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Effects of Experience and Body Size on Refuge Choice in the Crayfish *Orconectes immunis*

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ABSTRACT

We investigated whether refuge size or experience with a refuge affected the refuge use of male *Orconectes immunis* crayfish. Individuals were given choices among seven refuges for 10 consecutive days. Refuges were formed from equal length but different diameter PVC pipe and placed in an array in a random sequence. Three treatments were used. In the Novel Refuge treatment, individuals were placed in a new test arena with a new arrangement of cleaned refuges every day. In the Nonremoval treatment, individuals were left in the same arena with the same set of refuges each day. In the Removal treatment, individuals were removed from the refuges each day but placed back in the same arena with the same set of refuges after the refuges had been cleaned. We found that refuge occupation was correlated with an individual's size; smaller crayfish tended to use smaller refuges than larger crayfish, even though all crayfish could fit in all of the different sized refuges. When first tested, individuals initially chose larger refuges than they would subsequently settle in, suggesting that under duress, they were not as particular about refuge characteristics. Individuals in the Nonremoval and Removal treatments were significantly more consistent in their refuge use than those in the Novel Refuge treatment, suggesting that experience with a particular refuge increased use of that refuge. Individuals from the Novel Refuge treatment that were housed for a month with a single refuge did not increase their use of that sized refuge more than those that were housed without a refuge, indicating that simply occupying a refuge of a given size did not affect refuge preference.

INTRODUCTION

A wide variety of invertebrate and vertebrate animals use refuges to decrease their exposure to predators and/or unfavorable environmental conditions. Refuge availability potentially can determine levels of competition among individuals, affect population size and structure, and influence animal communities (Capelli and Hamilton 1984, Hill and Lodge 1994, Walters and Wethey 1996, Arsenault and Himmelman 1998, Gali-Muhtasib 1998). For instance, Beck (1995, 1997) showed that differences in the availability of suitably sized refuges could create a "demographic bottleneck" and thus influence the body size structure, and potentially the population size, of stone crabs (*Menippe mercenaria*). Also, Navarrete and Castilla (1990) found that the spatial distribution of two crab species (*Acanthocyclus gayi* and *A. hassleri*) appeared to be the result of *A. hassleri* aggressively excluding *A. gayi* from available refuges. Additionally, for species such as crayfish that are reared in captivity (e.g., for aquaculture), presence of appropriate refuges reduces aggression and cannibalism (Mason 1979, Capellia and Hamilton 1984, Alberstadt et al. 1995, Steele et al. 1997).

Individuals are often selective about using particular refuges, with several different factors potentially affecting an individual's choice of refuge and its use of that refuge. For example, when the predation risk is high, individuals may increase the amount of time they spend occupying refuges (Stein and Magnuson 1976, Stein 1977, Hill and Lodge 1994, Martín and López 1999) and may alter which refuges they use (Eggleston and Lipcius 1992). In addition, structural characteristics of refuges, such as the size, shape, texture and color, may also significantly affect refuge selection

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(Alberstadt et al. 1995, Blank and Figler 1996, Gregory and Griffith 1996, Walters and Wethy 1996, Steele et al. 1997, Arsenault and Himmelman 1998, Antonelli et al. 1999). For instance, Gregory and Griffith (1996) found that rainbow trout (*Oncorhynchus mykiss*) occupied refuges that closely corresponded to their body sizes. Likewise, Arsenault and Himmelman (1998) found that the size of crevice refuges occupied by scallops (*Chlamys islandica*) increased with the size of the individual. In uncontrolled field studies, such size relationships can either be because individuals of different sizes preferentially occupy different sized refuges, because larger individuals are physically incapable of fitting in smaller refuges even though no preference for size exists, or because all individuals prefer the same-sized refuges, but some individuals are aggressively excluded from these refuges by conspecifics or heterospecifics and forced to occupy other locations (e.g., Söderbäck 1991, Hazlett et al. 1992, Hill and Lodge 1994, Guiasu and Dunham 1999). Conspecifics can have less direct effects as well. Quinn and Graves (1998) found that male, female, and juvenile crayfish (*Orconectes virilis*) tended to avoid refuges that had been previously occupied by a male conspecific. Thus, to properly examine whether the size of an individual affects its preference for a refuge of a given size, preference must be tested in an environment in which an individual can physically fit into all available refuge sizes and no conspecifics are present.

Finally, an individual's experience may also affect refuge choice and use. Prior experience with particular locations or habitat types has been suggested to influence preference in other contexts (Partridge 1978, Klopfer and Ganzhorn 1985). For example, Switzer (1997a, 1997b) found that adult male amberwing dragonflies (*Perithemis tenera*) that mated at a territory were more likely to return to that territory than those males that did not mate. Female apple maggot flies (*Rhagoletis pomonella*) that were exposed to a particular host fruit species subsequently had higher oviposition rates and remained longer on that host species than females that had no experience with that host species (Papaj and Prokopy 1988) . However, few studies have examined whether experience with a particular refuge or with refuge characteristics affects an individual's preference.

In this study, we investigated whether an individual's size and experience affect refuge choice in the crayfish *Orconectes immunis*. Many studies have demonstrated that substrate type, presumably in providing access to suitable refuges, affects crayfish presence or abundance (e.g., Rabeni 1985, Lodge and Hill 1994) and many crayfish species use existing refuges or construct refuges of their own (e.g., Jonsson 1992, Foster 1993, Figler et al. 1995, Gali-Muhtsib 1998, Quinn and Graves 1998). In particular, *O. immunis* occupies existing refuges or constructs refuges in slow-moving or still bodies of water (Goellner 1943, Bovbjerg 1970, Page 1985, Hasiotis 1993). Despite being the most common crayfish in some habitats in parts of its range (Goellner 1943, Page 1985) and being a prime candidate for aquaculture use (e.g., Wetzel and Brown 1993, Huner and Lindqvist 1995), relatively little behavioral work has been done on *O. immunis* compared to other species of crayfish such as *Astacus astacus*, *Orconectes rusticus*, *Orconectes virilis*, and *Procambrus clarkii* (e.g., Bovbjerg 1956, Capelli and Hamilton 1984, Hazlett 1985, Söderbäck 1991, Figler et al. 1995, Steele et al. 1997, Quinn and Graves 1998, but see Bovbjerg 1970).

MATERIALS AND METHODS

Experimental Setup

This study was conducted from January to July 2001 with male crayfish captured from a small, shallow pond, 10 km south of Charleston (Coles County), Illinois. Crayfish were individually housed in 2 L plastic containers (16 cm diameter) containing tap water treated with Prime water conditioner (Seachem Laboratories, Inc.) and provided with a constant supply of air. Crayfish were housed in these containers without a refuge for at least one month prior to testing. Several days before a trial, we measured cephalothorax height and width at the location between the chelipeds and first set of walking legs.

Refuge preference trials were conducted in 12 L plastic testing arenas (L x W x H = 37 cm x 25 cm x 14 cm) that contained a refuge array of seven, 10 cm sections of PVC tubing, each of a different diameter (refuge number/size in mm: #1/40.3 , #2/34.5,

#3/26.0, #4/20.6, #5/18.0, #6/15.3, #7/12.4). Refuges were placed side by side in random order among 24 different arrays. Each refuge was secured to a black acrylic plastic base and backing (i.e., it was only possible to enter the tubes from one end) with non-toxic liquid polyurethane (Vantico Inc. # 6452). To minimize possible disturbances outside the testing arena, we covered the sides and the bottom of each testing arena with black plastic sheeting. Individual trials were started at approximately 1600 hr, and within minutes crayfish sought refuge in the tubes. At 1700 hr, we recorded the refuge in which a crayfish was located and we did this again the following morning (after 18 hrs.). Observations continued for 10 d. We defined an individual's "preferred" refuge as the refuge that it used the most during the 10 d, using the refuges from the morning observations to define preference. The morning observation was chosen because the individuals had at least 18 h to select refuges and because, if allowed to stay in the testing arena in the morning, they generally remained in those refuges for the remainder of the day.

Experimental Treatments

Groups of crayfish were subjected to one of three treatments: Novel Refuge, Nonremoval, and Removal. In the Novel Refuge treatment, we gave individuals 10 independent refuge choices. We removed the crayfish after recording its location in the morning and returned it to its holding container for 8 h. That evening, we placed the individual in a new testing arena with a new refuge array. All arrays and arenas were cleaned with soap and water before being used for the next individual.

In order to test for effects of experience with a particular refuge size, we randomly assigned individuals in the Novel Refuge treatment to two treatment subgroups – those that would have a subsequent one month period with a refuge and those that would have a subsequent one month period without a refuge (as a control). After the initial 10 d trial, individuals in the Novel Refuge treatment were placed back in their holding container. Those that were to be placed with a refuge were given a separate refuge of the size that was their second choice during their initial 10 d trial. Our reasoning in using their second choice was that we were interested in whether they would increase their use of a refuge following experience; therefore, choosing a refuge that they would use and yet did not prefer would give us the most sensitive test for changes in preference. In the event of a tie for second choice, the refuge given to an individual was chosen at random between the tied sizes. After the one month period, both treatment subgroups were retested for 10 d on the refuge choice arrays.

For the Nonremoval treatment, we examined whether preference was affected by experience with a particular refuge. Individuals were placed into a testing arena with a refuge array and not removed for 10 d. Refuge use was observed every evening and every morning; water in the arenas was changed every other day.

We conducted the Removal treatment to test for possible effects of disturbance differences between the Novel Refuge and Nonremoval treatments. In the Removal treatment, individuals were removed each day and arrays and arenas were cleaned. However, when the individuals were returned to the arenas after 8 h, they were returned to the same arena and same refuge array. Refuge use was recorded in the evening and the next morning.

Data management

Because no individuals used the smallest-sized refuge (i.e. , #7), we could not rule out the possibility that they were not using this refuge because they could not fit inside it. Therefore, we eliminated that refuge as a possible choice from our analyses.

We started with 160 individuals in our experiment. However, three types of individuals were excluded from our data prior to most of our analyses. First, some individuals died during the experiment prior to their trial being complete; these partial trials were not included in analyses needing all 10 observation days. Second, because molting will influence size and may influence behavior (Hazlett et al. 1974, Aiken and Waddy 1987), we excluded any individuals that molted while they were being tested. Third, in order to be confident that the crayfish in our analyses could use all of the provided refuges, we excluded all individuals that were larger than the largest individual who could use the smallest refuge (i.e., all individuals were small enough to fit into all six refuges). These three exclusions resulted in a sample sizes for the treatments of 34 individuals for Nonremoval, 51 for Novel Refuge, and 28 for Removal. Finally, individuals that did not have a clear first preference (e.g., use of two refuges was tied for first) were excluded from analyses of body size versus refuge preference, but not from analyses of preference strength.

RESULTS

Refuge preference and body size

We found refuge size related to refuge choice in three ways. First, using the first day for all treatments, we determined that individuals tended to choose larger refuges in the evening as compared to the next morning (Fig. 1; $\chi^2 = 27.5$, df = 5, $P < 0.0001$). Therefore, crayfish generally shifted their refuge choice from larger to smaller refuges after being initially introduced to the study arena. Second, individual crayfish exhibited a preference for a particular refuge size. Individuals chose their preferred refuges 47 ± 1.9 % (N = 113) of the time, which is significantly greater than the 17% of the time that would be expected if they were randomly selecting refuges (one-sample t-test, t = 15.6, $P < 0.0001$). Even though all individuals could physically fit in all refuges, the individual preferences for refuge size were not evenly distributed across all six refuge sizes. Considering only those individuals that had a single refuge that they used more than others (with refuge #1 being the largest), the refuge use was as follows: refuge #1, 1/95 individuals; refuge #2, 2/95; refuge #3, 31/95; refuge #4, 31/95; refuge #5, 24/95; refuge #6, 6/95 ($\chi^2 = 65.5$, df = 5, $P < 0.0001$). Third, the variation that did exist in individual refuge preference was related positively to body size. We looked at this size pattern in two ways. Our first method was to look for correlations between body size and refuge size; this correlation was significantly positive with all treatments combined for both body width (Spearman correlation, $r_s = 0.40$, z = 3.84, P = 0.0001, N = 95) and height (Spearman correlation, $r_s = 0.26$, z = 2.57, P = 0.01, N = 95). Looking at treatments individually revealed the same pattern for width for all treatments (Nonremoval: $r_s = 0.43$, z = 2.34, P = 0.02, N = 31; Novel Refuge: $r_s = 0.41$, z = 2.56, P = 0.01, N = 39; Removal: $r_s = 0.45$, z = 2.22, P = 0.03) and for height for the Novel Refuge treatment (Nonremoval: $r_s = 0.34$, z = 1.86, P = 0.06, N = 31; Novel Refuge: $r_s = 0.33$, z = 2.02, P = 0.04, N = 39; Removal: $r_s = 0.20$, z = 0.96, P = 0.34). Our second method was to look at the average size of the individuals occupying each refuge, using only refuges 3, 4, and 5 because they had large enough sample sizes for the analysis. Larger refuges had significantly larger crayfish preferring them overall (Fig. 2; ANOVA;Width: $F_{2,84} = 7.04$, P = 0.001; Height: $F_{2,84} = 3.55$, P = 0.03).

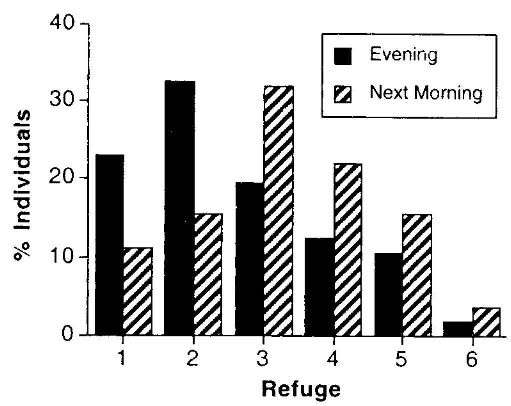

Figure 1. Percentage of *O. immunis* males (N = 160) occupying the six different sized refuges in the evening and the next morning for the first time individuals were introduced to an arena. Because all three treatments were the same for this first day, data from all treatments were combined. Refuge 1 was the largest and refuge 6 the smallest.

Effect of experience on refuge choice

We examined two possible effects of experience on refuge choice. First, we investigated whether the strength of preference for an individual refuge varied among treatments. Individuals in the Novel Refuge treatment tended to occupy their preferred refuge a lower proportion of the time (0.31 ± 0.016; N = 51) than those in the Nonremoval (0.60 ± 0.033; N = 34) and Removal treatments (0.60 ± 0.03; N = 28), and overall, preference strength varied among treatments (ANOVA; $F_{2,110} = 50.1$, $P < 0.0001$). This suggests that the crayfish refuge use was not adversely affected by daily removals (i.e., Nonremoval and Removal were equal) and suggests that returning to or remaining in a familiar arena and refuges had a positive effect on preference strength. Second, we examined whether extended experience with a particular sized refuge (i.e., within the Novel Refuge treatment) affected preference. Individuals that were housed with a refuge for an extended time were not more likely to switch to preferring that refuge when given a choice than those that were not housed with a refuge (11/23 individuals with experience switched to that refuge, while 7/20 without experience switched; $\chi^2 = 0.72$, df = 1, P = 0.39). Furthermore, the individuals housed with a refuge did not increase their proportional use of that refuge relative to other available choices (increase of 3.9 ± 3.6%, N = 23; paired t-test, t = 1.1, df = 22, P = 0.29). Taken together, these results indicate that experience with particular refuges, but not with a refuge of a particular size, affected refuge preference.

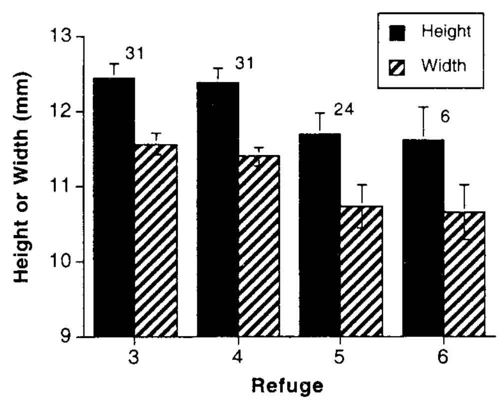

Figure 2. Mean height or width (± SE) of *O. immunis* males preferring the six different sized refuges. Number above bars refers to sample size for that refuge type; data from all treatments were pooled for this figure. Refuge 1 was the largest and refuge 6 the smallest.

DISCUSSION

In this study we found that crayfish occupied refuges nonrandomly; the refuges that they used were dependent upon their body sizes and their prior experiences with those particular refuges. These results reflect an individual's refuge choice relative to size and experience, because our design allowed us to rule out the possible positive or negative effects of conspecifics on refuge choice (e.g., Navarrete and Castilla 1990, Eggleston and Lipcius 1992, Hill and Lodge 1994, Quinn and Graves 1998) and rule out simple physical exclusion from some refuges because of body size. Other studies have also found that size of the refuge an individual used was related to its body size (Foster 1993, Gregory and Griffith 1996, Arsenault and Himmelman 1998, Cooper et al. 1999). For example, Foster (1993) found that crayfish (*A. pallipes*) were found under stones that were 2.3 times wider than their carapace length (width was not measured). In our study, individuals occupied refuges, on average, that were 1.44-2.25 times their carapace width. Therefore, some crayfish species appear to avoid overly large refuges but do not seem simply to choose the smallest refuge in which they can fit.

Occupying a refuge of "intermediate" size may represent a balance between defensibility from conspecifics and predators, flexibility for future growth, and perhaps ease of or response to water flow. Cooper et al. (1999) found that the refuges preferred by the lizard *Cordylus cordylus* reduced their detectability and decreased their likelihood of being dislodged. Gregory and Griffith (1996) suggested that rainbow trout preferred refuges that allowed for pectoral fin movement for maintaining position within water flow. In addition, occupying a refuge that is slightly larger than one's body would allow for an increase in size following a molt. Because individuals will be particularly vulnerable during a molt (Taugbøl and Skurdal 1992, Barki et al. 1997, Jonsson and Edsman 1998) and because individuals may use the same refuge for a period of time, occupying a refuge that is large enough to accommodate an increase in body size would eliminate the need for an individual to conduct a potentially risky search for a new refuge at this critical time. Indeed, Hazlett et al. (1974) found that *O. virilis* individuals tended to molt within their burrows; these individuals often would have been in the same location for weeks prior to the molt and then would move to a new location following the molt. However, Hazlett et al. (1974) also noted that this subsequent change in locations was unlikely to be due to a need for increasing the size of the refuge, since there was usually still space available within the current refuge.

Beyond anecdotally noting that crayfish in our study were noticeably more difficult to remove from the smaller refuges (i.e. relative to sizes #1 and #2), we do not have any data on how relative refuge size relates to defensibility, growth, or water flow. Interestingly, however, we found that individuals initially chose relatively larger refuges than they would subsequently use. This suggests that perhaps under high risk conditions (e.g. disturbed in an unfamiliar environment), individuals were less particular about refuge characteristics and instead tended to quickly occupy a refuge. Under such conditions, individuals may occupy refuges based on accessibility or conspicuousness rather than on more subtle relationships of relative size.

In our study, we intentionally limited the physical characteristics we were varying to refuge size in order to better assess how *O. immunis* reacted to this character. In addition, the entrance diameter for our refuges was equal to the diameter of the space within the refuge. However, in the field, other physical characteristics of a refuge may affect choice, and the space within a refuge may differ from the size of the entrance, either naturally or due to excavation by the inhabitant (e.g., Hasiotis 1993, Gregory and Griffith 1996, Arsenault and Himmelman 1998).

Because each individual was given a choice multiple times, we were able to assess the strength of an individual's preference for a particular refuge or refuge size. We found that individuals increased their probability of using a particular refuge when provided the opportunity to do so (i.e., our Nonremoval and Removal treatments). This suggests that familiarity with a particular refuge affects preference. Because refuges in the Removal treatment were cleaned between days, individuals must use spatial or tactile cues (e.g., Basil and Sandeman 2000) instead of relying solely on chemical cues (e.g., Hazlett 1985; Quinn and Graves 1998) to locate their previously occupied refuge. Based on our laboratory results, we would predict that in a natural setting, *O. immunis* would remain within a defined area and be faithful to particular refuges. To our knowledge, no field studies on *O immunis* have investigated the fidelity of individuals to particular refuges. Goellner (1943) found that individual *O. immunis* changed locations within a pond between captures; however, in his study he released all of the captured individuals from a pond at the same location, which might disrupt any site specific behavior. In other species of *Orconectes*, the tendency to remain for extended periods of time in the same burrow or under the same rock has been observed (i.e., *O. virilis*, Hazlett et al. 1974 and *O. juvenalis*, Merkle 1969). In any case, field studies examining the refuge fidelity and home range of *O. immunis* would be useful for determining the relevance of our laboratory experiment to field populations.

Experience with a refuge of a particular size, however, did not increase an individual's use of that sized refuge. Perhaps the benefit of experience with a refuge characteristic such as size, for which the availability of appropriate refuges may change unpredictably within a short period, may not be high enough to have led to selection for this ability (Stephens 1991). Alternatively, occupation of the refuge alone may not have been sufficient for altering an individual's preference. For example, if an individual has experience defending a refuge of a particular type, it may be more capable of defending a refuge of that type, and consequently prefer that type of refuge.

In conclusion, we found that an individual's size and experience with a refuge may affect the refuges that it occupies. These results suggest that patterns observed in the field, in particular spatial patterns in the distribution of different sized crayfish in relation to different sized refuges, need not be large individuals being physically excluded from small sites or of large individuals forcing smaller individuals to less preferred, smaller refuges (*cf.* Rabeni 1985). The results also indicate that refuge-based demographic bottlenecks, as observed for stone crabs (Beck 1995, 1997), could potentially affect *O. immunis* populations. However, while our study provides some interesting possible mechanistic bases for population distributions in the field, many areas of study remain. The defensibility of refuges of particular sizes and conformations and the relative importance of refuge availability versus preference are two such areas.

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