Avoidance of drilled gastropod shells by the hermit crab 
*Pagurus longicarpus* at Nahant, Massachusetts 

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Abstract 

Most hermit crabs depend on empty gastropod shells for shelter; competition for appropriate shells is often severe. This study determined whether shells that have been drilled by naticid gastropods are suitable for occupancy by the hermit crab *Pagurus longicarpus*. Differences in the characteristics of empty shells and those occupied by hermit crabs were assessed at two adjacent field sites in Nahant, Massachusetts. Drilling damage was far more frequent in empty gastropod shells than in shells occupied by hermit crabs, suggesting that individuals of *P. longicarpus* avoid drilled shells. They did not appear to avoid shells with other forms of damage. Laboratory experiments confirmed that these hermit crabs preferentially chose intact shells over drilled shells, even when the intact shells offered were most suitable for crabs half the weight of those tested. Final shell choices were generally made within 1 h. The hermit crabs apparently discriminated between intact and drilled shells based on tactile cues, since crabs kept in the dark showed the same preference for intact shells. The hermit crabs strongly avoided, to nearly the same extent, artificially drilled shells, naturally drilled shells, and shells with holes artificially drilled on the opposite side of the shell from where they would normally be located. Possible selective forces causing *P. longicarpus* to show such strong behavioral avoidance of drilled shells include increased vulnerability of crabs in drilled shells to osmotic stress, predation, and eviction by conspecifics. © 2000 Elsevier Science B.V. All rights reserved. 

Keywords: Behavior; Drill holes; Hermit crabs; *Pagurus*; Shell selection 

1. Introduction 

When hermit crabs metamorphose, they must quickly locate an empty shelter, usually
a gastropod shell, of appropriate size (Reese, 1963; Hazlett and Provenzano, 1965; Harvey and Colasurdo, 1993; Brodie, 1999). As they continue to grow, they must seek larger shells. If they fail to find (or commandeer) larger shells they may become increasingly vulnerable to predation (Vance, 1972; Angel, 2000), desiccation (Taylor, 1981; Brodie, 1999), and osmotic stress (Shumway, 1978), and may also suffer declines in growth rate and fecundity (Markham, 1968; Childress, 1972; Fotheringham, 1976, 1980; Angel, 2000). Many studies have shown that hermit crabs discriminate among shells of different gastropod species and of particular sizes, weights, or internal volumes (e.g. Blackstone and Joslyn, 1984; McClintock, 1985; Wilber, 1990; Carlon and Ebersole, 1995; Elwood, 1995; Wada et al., 1997; Elwood et al., 1998; Osorno et al., 1998; Barnes, 1999). Fewer studies have investigated discrimination based on shell condition (e.g. Conover, 1978; McClintock, 1985; Wilber, 1989, 1990), and none have specifically looked at the impact of holes drilled by predatory gastropods on shell suitability. At Nahant, Massachusetts, there is a large population of the hermit crab Pagurus longicarpus living primarily in shells of the periwinkle Littorina littorea; preliminary studies (Pechenik, Li, and Angel, unpublished data) showed that about one-third of the available empty gastropod shells at this site bore conspicuous, countersunk holes drilled by naticid gastropods, probably Euspira (=Lunatia) heros (Carriker, 1981; Dietl and Alexander, 1995). Yet, we found few hermit crabs in such drilled shells, despite their ready availability in many sizes. In this paper we document the selective avoidance of drilled gastropod shells by P. longicarpus in both the field and laboratory, and explore the mechanisms by which the crabs discriminate between drilled and intact shells.

2. Materials and methods

2.1. Shell availability and characteristics of shells occupied by hermit crabs in the field

All studies were conducted at an intertidal site in Nahant, Massachusetts. Part of the site is rocky, with dense populations of blue mussels (Mytilus edulis), barnacles (Semibalanus balanoides), and periwinkles (Littorina littorea). Adjacent to this is a muddy/sandy area that contains a few patches of eelgrass (Zostera marina). In July 1997 and in September 1998, about 300 and 450 gastropod shells, respectively, were collected haphazardly from both sites. In September 1999, over 900 shells were collected haphazardly from the rocky area. In both years, live snails were returned to the study site immediately. The remaining shells were identified to species and examined for condition (intact, drilled, other forms of apex or aperture damage) and whether or not they contained hermit crabs. The aperture length of each shell was measured to the nearest 0.1 mm with dial calipers, and a crowding index (index of shell fit) was determined for each shell occupied by a hermit crab; crabs that could withdraw far inside their shell were scored as ‘Hidden,’ those that fit perfectly inside their shell with the chelipeds lying flush with the aperture were scored as ‘Flush,’ and those unable to pull their chelipeds into the shell were scored as ‘Protruding.’ Because most of the crabs
were found in shells of the periwinkle *Littorina littorea* (see Results), our presentation focuses primarily on hermit crab utilization of those shells.

2.2. Shell choice by hermit crabs in the laboratory

Hermit crabs (in periwinkle shells exclusively) were collected at the study site at Nahant, Massachusetts in Fall 1998 and maintained individually in 100 ml plastic cups approximately half full of seawater at approximately 20°C. Although we did not note the sex of individuals used in this study, previous surveys of this population indicate that males and females occur in approximately equal numbers at this site (Pechenik and Li, unpublished data). In all experiments, water was changed daily; crabs were fed shrimp pellets between water changes. To study shell choice, hermit crabs were transferred to rectangular plastic boxes (approximately 8 × 12 cm) approximately half full of seawater. In all experiments, hermit crabs were offered two shells, one intact and the other drilled.

Four experiments were conducted to determine the extent to which hermit crabs would discriminate between drilled and intact periwinkle shells in the laboratory, and to determine how long it took crabs to make the distinction. We also assessed the relative important of visual and tactile cues, by running some experiments in darkness. In another experiment, we sought to determine whether the position of the drill holes influenced shell selection. In all four experiments, the two shells offered to each hermit crab were matched to crab size using the equation determined by Angel (2000) for crabs from the same Nahant population. The aperture diameters of all shells were measured, as were the drill hole diameters, so that we could determine whether the drilled and intact shells offered were equal in size, and whether mean drill hole diameter differed significantly between treatment groups. In each experiment, there was no significant difference in mean aperture diameter between intact and drilled shells offered to each hermit crab (for paired *t*-tests, all *P* values were > 0.21), so that pairing was effective. In experiment 4, in which we drilled holes into shells at either of two different locations, aperture diameters also did not differ significantly between intact and drilled shells (paired *t* = 0.8836, df = 39, *P* = 0.382; pairing effective, *r* = 0.823). The average size of the holes that we drilled was, however, significantly smaller than that of holes found on field-collected shells (field samples, \( \bar{X} = 3.8 \) mm, S.D. = 1.03 (*n* = 40); hand-drilled holes, \( \bar{X} = 2.9 \) mm, S.D. = 0.47 (*n* = 38); *t* = 4.93, df = 76, *P* < 0.0001).

In experiment 1, ten hermit crabs were carefully removed from their shells and each was offered a choice between an intact periwinkle shell or a naturally drilled shell of similar size. The experiment was performed under natural laboratory lighting. Final shell choices were recorded after 24 h.

The relative importance of visual and tactile cues was assessed in two experiments. In experiment 2, 50 crabs were carefully evicted from their shells. Twelve hours later, each crab was given two periwinkle shells of approximately equal size, one with a natural drill hole and the other intact. Half the crabs were kept in continuous light and their shell choices recorded several times over 24 h. The other 25 crabs were maintained in the dark and their shell choices were recorded only once, 24 h after shells were introduced. Experiment 3 was similar except that hermit crabs (from a separate collection) were initially forced to occupy drilled periwinkle shells. Forty crabs were gently evicted from
their shells and offered only periwinkle shells with drill holes. After crabs moved into these drilled shells, they were transferred into individual plastic boxes with an intact shell of comparable size. Half the crabs \((n = 20)\) were maintained in continuous light, while the remaining 20 crabs were maintained in continuous darkness. Mean drill hole diameter did not differ significantly between the light and dark treatments \((\text{Mann–Whitney } U = 177.5, \ P = 0.552, \ n = 40)\). Shell occupancy of crabs was recorded periodically at intervals over the next 24 h for crabs kept in the light, but only after 24 h for those kept in the dark.

Experiment 4 was designed to test whether the position of the drill hole would influence the ability of hermit crabs to distinguish between drilled and intact shells. Because *Euspira heros* drills with considerable site specificity \((\text{Dietl and Alexander, 1995})\), in the body whorl to the left of the aperture \((\text{Fig. 1})\), we hypothesized that hermit crabs might be unaware of holes placed elsewhere on the shell. Forty freshly-collected hermit crabs were gently evicted from their shells and maintained individually in 100-ml plastic cups. The next day, each naked hermit crab was given a choice between an intact periwinkle shell and an artificially drilled periwinkle shell of comparable size. Holes \((\text{mean diameter} = 2.8 \text{ mm}, \ S.D. = 0.42, \ n = 40)\) were drilled into intact periwinkle shells using a Dremel drill bit. In half of the drilled shells \((n = 20)\), holes were made in the position of natural drill holes, while in the other 20 shells holes were drilled in the opposite surface, \(180^\circ\) from the aperture. Drill holes in the two positions did not differ significantly in diameter \((\text{unpaired } t = 0.056, \ P = 0.956)\), although they were sig-

![Fig. 1. Shell of the gastropod *Littorina littorea* bearing the characteristic hole drilled by a predatory moonsnail. The hole is approximately 3.5 mm in diameter.](image-url)
significantly smaller in mean size than those found on field-collected shells (mean diameter for field-collected shells = 3.8 mm, S.D. = 1.03, n = 40; unpaired t = 4.93, df = 76, P < 0.0001). As before, the hermit crabs were given 24 h to make a choice of shells in both constant light and constant darkness, with more frequent observations being made in constant light.

Two final experiments were conducted using separate collections of hermit crabs, to assess the magnitude of bias against drilled shells. Appropriately sized drilled shells were paired with intact shells that were too small for each hermit crab, based on the relationship between crab weight and preferred shell size established by Angel (2000).

In experiment 5, 18 hermit crabs that had been evicted from their shell were given a choice between an intact periwinkle shell appropriate for a crab one-half of that crab’s wet weight and a naturally drilled shell of ideal size. For example, a crab weighing 0.39 g (wet weight) was offered a drilled shell with an aperture diameter of 13.0 mm and a noticeably smaller intact shell with an aperture diameter of only 10.8 mm. In experiment 6, 16 naked hermit crabs were given a choice between an intact periwinkle shell appropriate for a crab one-quarter of that crab’s wet weight and a naturally drilled shell of ideal size. For example, a crab weighing 0.34 g was offered a drilled shell with an aperture diameter of 12.5 mm and an intact shell with an aperture diameter of only 8.7 mm.

All hermit crabs were returned to the study site after use.

2.3. Data analysis

To determine whether hermit crabs were occupying periwinkle shells without regard to shell condition, we compared frequencies of crab-occupied and empty shells that were intact, drilled, or showed other damage using likelihood ratio (G) tests of heterogeneity. Crowding indices of crabs occupying drilled versus non-drilled shells were compared using a Kruskal–Wallis test of 2 × 3 singly ordered contingency tables, to test the null hypothesis that crabs in these two shell types show identical distributions across the three levels of crowding. Differences in mean aperture length as a function of shell condition (drilled vs. not drilled) and shell occupancy (with crabs or empty) were examined using two-way fixed effects ANOVA.

To test the null hypothesis that hermit crabs showed no preference for intact versus drilled shells in the laboratory, we used exact binomial tests. To test whether crabs exhibited the same choices in the light and in the dark, data were analyzed by contingency table analysis using StatXact 3.0 (Cytel Corporation). The same procedure was used to test whether drill hole position influenced the crabs’ ability to distinguish between intact and drilled shells.

3. Results

3.1. Shell availability and hermit crab occupancy in the field

At both the sandy and rocky sites, at least 94% of all hermit crabs were found in
periwinkle shells, *Littorina littorea*. Hermit crabs were not randomly distributed among periwinkle shells that were intact, drilled, or had other damage (Fig. 2; *G* test of heterogeneity for 1998 Rocky site *G* = 52.1, df = 2, *P* < 0.0001; for 1998 Sandy site *G* = 30.2, df = 2, *P* < 0.0001; for 1999 Rocky site *G* = 166.2, df = 2, *P* < 0.00001). In particular, while drilled shells constituted 33–73% of all empty shells across the three collections, crabs were found in drilled shells at much lower frequencies, ranging from only 2.2–12.4% (Fig. 2). Thus drilled periwinkle shells were occupied by hermit crabs considerably less often than would be expected based on their availability. In contrast, in all three collections, higher percentages of hermit crabs were recorded from shells with apex or aperture damage compared to the proportion of empty shells with such damage. This indicates that hermit crabs did not discriminate against shells with non-drilling damage.

In 1998 samples, hermit crabs in drilled shells were distributed fairly evenly over the three crowding categories (Fig. 3a; data combined from both sites); 33% of crabs in

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**Site and shell condition**

Fig. 2. Shell availability (open bars) and shell use by hermit crabs (*Pagurus longicarpus*) (stippled bars) related to shell condition at two sites in Nahant, Massachusetts in 1998 and 1999. Only shells made by the gastropod *Littorina littorea* were considered, as they made up at least 94% of all shells collected at this site. Rocky and Sandy refer to two adjacent sites at the same location. Other = shells with broken apex or damaged aperture edge. Numbers in parentheses indicate the total numbers of shells sampled that did or did not contain hermit crabs. The first pair of bars, for example, indicates that about 12% of the 65 empty shells collected at the Rocky site in 1998 were intact, while about 55% of the 113 shells containing hermit crabs were intact.
Fig. 3. Relationship between degree of crowding and shell damage for the hermit crab *Pagurus longicarpus*. (a) Combined field data from rocky and sandy sites sampled in 1998 at Nahant, Massachusetts; (b) Field data from rocky site at Nahant in 1999.
drilled shells were classified as ‘Protruding’, i.e. they were unable to retract their chelipeds into their shells. In contrast, hermit crabs in undrilled shells (those that were intact or those with apex or aperture damage) were much less likely to be crowded in their shells (Kruskal–Wallis test of $2 \times 3$ contingency table $H = 13.7$, df = 1, $P = 0.0002$); only 13% were unable to retract their chelipeds into the shells (Fig. 3a). A similar trend was observed in the 1999 sample (Fig. 3b), although the distributional differences were not significant (Kruskal–Wallis test of $2 \times 3$ contingency table $H = 0.8$, df = 1, $P = 0.41$).

Drilled periwinkle shells occupied by hermit crabs were significantly larger than intact shells occupied by hermit crabs in all samples (Figs. 4 and 5). Indeed, aperture lengths of drilled periwinkle shells, whether occupied or not, were significantly larger than those of non-drilled shells (two-way ANOVA for drilled versus non-drilled shells; 1998 $F = 34.4$, df = 1, 222, $P < 0.0001$; 1999 $F = 127.6$, df = 1, 915, $P < 0.0001$) (Fig. 5). Moreover, in 1999 crab-occupied shells in general were significantly larger than empty shells (Fig. 5; $F = 32.5$, df = 1, 915, $P < 0.0001$).

### 3.2. Crab behavior and shell choice in the laboratory

Hermit crabs examined shells with their chelipeds, as previously described (e.g. Elwood, 1995), and after occupying one shell they continued to investigate the remaining shell periodically. When examining drilled shells, many crabs inserted a
Fig. 5. The relationship between mean aperture length (+ 1 S.D.), shell condition (drilled by moon snails, or not), and shell occupancy by hermit crabs (*P. longicarpus*) in a rocky habitat at Nahant, Massachusetts in (a) 1998 and (b) 1999. Numbers above bars indicate sample sizes.
cheliped into the drill hole, sometimes from the outside of the shell and sometimes from the inside, after inserting the cheliped into the shell aperture.

In all four experiments, at least 88% of all hermit crabs preferentially chose intact periwinkle shells over shells with drill holes (Fig. 6), and most crabs made their final shell choice within 1 h (Fig. 7). Indeed, of those nine crabs that were not occupying

![Lab shell choice data: % In intact shells at end](image)

Fig. 6. Laboratory experiments documenting shell choices made within 6 or 24 h by hermit crabs (*P. longicarpus*) offered one intact shell and one drilled shell of comparable size. All shells offered were of ideal size for the particular crab recipient, based on the relationship between crab weight and preferred shell size established for crabs in this population (Angel, 2000). All hermit crabs were naked when the experiments began, except for experiment 3, in which all hermit crabs were initially forced to occupy drilled shells before the experiment began. In experiments 2 and 3, half of the crabs were maintained in the dark. In experiment 4, drill holes were not made by moonsnails. Instead, holes were made using a Dremel drill bit either in the natural position (Fig. 1) (*n* = 20) or in the opposite surface (*n* = 20). *n* represents the number of hermit crabs in each treatment within an experiment.
intact shells within 30 min in experiment 4, only two were in shells with drill holes; the other seven individuals had not yet made a choice and were still naked. Even in experiment 4, in which half of the drill holes were placed in the wrong position, the hermit crabs quickly occupied intact shells (Fig. 7), and did so regardless of drill hole position ($2 \times 2$ contingency table analysis $G = 0.001$, df = 1, $P = 1.0$). Hermit crabs appear to discriminate between drilled and intact shells using tactile cues, as there were no significant differences in choices made in the light and in the dark (Fig. 6; experiments 2 and 3; $2 \times 2$ contingency table analysis for experiment 2 $G = 4.5$, df = 1, $P = 0.23$; for experiment 3 $G = 1.4$, df = 1, $P = 1.0$).

Given a choice between drilled shells of ideal size and intact shells appropriate for crabs half of each crab’s actual wet weight, almost every hermit crab chose the smaller but intact shell over the larger drilled shell (Fig. 8; binomial test, $n = 18$: $P = 0.0007$). This was true even though, when occupying the smaller shell, much of the crab’s body protruded from the shell aperture. Moreover, the final choices were made very quickly, within 30 min. In contrast, given a choice between drilled shells of ideal size and intact shells appropriate for crabs one-quarter of each crab’s actual wet weight, almost every hermit crab selected the larger, drilled shell over the smaller intact shell (Fig. 8; binomial test, $n = 16$: $P = 0.0003$). Again, the final shell choices were largely completed within 30 min.
4. Discussion

Previous work suggests that hermit crabs at Nahant, Massachusetts are subject to severe competition for shells, as nearly 25% of them were in shells of suboptimal size (Angel, 2000). Our finding that shells with apex or aperture damage were occupied in proportion to their abundance further supports the idea that appropriately sized intact shells were rare relative to the needs of the hermit crab population, since crabs of this species choose intact over damaged shells in the laboratory (Wilber, 1990). The extent to which hermit crabs occupy damaged shells in the field has not been quantified very often. However, a few other studies have similarly reported widespread use of damaged shells by hermit crabs of many species (Fotheringham, 1980; Barnes, 1999), adding to the impression that shells are generally limiting.

Many empty shells were found at our field site, in a wide range of sizes, but a high proportion (33–73%) of all the empty shells that we gathered in our three collections had been drilled. Our field observations indicate that drilled periwinkle shells (Littorina littorea) at Nahant, Massachusetts were markedly underutilized by the hermit crab
Pagurus longicarpus relative to their availability. In contrast, the crabs occupied shells with other types of damage (broken apex or damaged aperture) in proportion to the availability of such shells.

Surprisingly, previous studies on the use or avoidance of damaged shells by hermit crabs do not specifically mention damage caused by predatory gastropods (e.g. Conover, 1978; Taylor, 1981; McClintock, 1985; Wilber, 1989, 1990; Kuhlmann, 1992; Barnes, 1999). Either the incidence of drilling is far lower at other sites, or this type of damage has simply been ignored previously. At Beverly, MA, fewer than 10% of nearly 500 empty periwinkle shells examined in Fall 1999 had drill holes (unpublished data). Dietl and Alexander (1995) mention collecting drilled shells with and without hermit crabs from a site in New Jersey, but they did not indicate the proportion of drilled shells in which hermit crabs were found.

Our laboratory studies provide strong behavioral evidence that individuals of P. longicarpus avoid using drilled shells. Hermit crabs rejected drilled shells very quickly, generally within 15–30 min. Only when intact shells were much too small — so small as to be suitable for a crab one-quarter the weight of the tested crab — did individuals choose drilled shells over intact shells.

Hermit crabs appeared to use tactile cues rather than visual cues to assess drilling damage: distinctions were made equally well in the light and in the dark, and crabs were often observed thrusting a cheliped through the drill hole before rejecting a shell. The importance of tactile cues in shell assessment has been noted previously (Mesce, 1993; Elwood, 1995). Moreover, Mesce (1993) has shown that hermit crabs of at least some species (P. hirsutiusculus) can locate empty shells in the light and in the dark with equal speed. However, the present study seems to be the first to demonstrate that hermit crabs can assess shell quality in complete darkness.

Pagurus longicarpus occurs over a large range, from Nova Scotia to Texas and Florida (Caine, 1975; Wilber, 1990). Thus, our results may indicate a key constraint on shell use over a considerable geographic range. At our study site, drill holes were a major form of damage, representing 22–48% of all damaged shells. Thus, predatory moon snails at this site are acting as ‘ecosystem engineers’ (Jones et al., 1994), essentially removing shells as a resource for hermit crabs by their drilling activity. At Nahant, 44–72% of the hermit crabs we collected occupied shells with either apex, aperture, or drill hole damage, and about 13% of individuals could not fully retract into their shells. Drilling by moon snails at this site is likely to greatly increase the competition for shells among hermit crabs. Because mean shell size was significantly greater ($P < 0.05$) for drilled shells than for intact shells occupied by hermit crabs at this site, and because large shells are often in particularly short supply (e.g. Kellogg, 1976; Carlon and Ebersole, 1995), the effects of drilling on competition for shells must be especially great for larger hermit crabs.

Although intact shells are selected by P. longicarpus over apex or aperture-damaged shells of comparable size in the laboratory, damaged shells are preferentially selected by P. longicarpus when the intact shells provided are too small (Wilber, 1990). Thus, our results indicate that drilled shells are treated by this species very differently from shells with other forms of damage. Only when intact shells were so small as to be appropriate for an individual 25% of the test individual’s weight did hermit crabs select a drilled
shell over an intact shell in our laboratory studies. The aversion to drilled shells was nearly complete, even when drill holes were smaller than natural.

Such extreme avoidance of drilled shells by individuals of _P. longicarpus_ suggests considerable selection against their use. Indeed, given a choice between a drilled shell of appropriate size and an intact shell appropriate for a crab half its weight, the crabs in our experiment all chose the intact shell; apparently, only a very desperate crab will take up residence in a drilled shell. Drill holes might increase vulnerability to desiccation. However, members of this hermit crab species typically burrow beneath the sand at low tide or congregate in intertidal pools (Wilber, 1990; Kuhlmann, 1992) where they would not be subject to desiccation. Moreover, hermit crabs (_Pagurus samuelis_ and _P. granosimanus_) in damaged shells did not show reduced resistance to desiccation stress in previous studies (Taylor, 1981). More likely, drill holes increase vulnerability to predators. A drill hole may weaken the shell and make it easier for crabs and other shell-crushing predators to capture the hermit crab resident, as does shell pitting (McClintock, 1985; Barnes, 1999), or it may allow access by small carnivores, such as juvenile nereid worms. However, shell damage (including holes in various parts of the shell) did not influence vulnerability of _P. longicarpus_ to predators in field studies conducted by Kuhlmann (1992). Note, however, that the hermit crabs we found occupying drilled shells at our field site tended to be too large for those shells (Fig. 3). Hermit crabs that cannot retract fully into their shells are considerably more vulnerable to predators (Angel, 2000; Vance, 1972), so that occupying drilled shells may increase vulnerability to predators indirectly. Drill holes may also increase vulnerability of brooded embryos to predation, although we noticed no differences in shell selection behavior among males and females, and none of the individuals used were brooding embryos (unpublished data). Drill holes may also facilitate eviction by other hermit crabs (Vance, 1972; Taylor, 1981; personal observations), either directly by increasing access to the occupant through the drill hole, or indirectly by altering the force or vibration frequency with which shell-rapping signals are transmitted to the occupant (Briffa and Elwood, 2000). Our data suggest, however, that the victor would be unlikely to take up long-term residence in a drilled shell. Finally, drill holes should make hermit crab occupants (and their brooded embryos) more vulnerable to osmotic stress (Shumway, 1978).

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**References**


