation has been shown to be consistent across many experiments with the rusty crayfish and other species within the genus *Orconectes* (Hazlett 1985, 1994, 1999, 2003; Hazlett & Schoolmaster 1998; Pecor & Hazlett 2003). A lowered posture was defined as the presence of the chelipeds on the substrate. A lowered posture is associated with antipredator behavior, as is use of a shelter. Non-ambulatory motion was considered any behavior that involved movement without locomotion (e.g. movement of the chelipeds). Locomotion was defined as ambulatory motion within the aquarium. In previous work with crayfish, stimulation with a resource cue, such as food cue, caused the animals to spend time near the pipette through which the stimulus was introduced into the aquarium (K. W. Pecor, personal observations). Thus, we also recorded the time spent within approx. 2 cm of the stimulus pipette. Relative to a stimulus pursuit response, an antipredator response would include increased time spent in a lowered posture and within a shelter and decreased time spent in non-ambulatory motion, locomotion, and in close proximity to the stimulus pipette. It was possible, at any given time, for a crayfish to exhibit none of the behaviors of interest or to exhibit multiple behaviors. The duration of each of these five behaviors was recorded in seconds using an event program on a laptop computer.

The behaviors were considered statistically as a suite of response variables and analyzed with multivariate analysis of variance (MANOVA), which was appropriate for two reasons. First, individual ANOVA analyses inflate the probability of type I error (Zar 1999; Scheiner 2001). Second, the relationships among the response variables have not been formally assessed, but casual observation suggests that the responses are correlated. For instance, crayfish within the shelter tend to assume a lowered posture. Separate ANOVA analyses would not take into account the interrelations of response variables (Zar 1999). A doubly-multivariate test (von Ende 2001) was used to assess the effects of both the between-subject factors (stimulus and frequency) and the within-subject factor (observation time). A doubly-multivariate test has three components (SAS Institute Inc. 1989). First, the between-subject factors are analyzed using composite responses that are a summation of the responses across time. For example, the shelter use in the first observation would be added to the shelter use in the second observation, and the sum would be used in the analysis. Second, the effect of time was assessed by testing the intercept effect using the differences between responses (e.g. shelter use in the second observation would be subtracted from the shelter use in the first observation). Third, the interaction of time and the between-subject factors was assessed by repeating the first analysis using the differences between responses. Pillai's Trace was selected as the multivariate statistic, because it is more robust than the other multivariate roots (Scheiner 2001) and the best root for general use (Zar 1999). All statistical calculations were made using SAS v8.2.

Results

The responses of the crayfish were significantly affected by stimulus (Pillai's Trace = 0.46, $F_{10,156}$ = 4.62, $p < 0.0001$; Fig. 1). Frequency of exposure to risk did not have a significant effect on crayfish behavior (Pillai's Trace = 0.10, $F_{10,156} = 0.85$, $p = 0.58$; Fig. 2), nor did the interaction of stimulus and frequency (Pillai's Trace = 0.20, $F_{20,320} = 0.83$, $p = 0.67$). Time was a significant effect (Pillai's Trace = 0.59, $F_{5,77} = 22.18$, $p < 0.0001$), indicating that responses changed between the two observation times. Most importantly, there was an interaction between time and stimulus treatment (Pillai's

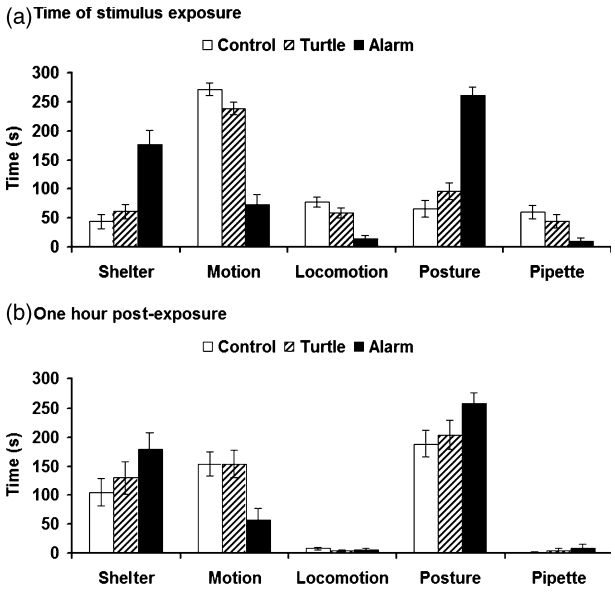

Fig. 1: Responses by the crayfish to the three stimulus treatments (a) at the time of stimulus exposure and (b) 1 h after stimulus exposure. The MANOVA for between-subject treatments used a summation of the responses between the two observations, whereas the MANOVA for within-subject treatments (i.e. time * stimulus) used the differences between the observations. Shelter: time spent within the clay pot shelter. Motion: time spent in non-ambulatory motion. Locomotion: time spent in ambulatory motion. Posture: time spent in the lowered posture. Pipette: time spent within approx. 2 cm of the pipette used for stimulus introduction. Bars represent mean responses ± SE

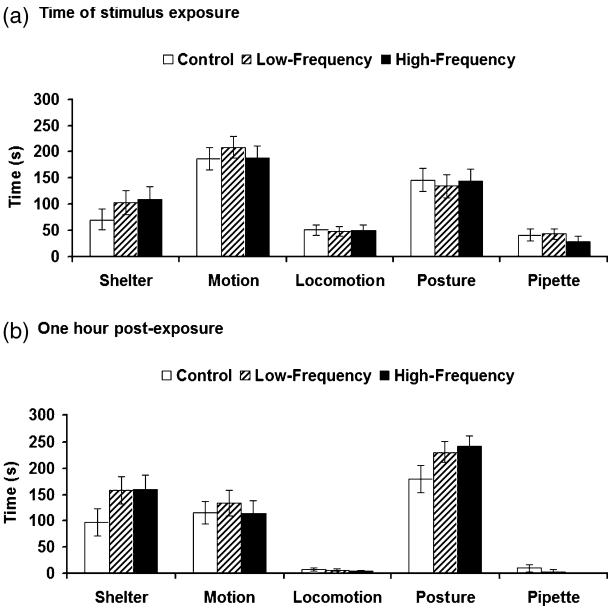

Fig. 2: Responses by the crayfish to the three frequency treatments (a) at the time of stimulus exposure and (b) 1 h after stimulus exposure. The MANOVA for between-subject treatments used a summation of the responses between the two observations, whereas the MANOVA for within-subject treatments (i.e. time * frequency) used the differences between the observations. Shelter: time spent within the clay pot shelter. Motion: time spent in non-ambulatory motion. Locomotion: time spent in ambulatory motion. Posture: time spent in the lowered posture. Pipette: time spent within approx. 2 cm of the pipette used for stimulus introduction. Bars represent mean responses ± SE

Trace = 0.40, $F_{10,156}$ = 3.91, $p < 0.0001$), indicating that the responses of the crayfish over time were dependent upon the stimulus treatment that they experienced. No significant interaction was found between time and frequency (Pillai's Trace = 0.14, $F_{10,156}$ = 1.18, $p = 0.31$), nor was the time * stimulus * frequency interaction significant (Pillai's Trace = 0.34, $F_{20,320}$ = 1.50, $p = 0.08$).

Based upon the significant interaction between stimulus treatment and time, we performed further tests to determine how the effects of cue and time were interacting. We analyzed the responses to the three stimulus treatments within each observation time and the responses to each stimulus between the two observation times. For such analyses, an adjustment is recommended to account for the increased risk of type I error associated with multiple comparisons (Quinn & Keough 2002). We adjusted the α level to 0.01 using a Bonferroni procedure.

The responses of the crayfish at the time of stimulus introduction were significantly influenced by stimulus treatment (Pillai's Trace = 0.58, $F_{10,168}$ = 6.90, $p < 0.0001$; Fig. 1a). To discern which treatments differed from one another, multivariate, pairwise contrasts were used. Multivariate post hoc tests are not shielded from the increased risk of type I error associated with multiple comparisons (Scheiner 2001), so we recalculated the critical value of the F-statistic to be F_{crit} = 1.61 using the procedure described by Harris (1985) and Scheiner (2001, equation 6.2). Alarm stimulus elicited responses that were significantly different from both the control stimulus (Pillai's Trace = 0.54, $F_{5,83}$ = 19.12, $p < 0.05$) and the turtle stimulus (Pillai's Trace = 0.45, $F_{5,83}$ = 13.59, $p < 0.05$). Control stimulus and turtle stimulus did not differ in the responses that they elicited (Pillai's Trace = 0.04, $F_{5,83}$ = 0.67, $p > 0.05$). The responses of the crayfish at 1 h post-exposure were not significantly affected by stimulus treatment (Pillai's Trace = 0.24, $F_{10,168}$ = 2.27, $p = 0.02$; Fig. 1b).

The responses to the control stimulus changed significantly between observation times (Pillai's Trace = 0.58, $F_{5,54}$ = 14.95, $p < 0.0001$; Fig. 3a). Responses to the turtle treatment also differed significantly between observation times (Pillai's

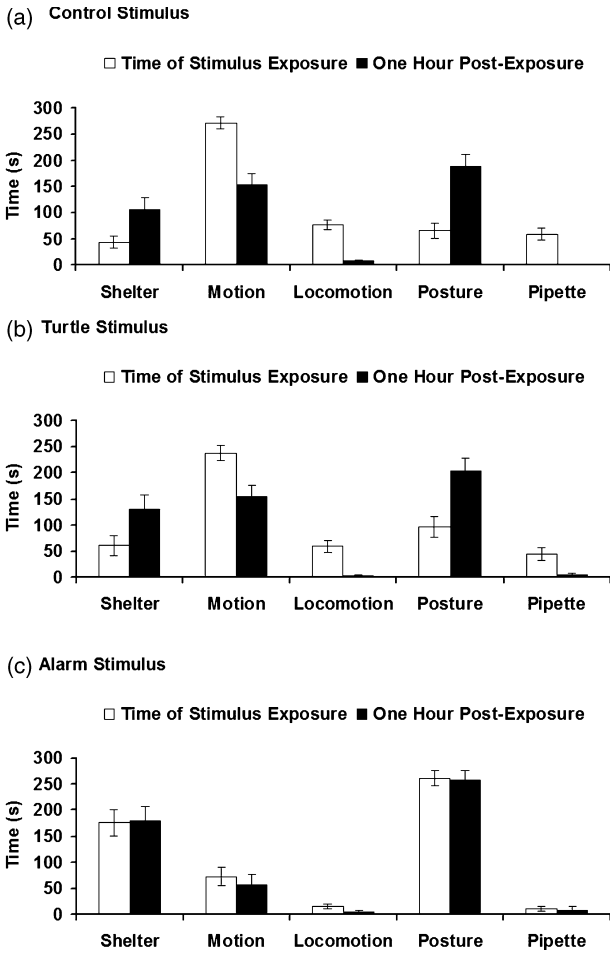

Fig. 3: Responses by the crayfish to the (a) control, (b) snapping turtle and (c) conspecific alarm stimulus treatments between observation times. Shelter: time spent within the clay pot shelter. Motion: time spent in non-ambulatory motion. Locomotion: time spent in ambulatory motion. Posture: time spent in the lowered posture. Pipette: time spent within approx. 2 cm of the stimulus pipette. Bars represent mean responses ± SE

Trace = 0.31, $F_{5,54} = 4.91$, $p = 0.0009$; Fig. 3b). Responses to alarm stimulus between observation times were not significant (Pillai's Trace = 0.18, $F_{5,54} = 2.44$, $p = 0.05$; Fig. 3c).

Discussion

The rusty crayfish did not respond to the snapping turtle cue as a predation risk stimulus, and their responses to conspecific alarm cue were not dependent upon the frequency with which it was encountered during the conditioning period. The latter result fails to support the predictions of the risk allocation model. If the RAH was supported, we would have seen significantly less antipredator behavior in the alarm cue treatment at a frequency of 12- and/or 6-h exposures than in the control frequency treatment. That is, there would have been a significant interaction between the stimulus and frequency treatments.

Our results contrast with findings from earlier work with the virile crayfish. Our stimulus treatments were similar to those used by Hazlett (1999) and Pecor & Hazlett (2003). Our control frequency treatment mirrored the protocol used by Hazlett (1999), in that it did not include prior exposure to risk. Our low- and high-frequency treatments were identical to those used by Pecor & Hazlett (2003). In those studies, virile crayfish both responded to snapping turtle cue as a risk stimulus and exhibited risk allocation. Virile crayfish exhibited less antipredator behavior and were more active in the food + turtle and food + alarm treatments when pre-exposure to risk cues was considered, whereas rusty crayfish were not affected in this way.

The different effects of frequent exposure to risk stimuli on these two species could be a result of their responses to starvation and/or sensory acclimation. The risk allocation model is based in part upon the assumption that the animal under consideration must meet an energetic requirement during the time of interest (Lima & Bednekoff 1999). Previous work suggests that the metabolic needs of rusty crayfish are less than those of the virile crayfish, and/or they do not respond to their metabolic needs in the presence of a single pulse of predation risk after as much as 10 d without food (Hazlett 2003). The protocol used by Hazlett (2003) was very different than the one used here, but his work suggests that our present study with a 48-h period of starvation may not have included the focal period during which the rusty crayfish needed to satisfy its energetic needs. We chose our protocol to allow for a direct comparison with the virile crayfish, but a test of the RAH with the rusty crayfish that includes a longer starvation period might support Lima & Bednekoff's (1999) model.

An alternative explanation is that increased foraging in the presence of predation risk after recent exposure to risk is a result of sensory acclimation. If the crayfish spend extensive time in the presence of chemical cues representing predation risk and do not receive additional inputs (visual, tactile, etc.), they may cease responding to the risk stimulus, as in the work with the virile crayfish (Pecor & Hazlett 2003). Previous work with the rusty crayfish suggests that its chemical ecology, in general, is much more sophisticated than is that of the virile crayfish

(Hazlett 2000; Hazlett et al. 2002). Sophistication may include a stronger resistance to sensory acclimation. This explanation is consistent with the combined results of work on risk allocation with these two species and deserves empirical consideration.

Given the generally sophisticated chemical ecology of the rusty crayfish, an unexpected result was the lack of a response to the snapping turtle cue. Snapping turtles are predators of crayfish (Ernst et al. 1994), and informal tests with one of the turtles used as a predator model suggested no aversion to the rusty crayfish by snapping turtles. (The second turtle was released before a feeding test was conducted.) Snapping turtles are present in the waters from which the crayfish were collected, and one of the two turtles used was collected in the same bay as the crayfish. The rusty crayfish is an introduced species in Michigan, but the snapping turtle is not a novel predator for Michigan populations. Snapping turtles are widespread in North America, including the southern Ohio River Valley (Ernst et al. 1994), which is the native range of the rusty crayfish. The lack of any antipredator response is an unintuitive strategy for a dangerous predator such as the snapping turtle and indicates that there are some scenarios in which the rusty crayfish is not as sensitive to chemical signals as its congeners.

We found mixed support for the hypothesis that estimation of the resource pursuit-risk avoidance tradeoff would be dependent upon observation time. The responses to the food and turtle stimulus treatments changed significantly between the two observation periods (Fig. 3a, b), whereas the responses to the alarm treatment did not change over time (Fig. 3c). The similar behaviors exhibited across risk treatments at 1 h after stimulus exposure (Fig. 1b) suggest that the animals in the control and turtle treatments were no longer responding to the food cue. The crayfish may have discovered the lack of a food substance accompanying the chemical cue, and/or the food cue used here may have a high rate of decomposition. The alarm cue is known to retain its effect for approximately 6 h (Hazlett 2003). Thus, it is not surprising that the crayfish in the alarm treatment did not change their behaviors during the observation periods, especially if the rusty crayfish is resistant to sensory acclimation.

This study adds to a growing empirical literature on temporal variation in risk, especially risk allocation (Hamilton & Heithaus 2001; Sih & McCarthy 2002; Van Buskirk et al. 2002; Pecor & Hazlett 2003; Sundell et al. 2004). The mixed results obtained thus far in empirical tests suggest that temporal variation in risk is an important consideration for studies of behaviors under predation risk. The results also indicate that the risk allocation model is sensitive to deviations from its parameters. For instance, the inability of voles to perceive changes in the level of predation risk that they experience likely led to a lack of support for the RAH (Sundell et al. 2004). Similarly, the rusty crayfish studied here may not have needed to forage during the time in which they were observed, leading to the negative result. The differences in degradation rates between risk and resource stimuli, and the influence of those differences on behavioral tradeoffs has received less attention than risk allocation, but the results obtained here suggest that this aspect of behavioral ecology deserves continued consideration.

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