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The use of artificial shells for exploring shell preference in the marine hermit crab *Pagurus longicarpus* (Say)

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Although recognition behavior is central to many aspects of an organism's biology, it has been difficult to effectively identify the individual recognition components (i.e., production, perception, and action) for most organisms. Among hermit crabs, a relatively well-studied system for recognition behavior, the precise shell cues that stimulate crabs to explore and choose empty shells are unclear. We have developed a novel method for studying shell selection in the hermit crab *Pagurus longicarpus*. Using rapid prototyping technologies, we have produced artificial gastropod shells based on 3-dimensional virtual models derived from the morphological parameters of shell geometry. In our study, individual *P. longicarpus* reliably inspected and occupied artificial shells thus enabling us to make specific modifications to test hypotheses of shell preferences. In addition to discriminating based on shell size, coating shells with crushed $CaCO_3$ from remnants of natural shells increased shell acceptance. This latter result supports prior speculation that calcium is a recognition cue for shell preference. Our results indicate that this novel method of shell design and fabrication has great potential for more detailed investigations of recognition behavior in hermit crabs.

Introduction

Hermit crabs are poorly sclerotized crustaceans that rely on shells produced by gastropods for protection (e.g., Agassiz 1876, Reese 1962, Hazlett 1981, 1993). Predation by hermit crabs upon living gastropods is rare; rather, hermit crabs compete with each other for shells of gastropods that die by other means (e.g., desiccation or thermal stress, or predation by other organisms). As hermit crabs age, they continually search for new shells to compensate for body growth and for shells of higher quality than their current shell. Because the remaining shells of dead gastropods become weaker with age post-mortem (LaBarbara & Merz 1992), hermit crabs forced to occupy these shells of lesser quality are more vulnerable to predators, physical stress, and eviction by other hermit crabs (Vance 1972, Pechenik *et al*. 2001). As hermit crabs have soft bodied abdomens and are readily consumed by a variety of predators, survival depends on shell quality. As such, the costs of acceptance errors — that is, misidentifying a poor shell as a suitable one — are high (Reeve 1989).

Hermit crabs have been shown to choose among empty shells of different gastropod species (e.g., *see* Reese 1962, Blackstone & Joslyn 1984), different sized shells within a given gastropod species (e.g., *see* McClintock 1985, Wilber 1990, Hazlett 1996, Osorno *et al.* 1998, Angel 2000), shells differing in extent of external damage (McClintock 1985, Wilber 1990, Pechenik & Lewis 2000), and shells whose weight or center of gravity have been artificially altered (McClintock 1985). When choosing among vacant shells, hermit crabs perform a series of stereotyped shell-assessment behaviors (summarized by Reese 1962, Jackson & Elwood 1989, Elwood 1995); a specific spectrum of actions carried out partially or in full for various durations depending on certain circumstances (Jackson & Elwood 1990). Once a shell has been deemed appropriate, the hermit crab inserts its abdomen into the shell, thus accepting it, and remains in the shell as it performs other tasks (e.g., foraging).

Shell selection in hermit crabs is an example of recognition behavior, a critical aspect in the life history of organisms across all taxa. Recognition behavior is essential for consistent discrimination of feeding and/or breeding habitats, of mates, and of kin. Indeed, recognition behavior is relevant for all inter- and intra-specific interactions in which organisms have to discriminate between one item and another. Because of its importance, considerable effort has been put forth to describe the underlying components of recognition systems (reviewed in Sherman *et al.* 1997). In general, the three components of recognition systems are called the production, perception and action components (Holmes & Sherman 1983, Reeve 1989). The production component refers to the manifestation of recognition cues, the perception component refers to the detection and assessment of cues, and the action component refers to the resultant behavior given the assessment of the cues. Using hermit crab shell selection as an example, cues related to shell phenotype represent the production component, the assessment of these cues represents the perception component, and the behavioral act of inserting, or not inserting, the abdomen into the shell (i.e., accepting or rejecting the shell) represents the action component. Investigations into shell selection may further develop our understanding of recognition behavior, in particular with respect to the recognition template.

The recognition template is hypothesized to be the organism's 'understanding' of the ideal object, be it kin, nestmate, or shell, for any given fitness context. The level of mismatch between the cues and recognition template is what drives discrimination; shells too dissimilar to the template will be rejected, while those more similar will be accepted. As an example of this, Pechenik *et al.* (2001) showed that hermit crabs will reject shells with drill holes left by moon snails without inserting their abdomen into the shell, thus suggesting a level of mismatch severe enough for the hermit crab to reject the shell. Although some components of shell preference may be unlearned (e.g., Reese 1962, 1963, Hazlett 1996), aspects of shell preference can clearly be shifted by experience (Hazlett 1995, 1996). It has been difficult to dissect out the singular shell characteristics — or recognition cues — that determine shell choice (the production component) or to explore the sensory mechanisms involved in shell choice (the perception component), because natural shells differ in a variety of characteristics that are difficult, or impossible, to control for. For example, shells of different geometries (i.e., shells produced by different gastropod species) will also differ in shell aperture dimensions, shell weight, how that weight is distributed, internal volume, and so forth.

Artificial shells for investigations of hermit crab shell selection behavior may reduce shell-to-shell variability. Experiments using plaster replicate shells made from reagent grade $CaSO_4$ and rubberized molds of interior shell surfaces have been conducted (Mesce 1993); however, these models were limited by shell geometries that exist in nature, and natural shells occupy only a small proportion of the potential gastropod shell morphospace (Raup & Michelson 1965, McGhee 1999). In this study, we present a new model shell unencumbered by previous limitations of design, size, texture, etc. Thus, it is now possible to address questions concerning shell preference relating to morphology, coloration, physical condition, weight distribution, and chemical effects by using engineering technologies to manufacture artificial shells.

The use of computer modeling provides for the design of shells with morphologies that do or do not exist in nature. This combined with the recent advent of rapid prototyping technology (*see* below), makes possible the design and production of artificial shells with finely controlled morphologies, which can be modified in subtle ways, one parameter at a time. Artificial shell manufacturing technology combined with behavioral tests may provide the ability to precisely define the ideal shell (i.e., the template) for shell choice.

Methods

Artificial shell production

Artificial shells used in the experiments were manufactured using Stereolithography, a Rapid Prototyping (RP) technology, where a 3-dimensional CAD (computer-aided design) model is replicated by stacking photo-cured resin layers into tangible representations of the virtual model. A virtual shell model was created using CAD software (Pro/Engineer 2000i^2, Parametric Technology Corporation) with similar dimensions and characteristics to that of the shell of the common periwinkle, *Littorina littorea* shell (Fig. 1). The shell model was developed by tracing a spiral curve equation having a decreasing radius with a circular cross section that decreased in diameter proportionally to the curve (automated with the software). The shell model uses three equations in cylindrical coordinates to define the spiral curve in a non-dimensional parameter, $t[0:1]$:

$$\theta = 360Nt \tag{1}$$

$$r = \exp(-8t/3) \tag{2}$$

$$z = 1.5\exp(-8t/2.5) \tag{3}$$

where θ is the angle of whorl (degrees), N is the number of revolutions around the central axis, t is the parameter that varies from 0 to 1 to define the spiral start and end point, r is the radius of the spiral measured from the centerline (cm), and z is the magnitude in the z-direction or height of the spiral (cm).

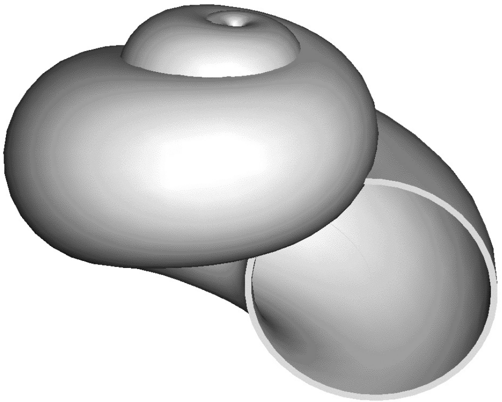

Fig. 1. Three-dimensional CAD model of the artificial shell used in Experiment 1 and modified for Experiment 2.

Artificial shells were manufactured from the three-dimensional model using outsourced stereolithography services (RP Innovations, Richardson, TX). The artificial shell was made on a 3d Systems Model 5000 SLA from DSM SOMOS® 9100 resin, an epoxy based photopolymer that mimics many key properties of polypropylene. The material exhibits exceptional durability and relatively low water absorption for use in aquatic environments (0.50%, ASTM D570-98) (ASTM 2003). In comparison with other known molluscan shell mechanical properties, DSM SOMOS® 9100 shows weaker strength properties (Jackson *et al.* 1988, DSM Somos® 2003). The resin has a tensile strength of 27.6–31.7 MPa where nacre from the shells of *Pinctada* bivalves are reported to have a tensile strength of 140–170 MPa (Jackson *et al.* 1988, DSM Somos® 2003). *Pinctada* shells also have a Young's modulus of 60–70 GPa, where the resin has a modulus of only 1.1–1.4 GPa; a much more flexible material (Jackson *et al.* 1988, DSM Somos® 2003). The artificial shells have similar geometries to that of a natural *L. littorea* shell, but are lighter in weight than natural shells of similar aperture size. The artificial shells are also semi-transparent which provides for observations of the crab's behavior inside the shell.

Artificial shells were manufactured to a prescribed size for use in all experiments (aperture length = 17.80 mm) and a second set of RP shells were modified to more closely mimic shell sizes preferred by hermit crabs of different sizes:

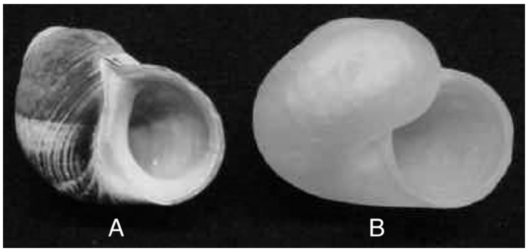

Fig. 2. Shells used in experiments involving hermit crab behavioral recognition and acceptance of shells. — **A**: Natural shell of the periwinkle snail (*L. littorea*). — **B**: Artificial shell.

$$Y = 0.2623X + 0.4342 \qquad (4)$$

where Y = log(shell aperture length) in millimeters and X = log(crab weight) in milligrams ($r^2 = 0.8625$, $p < 0.0001$) (Angel 2000). Modified shells were fitted to the average crab weight of the experimental population, taken from Nahant, Massachusetts. Modifications were made to the second set of shells using a Dremel Variable-Speed MultiPro® Rotary Tool with flexible shaft and cutting wheel. Patterns were traced onto the shells to ensure a low level of variance in aperture size of the modified shells.

These techniques resulted in a prototype artificial shell relatively similar to that of the prosobranch gastropod *L. littorea*, the common periwinkle (Fig. 2).

Experimental design

Pair-wise shell selection experiments were designed to test the recognition behavior of *Pagurus longicarpus* hermit crabs towards artificial shells. In the first experiment, the ability of the organism to discriminate between two different artificial shells was tested. In the second experiment, preference of the hermit crabs towards two shells, one coated with crushed shell material and one not, was examined. Hermit crabs in shells of the periwinkle snail *L. littorea* were collected in June of 2003 at low tide in Nahant, Massachusetts and maintained in laboratory aquaria on a diet of artificial crabmeat at room temperature (approximately 23 °C).

Experiment 1: Can *P. longicarpus* discriminate between artificial shells of differing sizes?

For this study, we tested the ability of 17 hermit crabs to discriminate between the original artificial shell and a modified version that mimicked the size preferred by the animal according to weight (equation derived by Angel 2000). The test population had a mean dry weight of 0.82 g (SD = 0.172, N = 17), which corresponds to a shell of aperture length = 15.79 mm according to Angel (2000). The unmodified shells had aperture lengths substantially larger than preferred by the crab (17.80 mm), whereas the modified artificial shells had a mean aperture length closer to that preferred by the hermit crab (mean aperture length = 15.64, SD = 0.2871, N = 17) (Angel 2000).

Each crab from the test population was gently removed from its shell using accepted techniques of physically pulling them out or applying a light heat source to the apex of the shell to remove them. Each crab was placed in a plastic arena (12 cm × 8.3 cm × 3.2 cm) holding about 220 ml of seawater and containing an unmodified artificial shell. The hermit crabs were allowed 24 hours to move into the unmodified artificial shell unprovoked, and those who did not after 24 hours (N = 3) were coaxed into accepting the shell by facing the individual toward the shell and initiating contact between the crab's antennae and chelipeds and the shell.

The experiment start condition had 17 hermit crabs occupying oversized artificial periwinkle shells. Modified artificial shells were added at time zero. Inspection and acceptance behavior of the crabs was recorded every 5 minutes for the first 30 minutes of the experiment, and every 30 minutes for the following 270 minutes; a total experiment time of 300 minutes with final shell selections recorded.

Experiment 2: Does a coating of $CaCO_3$ with organic material (taken from natural shells) increase acceptance rates by *P. longicarpus*?

The second experiment tested the hypothesis that hermit crabs prefer shells coated with calcium carbonate by offering 22 different hermit crabs a pair wise choice between modified artificial shells and modified artificial shells coated with $CaCO_3$. As Chiussi *et al.* (2001) and Mesce (1982) suggested calcium cues attract hermit crabs to objects resembling gastropod shells; hence, modified artificial shells (as described in the methods for Experiment 1) were coated with powdered calcium carbonate, obtained from finely crushed *L. littorea* shells, using a polymer adhesive. The uncoated, modified artificial shells had a mean aperture length = 15.38 mm (SD = 0.18, $N = 12$) and the coated artificial shells had a mean aperture length = 15.76 mm (SD = 0.30, $N = 12$). The test population, having a mean dry weight of 0.91 g (SD = 0.23, $N = 22$), was divided into two sub-populations, one of 10 crabs the other of 12 crabs, so that experiments could be staggered and thus fewer artificial shells were required.

All 22 crabs were gently removed from their shells and allowed to acclimate overnight. One uncoated artificial shell and one coated artificial shell were placed in opposite corners of one end of the previously described plastic arenas. Each crab was placed, naked, at the other end of the arena such that shells were equally in view of the crabs, an important element to testing calcium as a cue (Chiussi *et al.* 2001). Inspection and acceptance behavior of the crabs was observed over a 180-minute period with final shell selections recorded.

A control for the adhesive used to secure the $CaCO_3$ to artificial shells was conducted on natural shells. Eight naked hermit crabs (mean dry weight = 1.08 g, SD = 0.23, $N = 8$) were offered a pair wise choice between an uncoated natural shell and a natural shell coated with the polymer adhesive used in Experiment 2. Natural shells of similar size (mean aperture length = 16.76 mm, SD = 0.55, $N = 16$) were divided into two groups of eight, one group left untouched, and the other group coated with the adhesive. One coated shell and one uncoated shell were placed at one end of plastic arenas, and one naked crab was placed at the opposite end of each arena such that each shell was equally in view of the crab. Crabs were allowed to inspect shells for 180 minutes and final shell selections were recorded.

Fig. 3. Long-wristed hermit crab, *P. longicarpus*, occupying a modified artificial *L. littorea* shell. The artificial shell is lighter in weight than a natural shell and transparent, allowing ease of observation.

Results

Qualitative observations revealed hermit crabs not only accepted the artificial shells (Fig. 3), but also exhibited the same stereotypical behaviors when investigating the artificial shell as they do with a natural shell. Generally, the crab first contacted the shell with the antennae, and then wrapped its walking legs and chelipeds around the shell to begin an external investigation. The animal turned its body to gain access to the aperture and inserted a single cheliped into the shell, followed by the second cheliped and sometimes a walking leg. At this point, either the animal continued investigation, swinging its abdomen into the shell thus initially accepting it, or it rejected the shell. The recognition and investigation of a natural shell is a documented sequence of events (*see* Mesce 1993, Jackson & Elwood 1989, 1990, Elwood 1995, Hazlett 1996) that the hermit crabs generally exhibited when investigating artificial shells.

At the start of Experiment 1, all hermit crabs inhabited the large shells, however, many hermit crabs, including those coaxed into the shells, moved out during the experiment. Regardless, all hermit crabs performed thorough inspections of both shells and the expected outcome was a 50:50 choice split between large and small artificial shells. Of the crabs occupying shells at the end of 300 minutes, a significantly larger number accepted the modified shell, being more appropriate according to crab weight, over the larger shell ($\chi_1^2 = 6.23$, $p < 0.015$; Fig. 4a). Hermit crabs not selecting shells ($N = 4$) were excluded from the statistical analysis.

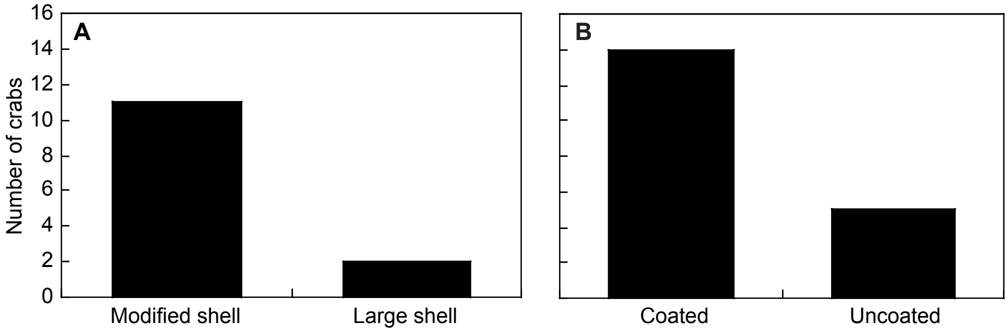

Fig. 4. Results of Experiments 1 and 2 showing number of crabs accepting given shells. — **A**: Experiment 1 results: $N = 11$ crabs accepted modified artificial shell, $N = 2$ crabs accepted large artificial shell. $\chi^2 = 6.23$, $p < 0.015$. — **B**: Experiment 2 results: $N = 14$ crabs accepted modified artificial shell coated with $CaCO_3$, $N = 5$ crabs accepted uncoated modified shells. $\chi^2 = 4.26$, $p < 0.05$.

In Experiment 2, it was expected that no preference would be shown between the coated and uncoated shell; however, of the crabs that selected shells, significant preference was shown toward the $CaCO_3$ coated shell after 180 minutes ($\chi_1^2 = 4.26$, $p < 0.05$; Fig. 4b). One crab made no movement, failing to inspect any shell, thus this animal was excluded from the statistical analysis. In the polymer adhesive control experiment, four crabs selected uncoated shells (50%) and four crabs selected coated shells (50%).

Discussion

Model results

The results of these experiments show that rapid prototyping technology can be used to produce artificial gastropod shells that hermit crabs will accept. *P. longicarpus* recognizes the artificial shell using a very similar exploration sequence as when inspecting natural shells such as grasping the shell with the chelipeds and using walking legs to investigate the inner geometry (as reported by Mesce 1993, Jackson & Elwood 1989, 1990, Elwood 1995, Hazlett 1996). Specific size modifications to the artificial shells increase acceptance rates (Fig. 4a), and coating the modified shells with calcium further increases acceptance (Fig. 4b), with no preference shown toward the adhesive used to coat the shells. These data do not rule out the possibility that hermit crabs chose shells based simply on texture; however, it would be easy to test for this by applying similar coatings that lack calcium. Regardless, this simple step-wise modification of the shell to be more desirable to hermit crabs shows the possibility for this technology in investigations regarding the recognition template. That is, because shells are first produced virtually using computer software and then manufactured to the exact computer-generated design, we can now manipulate shell characteristics to an extraordinarily fine degree. In doing so, we can create a range of shells that not only include all morphologies normally encountered by the crab, but also morphologies that do not currently exist in nature. As such, this technology makes possible the most complete exploration into preferred shell characteristics to date.

It should be noted, however, that these results represent just the beginning of the exploration and that our techniques must be refined. For example, although *P. longicarpus* adopted artificial shells of appropriate size, they quickly switched to natural shells of similar size and design when available. This suggests that recognition cues for artificial shells are highly mismatched by hermit crabs compared with natural shells. Despite mismatch, the hermit crabs treated artificial shells with similar inspection behavior to natural shells, thus warranting improvement of the current model to more closely match natural shells while retaining the ability to vary specific parameters.

Improvements to the current method will stem from observed geometrical differences between the artificial and natural shell. The development of a better 3D virtual model created using a best-fit representation of natural shell trajectories, aperture shapes, and global geometric parameters will, hopefully, improve response to and acceptance rate of the artificial shell by hermit crabs. We plan to modify internal and external geometrical features, theoretical morphology parameters such as whorl rate and generating curve shape, wall thickness, shell material, shell coloration, and weight distribution. The results of these preliminary studies warrant further development of artificial shell design to increase acceptability of the artificial shell by the hermit crab en route to determining the preferred shell characteristics.

Model applicability to recognition systems

To understand the potential utility of this technology to recognition system research, a short review of current issues is necessary. In recognition system research, generally, researchers assess the outcome of the action component (i.e., acceptance or rejection), and recognition is thus inferred through behavioral discrimination. However, two problems arise with this assumption: (1) lack of behavioral discrimination does not necessarily indicate lack of recognition, and (2) interactions between individuals blur the distinction between recognition components.

First, the complexity of discrimination depends on the fitness context of the experiment (*see* e.g., Starks *et al*. 1998); therefore, care must be taken not to suggest that recognition is absent when only behavioral discrimination is absent (*see* e.g., Pratte 1982). This problem is described well in Mateo (2002). Secondly, the behavioral response of one individual is confounded by the behavior of others. In these instances, the behavior of the interactors cannot be subdivided into a single component of the recognition system, but rather must be considered part of multiple recognition components.

This form of component blurring is often the case even when studying kin discrimination in arguably the best current invertebrate model recognition system: *Polistes* paper wasps (*see* Gamboa 1996). For an example, consider the neutral arena behavioral assays commonly used to detect kin (or nestmate) discrimination in paper wasps (*Polistes* spp.). In these assays, observers typically place a small number of individuals (2–4) in neutral arenas and then score the level of aggressive behavior in interactions between nestmates and between non-nestmates. Unfortunately, when examining interactions between live animals the behavior of one animal — e.g., appeasement, aggression, or avoidance — becomes a reliable cue of, in the case of the paper wasp, nestmate status and thus the action component becomes part of the production component.

Many researchers have avoided this problem by examining behavior directed at dead animals (e.g., *see* Dani *et al*. 1996), at inanimate objects that contain nestmate cues (e.g., the nest material, *see* Ferguson *et al*. 1987, Espelie *et al*. 1990, Pfennig 1990, Starks *et al*. 1998, Starks 1999, 2003, Lorenzi & Caprio 2000), or (although not yet with paper wasps) video/audio cues (e.g., O'Loghlen & Rothstein 2002, Hauber *et al*. 2002, Hauber 2002, Uetz & Roberts 2002). Recent results, however, have shown that recognition studies using dead conspecifics are prone to replication problems (*see* Roulston *et al*. 2003), suggesting room for improvement in a widely accepted method for controlling component blurring.

Conclusions

Previous studies and results presented here suggest that shell selection behavior by hermit crabs can be considered a model recognition system. Because shell characteristics are vital to the hermit crab's survival, recognition without discrimination is highly unlikely. Because shells selected by hermit crabs are abandoned, and thus inanimate, we need not concern ourselves with the contamination of interaction-dependent emergent behavior. Cues related to the shell are thus a pure representation of the production component: controlling these cues will allow us to determine optimal shell condition for hermit crab usage. Precise identification of preferred shell cues will allow for tests of the level at which hermit crabs can perceive cue differences (i.e., the perception component) and alterations in the experimental environment will allow us to quantify the level of flexibility of the hermit crab acceptance behavior (i.e., the action component). As such, we believe that artificial shell manufacturing technology aiding investigation into shell selection behavior in the hermit crab *P. longicarpus* is an ideal combination, potentially making hermit crabs a preferred model system in recognition behavior research.

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