

Learning in Stomatopod Crustaceans

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The stomatopod crustaceans, or mantis shrimps, are marine predators that stalk or ambush prey and that have complex intraspecific communication behavior. Their active lifestyles, means of predation, and intricate displays all require unusual flexibility in interacting with the world around them, implying a well-developed ability to learn. Stomatopods have highly evolved sensory systems, including some of the most specialized visual systems known for any animal group. Some species have been demonstrated to learn how to recognize and use novel, artificial burrows, while others are known to learn how to identify novel prey species and handle them for effective predation. Stomatopods learn the identities of individual competitors and mates, using both chemical and visual cues. Furthermore, stomatopods can be trained for psychophysical examination of their sensory abilities, including demonstration of color and polarization vision. These flexible and intelligent invertebrates continue to be attractive subjects for basic research on learning in animals with relatively simple nervous systems.

Among the most captivating of all arthropods are the stomatopod crustaceans, or mantis shrimps. These marine creatures, unfamiliar to most biologists, are abundant members of shallow marine ecosystems, where they are often the dominant invertebrate predators. Their common name refers to their method of capturing prey using a folded, anterior raptorial appendage that looks superficially like the foreleg of a praying mantis. However, the appellation "mantis shrimp" is quite misleading. The animals have little resemblance to shrimps or prawns, looking instead more like miniature, clawless lobsters. Indeed, some species rival lobsters in size. More importantly, they are only distantly related to shrimps. Their order, the Hoplocarida, diverged from all other modern crustaceans nearly half a billion years ago (Hof, 1998; Schram, 1969). This ancient separation has produced a group of about 500 anatomically similar modern species, most of which are instantly recognizable as stomatopods even to an untrained observer. Of more significance to this review, this group also has evolved a suite of unusual, even

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unique, characteristics that make the group particularly interesting to behavioral biologists and others interested in behavioral flexibility and learning.

Stomatopods are pugnacious predators that use their raptorial appendage sometimes in defense, but more often to disable prey either by a rapid snatching or spearing movement, or by powerful smashing blows (see general descriptions by Caldwell & Dingle, 1976; Reaka, 1981; for a more formal review, see Caldwell & Dingle, 1975). In the "speareers," the terminal joint, the dactyl, of this appendage folds back like a jackknife, and the edge of the dactyl (corresponding to the blade of the knife) is lined with spines that slice or impale prey. In "smashers," the dactyl is pointed, relatively reduced in size, and normally folded back along the second segment of the raptorial appendage (Figure 1). Their strikes are most often made with the armored heel of this terminal joint, which can crash into hard-bodied prey in one of the fastest movements made by an animal (Burrows, 1969, Patek, Korff, & Caldwell, 2004). When hitting soft-bodied prey (an excellent example is a human finger), the sharpened dactyl can be extended to pierce the target.

Use of such a powerful raptorial appendage requires care. The predator itself may be damaged or disabled if the blow is misaimed or launched inappropriately, so the intended target has to be accurately identified and precisely located in space. Mantis shrimps, therefore, must have some conception of three-dimensional space and must know both their predators and prey. This requires high-quality sense organs for range-finding and correct decision-making. Mantis shrimps also defend themselves aggressively from competitors but normally offer much gentler treatment to prospective (or permanent) mates, so they must know something about animals with whom they are grappling. Particularly in smashers, the raptorial weapon is so destructive that it is risky for an animal to accept a blow from a conspecific; stomatopods are among the very few animals that can almost instantly disable or kill a same-sized opponent. Such competence encourages the evolution of efficient means of sizing up opponents and communicating fighting competence (but not always honestly).

The stomatopods' mode of predation demands behavioral flexibility and efficient learning. Likewise, other aspects of their lifestyles and ecology require similar capabilities. Mantis shrimps commonly occupy holes and burrows (Figure 1), and many species (mostly smashers) leave their refuges to hunt out in the open where they, themselves, are vulnerable to predation. Consequently, a foraging mantis shrimp must be able to identify its own home and be able to reach it quickly in the event that a predator or competitor approaches. It also must be able to find a new burrow quickly if displaced. In addition, mantis shrimps have an interesting diversity of mating systems, ranging from long-term monogamy in many speareers to extreme promiscuity in some smashers (Caldwell, 1991). In at least one species, it is the females that initiate courtship (Hatzios & Caldwell, 1983). As in most animals, stomatopod courtship is ritualized, but the flexibility that is seen in the flow of the behavior and in the decisions that need to be made suggests that learning is probably involved. Many mantis shrimp species (mostly smashers) are very colorful, and the colors appear to play critical roles in visual communication between potential mates, competitors, and even interspecifically (Caldwell & Dingle, 1975; Chiao, Cronin, & Marshall, 2000; Hazlett, 1979). Thus, learning may also be involved in intraspecific and interspecific communications.

These demands and the behavioral characteristics to which they have led have produced a group of arthropods that seem unusually aware and intelligent. Land (1984) has called them "crustacean primates" because of their air of inquisitiveness and their ability to manipulate their environment. Their maxillipeds (anterior, food-handling appendages) make effective "hands," giving stomatopods the means to interact with their environment much more precisely than is the case for many other animals. This also gives them the ability to select and manipulate objects for burrow construction, prey handling, and even for mating or other intraspecific behavior. The smashers generally have the most complicated behavior and probably benefit the most from behavioral flexibility (see also Reaka & Manning, 1981). They are also relatively attractive to study because they spend time in the open, making their behavior easy to observe. Consequently, almost all studies on learning in stomatopods have been carried out on smashing species.

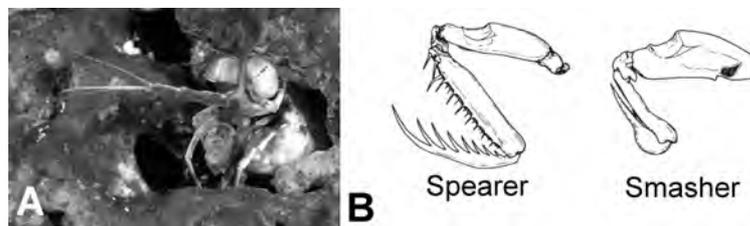


Figure 1. (A) The stomatopod *Haptosquilla stoliura* (a smashing species) at its burrow entrance. Note the long antennules and the stalked compound eyes extending out of the burrow. The medial flagellum of the antennule, which is chemoreceptive, appears shorter and white in this photograph. The longer, banded flagellae are thought to be only mechanoreceptive. Note the three-part compound eyes, most noticeable in the left eye facing the camera. (B) Raptorial appendages of a typical spearer (*Haptosquilla harpax*, left) and a typical smasher (*Odontodactylus scyllarus*, right). Note the numerous spines on the terminal segment of the spearer type, and the sharp "finger" and armored heel on that of the smasher.

In this review, we will briefly introduce the nervous systems of stomatopod crustaceans and describe their highly specialized sensory systems—especially their vision—in some detail. We will then discuss laboratory studies of learning in these fascinating arthropods, including the evidence for stomatopod learning and behavioral flexibility from field studies and ecological work, and we will conclude with some suggestions for promising future avenues of research.

Stomatopod Nervous Systems

Despite the stomatopods' relatively large size and a continuing interest in their behavior, their neuroanatomy has been only superficially investigated.

Central Nervous System

Studies of the brain and ventral nerve cord had an early start (reviewed in Bullock & Horridge, 1965; Ferraro & Burgni, 1989). An excellent historical review of this topic, with many citations to 19th and early 20th century literature, can

be found in Ferraro and Burgni (1989). Unfortunately, modern investigatory techniques have rarely been brought to bear on these systems. A notable exception is work on the midbrain of the smasher *Neogonodactylus oerstedii* in studies of antennular sensory function by Derby, Fortier, Harrison, and Cate (2003). Virtually all other work on the brain itself has focused on spearers, especially *Squilla mantis*.

Kleinlogel, Marshall, Horwood, and Land (2003) provide a recent, thorough investigation of the neuroanatomy of the optic ganglia in the eyestalks in several species of smashers. In some respects, particularly the modularity of functional units, this anatomy is quite different from that of other crustaceans (Bullock & Horridge, 1965; Strausfeld & Nässel, 1981). How these visual structures might be involved in learning, or even behavior, has not been studied. Looking still further from the brain, Heitler, Fraser, and Ferraro (2000) described the functional morphology underlying the escape response of the spearer, *Squilla mantis*, which is controlled by giant axon systems in the ventral nerve cord like those of decapods and other crustaceans. This close connection of neuroanatomy and behavior contributes to strongly reflexive behavior. How such a behavior might be modified by experience (e.g. through facilitation or habituation), and how this might relate to neurophysiological events, remains uninvestigated.

Stomatopod Sensory Systems

Much recent research has been devoted to understanding stomatopod vision and, to a lesser degree, chemoreception. These senses play central roles in all aspects of stomatopod learning examined thus far. Mantis shrimps also have an array of mechanoreceptors, but oddly, essentially nothing is known about their function or role in behavior; studies on mechanoreception thus far have concentrated only on internal receptors (e.g. Wales & Ferrero, 1987; Wales, 1989). Stomatopods are very responsive to mechanical disturbance and apparently communicate using this modality, so mechanosensory input probably affects their behavior. They also make sounds by rapping on the substrate with their raptorial appendages or by vibrating body parts. Research in the area of mechanoreception and hearing will be very welcome.

Chemoreception. Like most crustaceans, stomatopods probably have chemoreceptive sensillae on many body parts. However, the primary chemoreceptive appendages are the first antennae, commonly called the antennules. These triramous, often feathery, sense organs extend quite far from the anterior region of the animal (in some species, more than one-third of the body length). Mantis shrimps benefit from being able to sense their surroundings while remaining secure within their burrows (Figure 1). The two outer flagellae of each antennule are probably mechanoreceptive in function, but the third flagellum is lined with chemosensory aesthetascs (Derby et al., 2003; Mead & Koehl, 2000; Mead, Wiley, Koehl, & Koseff, 2003). Sensory afferents originating in each antennule enter two neuropils in the midbrain, of which one, the olfactory lobe, is certainly chemosensory (Derby et al., 2003). The olfactory lobe is glomerular in organization, like homologous lobes of decapod crustaceans, but *N. oerstedii* has many fewer glomeruli per lobe than any known decapod. The generally similar organization of

tracts and central structures suggests that many principles derived from the lengthy work on decapod chemoreception may apply to stomatopods as well.

Like other crustaceans, stomatopods sample the chemical environment by flicking the antennules, and the rate and amplitude of the flicking often increases when the animal is aroused. Flicking movements splay out the aesthetac sensillae, capturing a new mass of water for chemical analysis (Mead & Koehl, 2000; Mead et al., 2003). Chemosensation is important for feeding, sensing the presence of other animals, communication, and it plays a role in learning the identities of conspecifics. Considering the significance of chemosensation in the lives of stomatopods, it is surprising to learn that there are many fewer types of sensillae on the antennules than in homologous structures of decapods (Derby et al., 2003).

Vision. Given that stomatopods inhabit shallow, well-lit marine ecosystems, it is no surprise that vision is their most highly developed sensory modality. In fact, it is the mantis shrimps' large and active eyes that give them the air of intelligence and alertness. Like the antennules, the eyes are mounted as anteriorly as possible and can extend beyond the burrow entrance when the animal is alerted (Figure 1). The compound eyes vary in shape and overall structure among species and are in fact useful for taxonomic assignment (Harling, 2000; Manning, Schiff, & Abbott, 1984). However, the general features are the same in most stomatopod groups. The eyes are on mobile stalks driven by an array of muscles (Jones, 1994), and eye motion is essential for seeing in these animals as in others, including humans (Land, Marshall, Brownless, & Cronin, 1990). Cronin, Marshall, and Land (1994) and Cronin and Marshall (2004) provide reviews of stomatopod vision.

Compound eyes of stomatopods are of the apposition type; each ommatidium is optically isolated from all others (Figure 2 and Figure 3) and thus serves as a single sampling unit. Stomatopods, uniquely among modern animals, take advantage of this to produce triply overlapping visual fields within a single eye in some directions of view (Cronin, 1986; Exner, 1891; Horridge, 1978; Marshall & Land, 1993; Marshall, Land, King, & Cronin, 1991a, 1991b;). This multiple sampling of a specific area of the visual field is probably involved in rangefinding. The overlapping visual fields provide another, unexpected, benefit. The visual receptors devoted to color vision and polarization vision are restricted to a single eye region called the midband, usually made up of six parallel rows of ommatidia that wrap around the eye like a broad equator (Figure 2; Marshall, 1988; Marshall et al., 1991a, 1991b). Photoreceptors within these ommatidia contain several functional and anatomical adaptations that enhance the perception of color and facilitate the visual analysis of polarized light. Ommatidia in the rest of the eye are most likely devoted to spatial vision and motion vision (Cronin & Marshall, 2004).

Preprocessed information flows from the eye to the central nervous system within parallel data streams that provide, respectively, information about object location, distance, motion, and the color and polarization features of a stimulus (Cronin & Marshall, 2001). In fact, with so many different features of each stimulus being provided by the eye, learning could very well be necessary to recognize and discriminate among most of the biologically relevant objects that come into view.

Color Vision. Seeing in color requires that two or more spectrally different photoreceptor classes be present in the retina. Mantis shrimps more than meet this requirement with a greater array of spectral classes than is found in any animal group. In a single retina, stomatopods have as many as ten different visual pigments, each with a different peak sensitivities, in the human "visible" spectrum (400 to 700 nm; Cronin & Marshall, 1989a, 1989b). Of these, eight are located in a group of specialized ommatidia located in the dorsal four midband rows. Each of these ommatidia contained different, paired photoreceptor classes, one atop the other ("Color System", Figure 3). This arrangement causes the light reaching the more basal receptor type in each row to be filtered first through the receptor above it, sharpening its spectral tuning (Cronin & Marshall, 1989a, 1989b). The second and third of these rows of ommatidia also contain brightly colored filters that fine tune receptor sensitivity (Cronin, Marshall, & Caldwell, 1994; Marshall, 1988; Marshall et al., 1991b). Together, this receptor set has the potential to provide a richer sense of color than exists in any other type of animal (Cronin & Caldwell, 2002; Cronin, Caldwell, & Erdmann, 2002; Cronin, Caldwell, & Marshall, 2001; Cronin, Marshall, & Caldwell, 2000; Cronin, Marshall, Caldwell, & Shashar, 1994; Schiff, Manning, & Abbott, 1986).

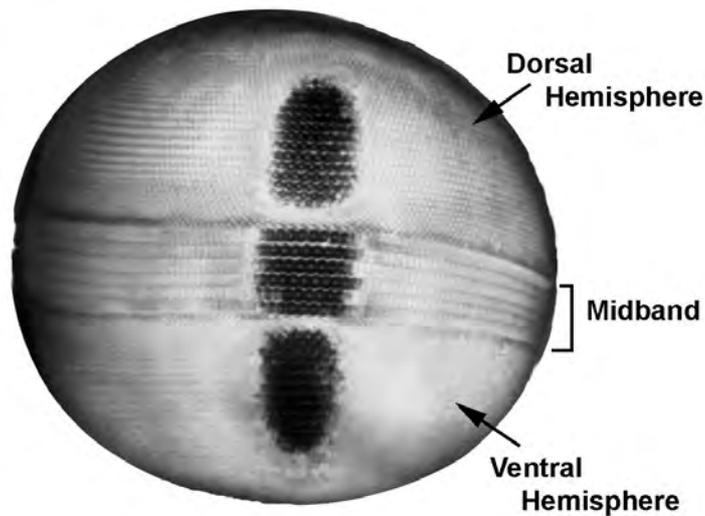


Figure 2. A frontal view of the compound eye of *Odontodactylus scyllarus*. The dorsal and ventral hemispheric ommatidial arrays are noted. These eye regions are much like the typical organization seen in crustacean apposition compound eyes. The midband region of six parallel ommatidial rows extending completely around the middle of the eye is unique to stomatopods. The dark patch in each of the three eye regions is the "pseudopupil", which looks dark because it absorbs the light in the direction of the camera; thus, the three separate pseudopupils indicate the ommatidial patches looking at the camera. The pattern indicates that three different regions of the same eye sample the same spot in visual space.

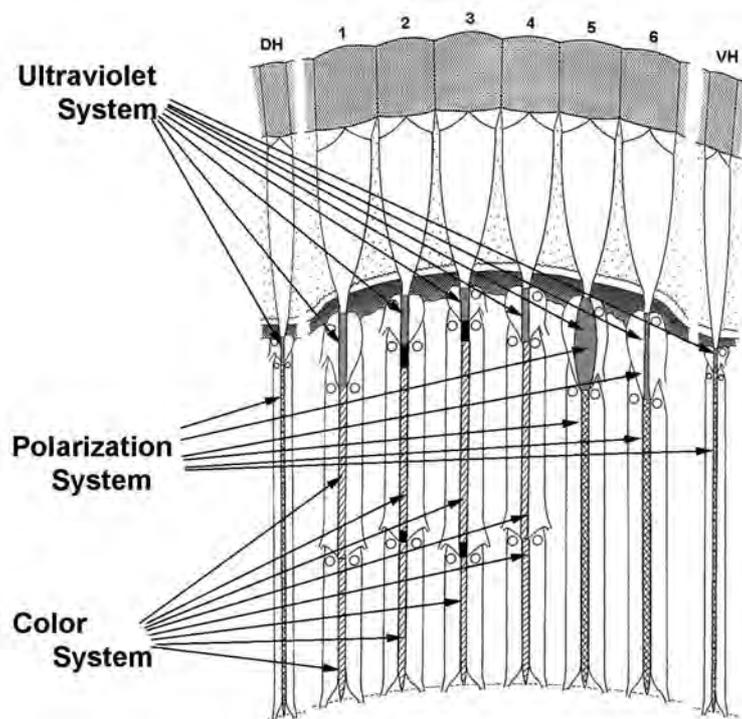


Figure 3. A diagrammatic view of the retina of a typical stomatopod crustacean that has a 6-row midband (like most species discussed in this review; see also Figure 2). The cornea with its facets is located at the top of the figure, and is underlain by a set of crystalline cones, one per ommatidium. Next are the distal photoreceptor cells, all of which contain ultraviolet-sensitive visual pigments in their rhabdoms ("Ultraviolet System"); the rhabdoms themselves are indicated by fine diagonal hatching. The main photoreceptors lie under these, and are labeled according to whether they contribute to the polychromatic color-vision system ("Color System"; rhabdoms with coarse diagonal hatching) or the polarization-vision system ("Polarization System"; rhabdoms with cross hatching). Note that some of the ultraviolet-sensitive cells have an additional role in polarization vision. Circles in the receptor cells indicate cell nuclei, and the black sections in main photoreceptors of midband rows 2 and 3 indicate the locations of intrarhabdomal colored filters. (DH: dorsal hemisphere, VH: ventral hemisphere, 1-6: ommatidial rows of the midband).

Besides the receptor system just described, many stomatopods have numerous spectral classes of ultraviolet-sensitive photoreceptors ("UV System", Figure 3; see Cronin, Marshall, Quinn, & King, 1994; Marshall & Oberwinkler, 1999). Whether these play a role in color vision is not known, nor is it clear what information they add to this already rich visual experience.

A third set of receptors, found both in the two ventral-most rows of midband ommatidia and throughout the main receptor sets of the rest of the eye, is anatomically specialized for the analysis of polarized light ("Polarization System", Figure 3). This sensory capability, widespread among arthropods, is particularly well developed in many stomatopod species (Marshall, 1988; Marshall et al., 1991a). Some mantis shrimps have specialized body parts that reflect polarized light, apparently for communication (Cronin et al., 2003a, 2003b). It is likely that polarization vision plays key roles in visual communication, predation, and possi-

bly in navigation as well, but this has not yet been investigated. However, as will be seen later, stomatopods can be trained to use both color and polarization vision to make visual discriminations.

Stomatopod Learning

Stomatopods are active animals, ecologically diverse and behaviorally complex. Their behavior is flexible, varying with context and experience, making mantis shrimps excellent models for research on learning in so-called "simple" animals (e.g., Prete, 2004). In this section, we review what is known about stomatopod learning, and in the concluding section of this paper we suggest some directions for further work that seem promising. As with other animals, the most effective research on stomatopods has taken advantage of the animals' normally occurring behaviors rather than attempting to train the animals to exhibit rather artificial responses.

Predator Recognition

An inborn ability to react to stimuli associated with danger can be useful to any animal. Some stomatopods can learn chemical cues that identify a potential predator. For instance, the Caribbean smasher, *Neogonodactylus bredini*, has an uneasy relationship with the small octopus *Octopus joubini*. Both species occupy crevices and cavities in coral, and similar-sized individuals will battle for possession of such a cavity. Their size ranges overlap, but when there is a great size disparity between two animals, the larger of either species can subdue and consume the smaller. Caldwell and Lamp (1981) investigated chemically mediated recognition of *O. joubini* by *N. bredini* by allowing naïve stomatopods to approach a cavity occupied by an octopus. Generally, the first time *N. bredini* encountered an occupied cavity, they readily entered it until they came in contact with the octopus, at which time they usually became aggressive. However, experienced stomatopods became significantly more cautious when approaching a cavity that had been filled with water that contained octopus odor (i.e., water from a container with an octopus in it). They were significantly slower to enter such a cavity and took up defensive postures at the burrow's entrance; they had learned chemical cues that indicated the presence of their competitor. At the sizes tested, the octopus probably did not pose a serious threat, but its bite could have been lethal. It would be interesting to know whether conditioned stomatopods would avoid larger octopus entirely.

Burrow Identification

Most species of mantis shrimp smashers inhabit holes or cavities in coral or rubble, often modifying these naturally occurring spaces to make them most suitable for occupation. In fact, it seems likely that particularly suitable cavities are continually reoccupied by many animals in succession over periods of months or years. Cavities are limiting resources for natural populations of stomatopods (Steger, 1987), and when artificial cavities are added to areas inhabited by stomatopods, almost every new site becomes inhabited within a few weeks (Cald-

well, Roderick, & Shuster, 1989). Individuals of most species will aggressively defend their home burrow, often to the death, especially when the cavity is of the preferred size (Caldwell, 1987). Thus, for stomatopods, burrows are a critical, highly valuable commodity.

Using a type of burrow never seen before by her subjects, Reaka (1980) examined learning in the Indopacific *Gonodactylaceus falcatus*, a species that normally occupies cavities in coral. Animals living in aquaria without other refuges available were provided with small Ehrlenmeyer flasks, painted black and lying on their sides on the aquarium sand. Animals were tested over a period of several days, measuring the time until the flask was occupied; once the animal had used the flask for one hour, the novel burrow was removed from the aquarium until the next day. On the first day, animals investigated the novel items at length, taking up to 18 hours before making their first entry. However, the median time to enter decreased very rapidly on subsequent presentations (Figure 4); after only three days entry into a flask typically occurred within just a few minutes, and by the fifth day most animals entered the flask immediately after a quick look to determine which end was the entrance. Learning was similar even if flasks were presented at 3-day, rather than 1-day, intervals, but the ability to recognize the flask waned after a week without exposure to the novel hiding place. However, even after a period of two weeks, experienced stomatopods relearned the task more rapidly than naïve animals (Reaka, 1980).

So, stomatopods (at least some species) can adjust to accept novel abodes. In nature, however, both novel and traditional burrows might already be occupied. Consequently, when approaching a burrow, most mantis shrimps are cautious, touching the entrance and testing its contents with their antennules; Reaka (1980) observed similar behavior when stomatopods first encountered her experimental burrows. In fact, stomatopods can even estimate the size of an occupant from the burrow's chemical contents (Caldwell, 1987).

There is also a growing body of evidence that stomatopods can remember other individuals that they have encountered, and that they remember animals with whom they have fought as well as the outcomes of those fights (Adams & Caldwell, 1990). They can even use their reputations as good fighters to deceive intruders they have met previously, if they encounter the same intruder when they are at a disadvantage; for example, when they are vulnerable just after molting (Caldwell, 1986).

Individual Recognition

Aggressive encounters between stomatopods are dangerous for both combatants; even the winner can be seriously injured in the course of a fight. This places a high value on remembering past encounters and knowing, in advance, who is likely to win. The earliest evidence for individual recognition by stomatopods was obtained from a Pacific smasher, *Neogonodactylus festae*, in the context of recalling past aggressive events (Caldwell, 1979). Pairs of individuals, size and sex-matched, interacted as follows: One individual was introduced to an empty aquarium and allowed to enter an artificial burrow. After it had been resident for 15 min, a second individual was introduced and interactions were recorded for 5

min. If the animal originally in the artificial burrow continued to retain it, it was considered the "resident" of the burrow, and both animals were removed. Fifteen minutes later, the animal that was unable to dislodge the resident was reintroduced to the same aquarium, which had been completely cleaned and refilled with new water, and faced a cavity that had been filled with one of three water sources: (1) water from the former, victorious resident (collected before the animals first encountered each other), (2) water from an individual it had never encountered before, and (3) fresh seawater. All animals quickly entered the cavity when it only contained seawater, and delayed only slightly when it contained water from a stranger, but most test animals never attempted to enter the cavity when it was filled with water from the former victor's burrow. The results imply that *N. festae* learn the identities of individuals that have defeated them in the past and identify them via chemical cues in the water. Since the test only included "losers," however, the possibility remains that all animals that have been met in the past are recalled, not only victors. This question was addressed in a following study (Caldwell, 1985).

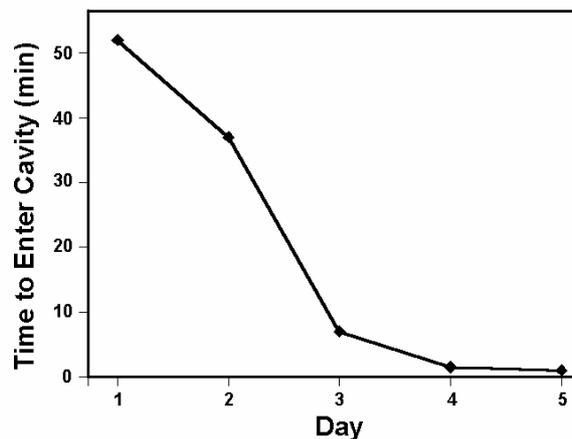


Figure 4. Learning of burrow recognition in the stomatopod *Gonodactylaceus falcatus*. The graph is based on data from Reaka (1980) and plots the median time to enter a novel burrow vs. day of the experiment; see the text for further information.

In these later experiments, similar in overall design to the ones just described, each animal was introduced to the test aquarium twice, 30 min apart, before being tested. One time it met a smaller resident, which it successfully displaced, and the other time it met a larger resident that it could not dislodge; the order of these two encounters was randomized. 30 min after the second encounter the test animal was placed in the cleaned and refilled test aquarium, with the now-empty cavity containing the water of either the defeated or the victorious former resident, and after another 30 min this was repeated with the water of the other former resident. Animals were significantly slower to enter the cavity if it contained water from the victorious resident than if the contents were from the evicted resident, suggesting that both previously encountered animals were not only remembered, but that their chemical signature was associated with the memory of their fighting prowess. Thus, they were likely recalled as individuals.

Individual recognition even occurs across species in species of *Neogonodactylus*. When individuals of *N. zaca* met and were defeated by resident *N. bahiahondensis* in a test situation like that just described, and were later exposed to a cavity containing either the odor of the former victor or that of an unknown *N. bahiahondensis*, they were significantly more hesitant to enter when the artificial burrow contained the odor of the known victor than when it contained that of the stranger (Caldwell, 1982).

Recent tests of individual recognition have extended work to other species and to more naturalistic experimental situations. In these, which were conducted by one of us (RLC) and not reported previously, pairs of individuals of *Neogonodactylus bredini* were maintained in single 38-liter aquaria and allowed to establish a dominant-subordinate relationship. Each animal had its own artificial burrow (a piece of plastic tubing), and pairs were observed daily for two weeks to ascertain dominance. Dominant individuals evicted subordinates from their homes, defended their own cavities, and/or pursued the other animal more often. After this time, each animal was tested for odor recognition in its own aquarium by being exposed to flowing water (using a peristaltic pump) that had contained either its former tank-mate or a size and sex-matched stranger. Water was drawn from a 200 ml reservoir that had contained the sample animal and was pumped at 10 ml/min, 2 cm from the entrance to the home cavity of the test animal. Pumping occurred for 15 s every 2 min for a total observation period of 20 min. Before pumping odor, clean seawater was first pumped on the same schedule until the test animal no longer responded to the stimulus. Half the animals were presented with the familiar odor first, and the other half with the stranger's odor first. Test animals were scored as "vigilant" during each 2 min pumping sequence by recording whenever any part of its eyes extended across the plane of the cavity entrance.

In these experiments, both dominant and subordinate animals became more vigilant when presented with either familiar or strange chemical odors than during the baseline period when only clean water was delivered (Wilcoxon, p always < 0.05 for dominants or subordinates, familiar or unfamiliar odors). Figure 5 shows results for tests with dominant animals (top panel) and subordinates (bottom panel). Dominants were significantly less vigilant in response to the odors of familiar subordinates than strangers in the first, third, and fourth intervals (Wilcoxon, $p < 0.05$ for interval 1; $p < 0.01$ for intervals 3 and 4). In contrast, subordinate test animals' responses to the odors of familiar, dominant animals and strangers were not significantly different. Comparing across groups, subordinate and dominant animals did not respond differently to strange odors (Mann-Whitney, $p > 0.05$), but dominants were significantly less vigilant when presented with familiar odors than were subordinates in intervals 1, 3, 4, and 5 (Mann-Whitney, $p < 0.05$ for intervals 4 and 5, $p < 0.01$ for intervals 1 and 3).

These results demonstrate that dominant neighbors recognize subordinates in pair-wise relationships that exist over a period of time and in an experiment that attempts to provide a naturalistic social environment. In these experiments, it is best to think of "individual recognition" as the use of a sufficient number of cues so that no two animals will be confused (Barrows, Bell, & Michener, 1975). While the study did not demonstrate that one *N. bredini* can recognize all conspecifics with which it has interacted, it does show that there exists a chemical recognition

system capable of distinguishing those individuals previously defeated from those not yet encountered.

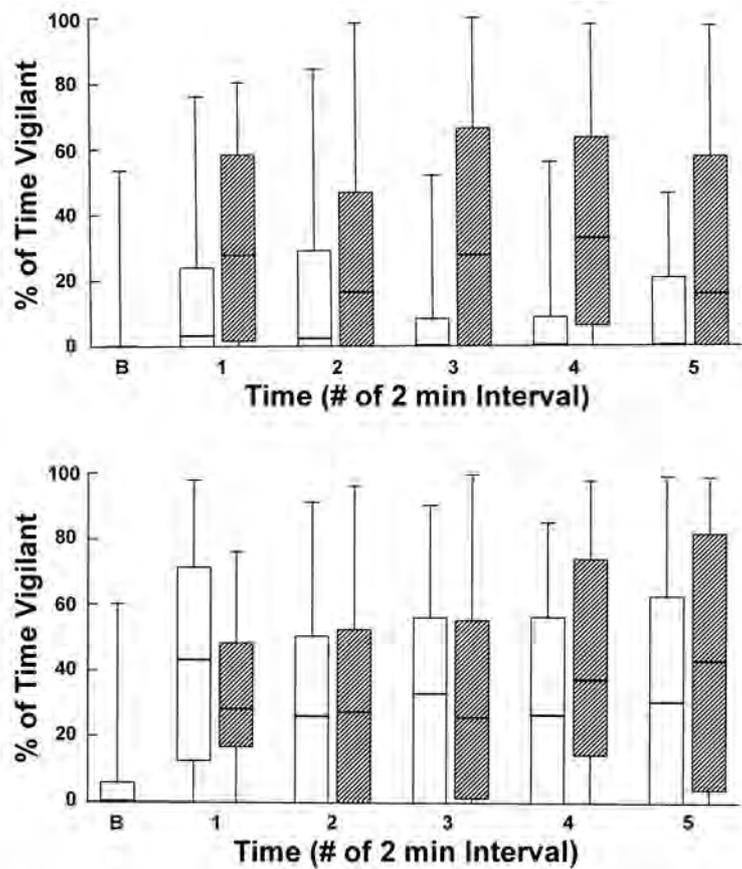


Figure 5. Chemically mediated individual recognition in *Neogonodactylus bredini*. The graphs are box and whisker plots of test animals' response in percent time vigilant to the pumping of clean water during the baseline period, and to the first five intervals of odor presentation. Boxes range from the 25th to the 75th percentile, with the horizontal line indicating the median. Whiskers extend to the 5th and 95th percentile of responses. Clear boxes show response to familiar odor; hatched boxes show response to strange odor. Top panel, responses by dominant animals; bottom panel, responses by subordinate animals.

If stomatopods remember those with whom they have warred, it should come as no great surprise to find that they also recall the ones they have loved. The species *Neogonodactylus bredini*, the same smashing stomatopod used in the socialization studies just described, forms temporary pairs that last only a few days. During this time, one male and one female share a cavity; the male guards the entrance and mates with the female until she spawns within the cavity (Dingle & Caldwell, 1972; Shuster & Caldwell, 1989). Once the female has released her eggs, the male departs, leaving the cavity to the female; she remains to care for the eggs for several weeks until the larvae hatch and become free living. During this extended period of egg care, it is possible that the former male mate might return

while searching for a home. If so, the male's fitness would be severely degraded if he evicted his former partner and allowed his offspring to perish, so there is good reason for him to remember her and avoid conflict.

To study mate recognition, Caldwell (1992) established breeding pairs of *N. bredini* in the laboratory. After egg deposition, each female was moved to a new burrow and either the former male mate or an unknown male was introduced (each mated female eventually encountered both males). Aggression between former mates occurred at extremely low levels; the number of pairs in which an aggressive act was scored was nearly six times as high between strangers than between former mates. Not only did males express lower levels of aggression to former mates, but the females also were much less likely to initiate any aggressive acts towards mates than strangers. The lowered aggression by males was seen even when the female had been moved to a new burrow without her eggs, strongly implying that the female's identity was the key factor in reducing aggression. Former mates remembered each other for surprising lengths of time; aggression between these individuals remained low even after two weeks of separation (Caldwell, 1992). Based on the observation that approaching males used their antennules actively to explore each burrow entrance, females are probably recognized chemically. Females also gave a specific maxilliped display that created a water current flowing out of the burrow, which would facilitate the transfer of chemical information to the male. (Female lobsters do much the same thing to direct chemicals towards courting males; Atema, 1986). Whether females can recognize approaching males visually is uncertain, but results from another burrow-dwelling smasher suggest that visual recognition of conspecifics is possible.

Haptosquilla glyptocercus is an Indopacific species that occupies cavities in reef and coral rubble and is noteworthy for its extremely polymorphic appearance. Animals in one reef flat region vary in color from black through green and brown to tan or cream-colored, with mottling or speckling on the background color. They often forage in the open and must frequently encounter their neighbors in the field. One of us (RLC) tested visual recognition of neighbors in a laboratory setting. Animals were collected from rubble near Lizard Island, Australia, and maintained individually in aquaria with a black, plastic tube as a burrow. For testing, individuals were allowed to enter a black glass vial attached to one end of a gray plastic box, 18 x 12 x 7 cm in size, and allowed to settle in for at least 24 h. The long dimension of the box was divided by a watertight, clear divider that formed a small compartment opposite the home of the test animal. The arena was lit so that this animal could clearly see another individual *H. glyptocercus* released into the distal compartment, but this new animal could neither see nor react to the presence of the resident.

After the 24-h settling-in period, a selected animal was introduced into the distal compartment behind an opaque card, and the card was removed once the introduced partner settled down. Each resident could face one of two partners. Both were the same sex and differed in length by no more than 2 mm, but they were noticeably different in coloration. The test partner was present for 1 h, after which it was again removed from behind the opaque card. Five minutes later, an animal was placed in the observation section as before. Half of the time, this was the same test partner (the one just seen); the other half, it was the other, differently

colored one that had not been seen before. Vigilance on the part of the resident was scored as the percent of the time over the next five minutes that it extended its eye-stalks beyond the entrance of the artificial burrow. After this five-minute period, the animal being viewed was removed from behind the card and the resident was returned to its home aquarium. One day later, the resident was placed back in the test chamber, and the test was repeated exactly as before, except that this time the viewed animal was the one not seen the day before.

Twelve residents were tested successfully. Of these, ten were more attentive to the animal they had not seen before (i.e. they had a higher vigilance score), and two were more attentive to the familiar animal (Sign Test, two-tailed; $N=12$; $p = 0.038$). This is a fairly crude experiment in that the differences among test partners were selected using human, not stomatopod, vision, but the results suggest that *H. glyptocercus* can remember and recognize conspecifics based on appearance. Typically, the animal being viewed was relatively inactive throughout the time it was being seen, so it is reasonable to hypothesize that the differences being recognized were not behavioral but were likely the color and/or pattern of the viewed stomatopod.

Training Experiments With Stomatopod Crustaceans

All experimental work with learning in mantis shrimps reviewed to this point has been concerned with recognition of critical organisms or of structures in the environment. The animals learned more-or-less as they naturally would in the course of their lives, and were not rewarded beyond the natural reward of reducing risks of aggression or finding security in a burrow. Stomatopods have also been trained to perform particular tasks in order to obtain a food reward. These experiments examined visual function and took advantage of a characteristic behavior of smashers, their tendency to pick up objects that they can handle and tap or bash them with their raptorial appendage, evidently in an attempt to learn whether they are edible. Two sets of experiments will be described.

Tests of Color Vision in Stomatopods. The complexity of the stomatopod retina, with its large number of spectrally distinct photoreceptor classes (Figure 3), implies that knowing the spectral features of stimuli, in other words, their colors, is very important to stomatopods. Color vision could be important in predator and prey detection and recognition in the difficult viewing conditions that exist underwater, and could serve roles in signal interpretation or individual recognition (as just described). Like *Haptosquilla glyptocercus*, many stomatopod species are both colorful and polymorphic (Dingle, 1964; Caldwell & Dingle, 1975). Although the stomatopods' retinal organization strongly implies that color vision exists in many species, finding behavioral evidence of the ability to discriminate among stimuli on the basis of color is the required proof. Marshall, Jones, and Cronin (1996) undertook this task by training stomatopods to discriminate among different colors. They selected the large smasher, *Odontodactylus scyllarus*, for the study, and trained individuals to break into a small, hollow plastic cube. Five sides of the cube were covered with thin glass which could be broken to obtain a food reward, and the sixth side was covered with a thin square piece of plastic, either of one of four

colors or one of six shades of gray, from white to nearly black (Figure 6). Individual animals were trained with cubes of one color, or one shade of gray, in a training paradigm in which the correct cube was primed with food and two other cubes, empty and of different shades of neutral gray, were placed with it in a random order. During actual tests, no food was provided, and the first cube touched was scored as the selected cube.

Animals never learned to discriminate among shades of gray (a common result in studies of color vision with many animals), but they became quite competent at discriminating red, green, and yellow from gray (Figure 6). They could do this even if the colors were darkened by overlaying them with transparent, gray plastic. Thus, they both learned the task and demonstrated that they have true color vision. Interestingly, they never were able to discriminate blue from gray. Marshall et al. (1996) noted that the particular shade of blue that was selected for the experiment stimulates blue-sensitive receptors in the retina almost identically to a neutral (colorless) stimulus. Thus, the results with blue were actually consistent with our understanding of stomatopod color vision. It would, of course, be interesting to test this species using a different shade of blue which is expected to cause a different set of receptor responses than a gray target. It would also be very interesting to learn whether stomatopods learn to discriminate targets that differ only in their ultraviolet coloration.

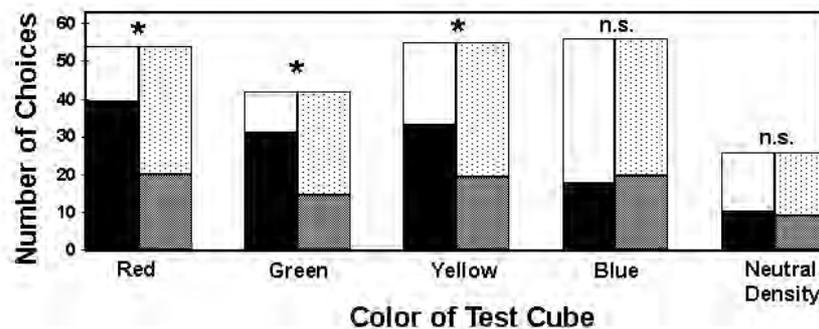


Figure 6. Tests of color vision in the stomatopod *Odontodactylus scyllarus*. The figure shows the results of tests for four differently colored cubes as well as for an attempt to train the animals to a specific level of gray or neutral density (ND). For each color, expected choice numbers are shown by the right grey (correct) and dotted (incorrect) bars and the observed choices by the left, black (correct) and white (incorrect) bars. * indicates a significant difference between observed and expected choices ($p < 0.001$ in chi-square test); n.s., not significantly different. Further details in text and in Marshall et al. (1996).

Tests of Polarization Vision. Most stomatopod retinas contain an array of polarization-sensitive photoreceptors types similar in complexity to that of the color system (Figure 3). Furthermore, these animals are thought to use patterns of reflection of polarized light as visual signals, much as they use color patterns (Cronin et al., 2003a, 2003b). All this suggested to us that mantis shrimps could have true polarization vision and thus be capable of discriminating among stimuli using only differences in the reflection of polarized light. This was tested in a series of training experiments very much like those just described to investigate stomatopod

color vision (Marshall, Cronin, & Shashar, 1999). Stomatopods were trained to select an object containing food and break into it through a thin cover glass window. The objects on which they were trained differed only in the orientation of polarized light they reflected; pieces of polaroid sheet were affixed to the front face of the food-containing object to create either a given *e*-vector orientation or a simple pattern of polarization. The test objects were either cubes, used with *Odontodactylus scyllarus* as in the earlier work with color vision (Marshall et al., 1996), or short plastic tubes, used with the aggressive smasher *Gonodactylus chiragra* (Marshall et al., 1999). As in the earlier work, during testing the trained object contained no food and was placed in a group of three objects, two of which were faced with non-polarizing, neutral density filters. And again, as a control, animals were tested for their ability to learn a particular shade of gray.

Results were quite similar to those obtained when animals were trained to colors or grays (Figure 7). Animals of both species became adept at discriminating the polarization object to which they were trained from unpolarized grays, but neither species learned to discriminate shades of gray from each other. The results show that mantis shrimps recognize polarization aspects of objects in much the same way as they do colors and that they can be trained to permit researchers to investigate their sensory capabilities using innovative psychophysical and behavioral approaches.

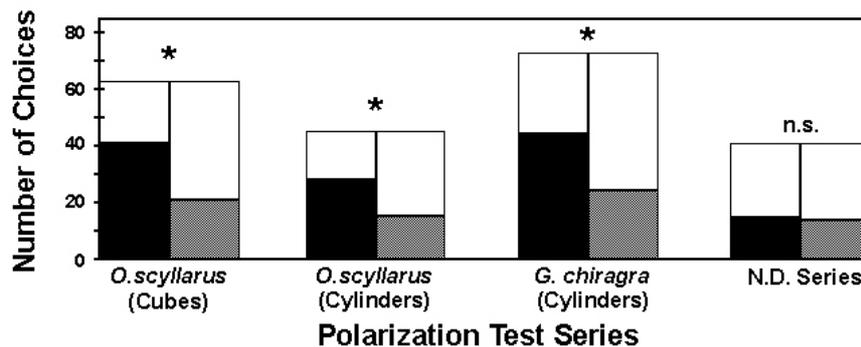


Figure 7. Tests of polarization vision in the stomatopod species *Odontodactylus scyllarus* and *Gonodactylus chiragra*. The figure shows results from 3-way choice tests and follows the same layout and data coding as Figure 6. Each pair of bars is from a different experiment, varying in test species and/or training object. These different types of tests were devised to overcome possible edge effects and artifactual patterning in cubes (see Marshall et al., 1999 for further details). Both *Odontodactylus scyllarus* and *Gonodactylus chiragra* were tested for their ability to discriminate cubes that differed only in neutral density (rightmost data set).

Future of Research on Stomatopod Learning

The research on stomatopod learning reviewed here amply confirms that these exciting animals have flexible and trainable behavior and demonstrates that they learn salient tasks quickly and reliably. The key to progress in studying the learning abilities of various stomatopod species is to use natural tasks and to select a naturally motivating reward. The animals desire food and shelter, and they will learn the identities of specific individuals to minimize risks when confronting oth-

ers. As in working with many other animals, punishment is often much less effective than reward in encouraging learning, in our experience. We unsuccessfully attempted to teach stomatopods to reject a cube of a particular color, in favor of one of a different color, by shocking the animal whenever it selected the incorrect cube. Its response was to learn to avoid all cube-shaped objects, not to discriminate between cubes differing in their colors. Although the work reported in this review has looked at stomatopod learning from several perspectives, there are many features of stomatopod biology where learning could be of great selective benefit that have received little or no attention.

One such area is predator and prey identification. As described, some features of predators can be learned. While there is good reason to expect stomatopods to have genetically programmed responses to many characteristics of predators, learned traits, including chemical signatures or features of predator behavior, could reduce the odds of a lethal encounter. Regarding prey, stomatopods prefer specific types within the range of animals they can catch and subdue. For example, *Odontodactylus scyllarus* prefers snails over hermit crabs (both of which may occupy identical shells) and when presented with moving mimics of both prey types, it generally attacks the smoothly moving snail mimic (Caldwell & Childress, 1990). Whether either the feeding preference or the movement characteristics of prey are learned remain to be investigated. We do know that stomatopods vary their attack techniques; crabs are struck vigorously and rapidly until subdued, whereas snails and hermit crabs are leisurely dragged back to the home burrow for treatment (Caldwell & Childress, 1990). (However, a hermit crab might be hit a few times to encourage it to withdraw into the shell before it's hauled away; Caldwell et al., 1989.) Learning likely plays some role in these behaviors and could be involved in optimizing the handling of other types of prey as well.

Another, related area where learning is known to exist but has not been much studied is food handling. Breaking an aragonite snail shell using crustacean exoskeleton is risky. If the stomatopod damages its raptorial appendage it may starve and will be greatly disadvantaged in aggressive encounters. However, stomatopods select prey, choosing intermediate and small snails over large ones (Full, Caldwell, & Chow, 1989). Again, whether or not learning plays a role in this prey selection task is uncertain. On the other hand, the Indopacific species *Odontodactylus scyllarus* learns how to handle and break novel prey. When it is provided with a thick-walled snail it would not normally encounter (*Tegula funebris*, from California), over a period of days it learns how to open the shell with progressively fewer strikes (Caldwell & Childress, 1990).

Finally, stomatopods often leave their burrows searching for food. How well they learn the features of their neighborhood, and whether they learn routes through it for attack or defense, has not been investigated but offers an interesting area for future research as well. The mantis shrimps are wonderful animals to study, with charismatic characters and fascinating, if pugnacious, personalities. We biologists have much to learn from them.

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