Chapter 2
Individual Recognition in Stomatopods

Kristina Mead Vetter and Roy L. Caldwell

Abstract Many stomatopod species seem capable of individual recognition. This ability appears most often in species that face severe competition for shelter, or that create shelters that are costly to reproduce. Mantis shrimp identify specific individuals (conspecific or otherwise), and adapt their defensive or offensive strategies in response to previous encounters with that opponent. Stomatopods also use individual recognition in reproductive contexts: to recognize current mates and young, and to avoid previous mates. Current thinking is that individual recognition serves to limit lethal aggression, always a risk due to the legendary strikes of their powerful raptorial appendages. The most aggressive species, with the most complex behavioral repertoires, appear to be most capable in this arena. This chapter describes the well-developed visual and chemical senses and the learning that supports this survival strategy, and then focuses on the evidence supporting chemically-mediated individual recognition. This is followed by accounts of the roles played by visual and auditory cues in individual recognition.

Introduction

Basic Stomatopod Biology

Members of the order Stomatopoda, also known as mantis shrimp, are the only living order of the subclass Hoplocarida. Stomatopods are marine carnivorous malacostracan crustaceans that mostly live in tropical or subtropical oceans, although a few temperate

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species are known. Species of mantis shrimp typically obtain a maximum body length of 2–35 cm. Identifying features include specialized stalked eyes, tripartite antennules that are highly sensitive to a variety of odors, and raptorial appendages capable of very rapid and powerful strikes. Compared to many other crustaceans, mantis shrimp exhibit complex aggressive behaviors. They also are capable of relatively sophisticated learning. These traits set the stage for the development of individual recognition.

The Importance of Shelter and Raptorial Appendage Type

With few exceptions, most adult mantis shrimp spend much of their time in some kind of shelter. They often lurk at the entrance, and emerge to hunt prey with startling swiftness. Their raptorial appendages (enlarged second thoracopods) are typically either long, spiny spearing appendages, or hardened smashing appendages with enlarged muscle mass, although other forms exist (Schram et al. 2013). The designation as "smasher" or "spearer" refers to the mode of hunting prey, but these categories also often relate to broad differences in habitat, anatomy, and behavior (Mead and Caldwell 2011). Families with spearing raptorial appendages include Bathysquillidae, Erythrosquillidae, Eurysquillidae, Indosquillidae, Lysiosquillidea, Nannosquillidae, Parasquilloidea, Squilloidea, and Tetrasquillidae. Smashers include the Coronididae, Gonodactylidae, Odontodactylidae, Protosquillidae, and Takuidae. There are, of course, exceptions to this division, as detailed in Schram et al. (2013), and some groups, especially among the Squillidae, have not been studied sufficiently to determine if their life style deviates from these patterns.

Stomatopod species vary greatly in the type of refuge occupied, the time and effort required to secure a home, and in their vulnerability to predation when they leave their shelter. The type of refuge preferred is strongly, but not perfectly, correlated with their raptorial appendage (Caldwell and Dingle 1975, 1976). Most spearing species excavate burrows in soft substrata (Fig. 2.1a), while most smashing species occupy cavities in coral rubble (Fig. 2.1b) or other hard substrata. Pseudosquillidae, spearers that group functionally with smashers¸ start their post-settlement life in coral or coral rubble and thus face many of the same constraints as smashers. Burrows or cavities are critical for many aspects of mantis shrimp ecology. They provide shelter from predators, a location for processing prey, and a safe haven for mating and for the guarding of eggs and larvae. Species that live in preexisting cavities in hard substrata such as coral, rather than burrows that they excavate themselves, often face strong competition for these cavities. This competition is intense due to defensive needs and reproductive constraints. Effective defense requires that the entrance diameter match the body diameter. Since stomatopods have indeterminate growth, they must modify or exchange their shelters after each molt. Species living in sand or mud can usually expand their burrows without abandoning them, but species living in rock or coral cavities cannot easily enlarge their dwellings and must often fight the current inhabitant to take control of a new, larger cavity. Furthermore, in non-monogamous species, the animals often face eviction from burrows during mating periods. In many species, the males, females, or both

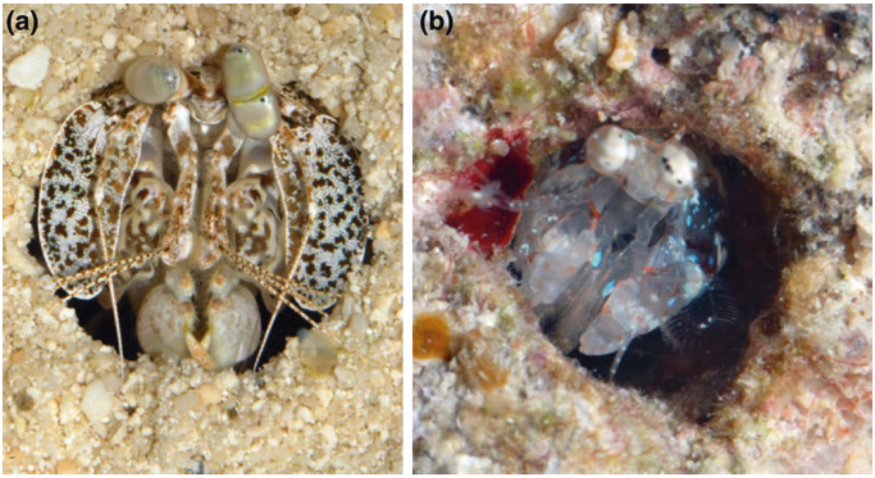

Fig. 2.1 Stomatopod shelters. **a** *Lysiosquilla maculata* in burrow in consolidated sand. **b** *Gonodactylus affinis* in coral cavity

leave their shelter as often as every lunar cycle to search for a mate (Caldwell 1991). The scenario is especially grim for a male: he leaves his cavity to search for a mate, risking that it will be occupied during his absence. If he finds a mate and guards her in her burrow, he must still leave once she lays her egg mass, and hunt for a new cavity. Either the resident mating partner is evicted, or the visitor returns to find its burrow occupied and must fight for it. This frequent exposure to predation and to competition over cavities exerts a heavy toll (Caldwell 1991).

Coral-dwelling mantis shrimp face limited availability of crevices suitable for shelter. Large cavities are scarcer than small ones (Reaka and Manning 1981). This situation leads to increased aggression with an increase in body size, both within and among species (Reaka and Manning 1981). For example, the largest cavity-living Costa Rican stomatopod, *Gonodactylus festae*, shows the most intense aggression, and has the highest incidence of wounds of the five species studied (Reaka and Manning 1980).

Even though the smashing species usually face greater competition for suitable cavities than spearers, both groups experience aggression, and animals with either type of raptorial appendages are capable of dealing lethal blues to conspecifics as well as to prey.

This fierce competition for burrow space, combined with the potentially lethal weapons at their disposal, places a premium on rapid, accurate information that can reduce the risk involved in assessing and fighting other stomatopods and other dangerous competitors. As a consequence, the visual and olfactory systems of stomatopods, particularly smashing species living in hard cavities, are very well developed. Complex behaviors, involving displays, assessment of aggression, learning, and individual recognition are well established. These features of stomatopod biology serve to mitigate the risk that competitive encounters will become lethal.

Patterns of Individual Recognition in Mantis Shrimp

Although this book is on the wider topic of social recognition, this chapter focuses on the subset of interactions governed by individual recognition. Individual recognition is defined here as the ability to identify and remember (at least for a period of time) specific individuals, based on previous experience. The idea, as expressed in Caldwell (1985), is that animals "use knowledge of their opponents gained during previous encounters [to choose] the aggressive strategies and tactics to be employed during subsequent interactions." This is in contrast to some forms of social recognition, where identification is to group, such as members of a species, males versus females, previously encountered animals versus strangers, or juveniles versus sexually mature animals, rather than to a specific individual.

Individual recognition in stomatopods was first studied in the context of aggressive interactions, specifically in regards to contests over shelter. This focus still represents the majority of the studies of individual recognition in mantis shrimp, but subsequent research has included the roles of individual recognition in reproduction. Here, too, the threat of violence is ever present, since a potential mate could also be a combatant.

It should be noted, however, that there is a continuum between social recognition (i.e., members of a group) and individual recognition. Individual recognition occurs when animals classify other creatures by a sufficient number of criteria so that the probability of confounding one individual with another becomes vanishingly small. What constitutes sufficient criteria will most likely vary with the type of sensory cues being used, the precision of the signal and the acuity of the receptor, the number of individuals that must be distinguished, and a variety of other factors that we can only guess at, especially since we do not know the exact natures of the cues involved. Given their sensory acuity and the large number of available cues, it is likely that most or all stomatopods practice at least some form of social recognition. For example, all mantis shrimp can probably recognize conspecifics and sex. In some, as described below, this ability has been honed to the level of identifying and remembering specific individuals.

Individual recognition occurs in a subset of mantis shrimp species (Table 2.1), and plays a variety of different roles, although many of them are related to the

Table 2.1 Individual recognition in mantis shrimp families

Superfamily and family	Raptorial appendage	Habitat and burrow	Contact, mating	Aggression	Individual recognition
Bathysquilloidea					
Bathysquillidae	Spearer	Burrow in mud, sand	Mate search	Low	Probably not
Indosquillidae	Spearer	Burrow in mud, sand	Mate search	Low	Probably not
Erythrosquilloidea					
Erythrosquillidae	Spearer	Burrow in mud, sand	Mate search	Low	Probably not

(continued)

Table 2.1 (continued)

Superfamily and family	Raptorial appendage	Habitat and burrow	Contact, mating	Aggression	Individual recognition
Eurysquilloidea					
Eurysquillidae	Spearer	Burrow in mud, sand	Mate search	Low	Probably not
Gonodactyloidea					
Alainosquillidae	Smasher	Cavity in rock, coral	Many new partners	Moderate	Unknown
Gonodactylidae	Smasher	Cavity in rock, coral	Frequent contact	Very high	Yes, odor
Hemisquillidae	Blunt[a]	Burrow in firm sand	Some contact	Can be high	Probably
Odontodactylidae	Smasher	Burrow in sand, gravel	Many new partners	Moderate	Probably
Protosquillidae	Smasher	Cavity in rock, coral	Mate guard	High	Yes, visual cues
Pseudosquillidae	Spearer[b]	Cavity or burrow	Many new partners	High	Yes, odor and visual?
Takuidae	Smasher	Cavity in rock, coral	Mate guard	High	Unknown
Lysiosquilloidea					
Coronididae	Smasher	Cavity in rock		Low	Unknown
Lysiosquillidae	Spearer	Extensive burrow[c]	Mono-gamy	Low	Yes
Nannosquillidae	Spearer	Extensive burrow[c]	Some in pairs	Low	Probably
Tetrasquillidae	Spearer	Extensive burrow[c]	May pair	Low	Probably
Parasquilloidea					
Parasquillidae	Spearer	Burrow in mud, sand	Mate search	Low	Probably not
Squilloidea					
Squillidae	Spearer	Burrow in mud, sand	Some guarding[d]	Low	Likely in *Meiosquilla*

Columns are explained as follows: Many features of a group's ecology and behavior correlate with the type of raptorial appendage. Species that find refuge in preexisting cavities or that create extensive burrows are more likely to have some form of individual or social recognition. Species that come into frequent contact with a limited number of individuals on a long-term basis, engage in monogamy or mate-guarding, or are more aggressive, are more likely to use individual recognition. Some characteristics show too much variability within a family to describe. *Notes* [a]The Hemisquillidae possess raptorial appendages that are blunt, and fit neither the smasher nor the spearer category. They may be basal. [b]While morphologically a spearer, with two spines, the Pseudosquillidae are often grouped with the smashers because of habitat and behavioral reasons. [c]These burrows in sand and rubble are extensive and mucus-lined, and thus very expensive to build. [d]*Meiosquilla* is thought to have a mating system similar to that of *N. bredini.* Information for this table comes from Caldwell (1991), Caldwell and Dingle (1975), Reaka and Manning (1981), Schram et al. (2013)

need to modulate aggression. There are several conditions that must be met, before individual recognition is likely to be established. First, there must be variation in individual presentation, via the sensory modality utilized (visual, chemical, audio cues, or a combination thereof). Second, the sensory apparatus must be sufficiently sophisticated to detect individual differences. Third, there must be an element of learning and memory so that the initial encounter is remembered and can affect subsequent meetings. Lastly, (at least for us to recognize the event!) the animal must have a flexible behavioral repertoire, so that distinct behavioral outcomes can result from the encounter and recognition of different particular individuals.

As will be described below, smashers generally have more sophisticated visual senses than spearers (except for pseudosquillids). Smashers often live in clear, well-lit habitats, and make the most of these signaling opportunities. The stomatopod families exhibiting the greatest aggression, behavioral complexity and flexibility are the Gonodactylidae, Protosquillidae, Takuidae, Odontodactylidae (all smashers), and Pseudosquillidae (functionally grouped with smashers). We can thus expect a greater reliance on individual recognition among these groups (Table 2.1), although there are exceptions.

Learning and Memory in Mantis Shrimp

Learning is an important part of the visual, olfactory, and vibrational communication between mates, competitors, and even among species (Cronin et al. 2006), and is essential to the rapid decision making attending courtship and mating. The facility with which mantis shrimp learn accurately and quickly is probably a product of numerous factors, including the probability of damage from aggressive contests, predation pressure, the strong need and capacity for behavioral flexibility, the complexity of their visual system, and the ecology of their environment (Cronin et al. 2006). Mantis shrimp are one of the few animals able to disable or kill a conspecific opponent with a single strike of their raptorial appendages. Use of such a fearsome appendage requires care, especially since a misaimed or poorly timed blow can damage the perpetrator. Since the attacker itself is vulnerable, it must be able to size up opponents and make quick decisions about whether or not to engage (Cronin et al. 2006). This careful, but rapid evaluation is especially important since an animal that is a prospective mate one day may be an unwelcome intruder on the next day. Given that the smashers generally have the most complicated behavior and probably benefit the most from behavioral flexibility, learning is probably most developed in these groups (Cronin et al. 2006).

Social conditions are also important, because there is a finite limit to how many other animals an individual can "remember", or the time over which this learning persists. For instance, if a mantis shrimp lives in a solitary manner, or if it encounters many tens of individuals a day with no repeats, then individual recognition is unlikely to play a pivotal role for that animal. In contrast, social and environmental factors leading to repeat interactions increase the likelihood of individual recognition playing a role. Examples include multiple Neogonodactylids occupying individual cavities in the same rock, or a monogamous pair of *Lysiosquillina* inhabiting the same burrow. R. L. Caldwell (*pers. obs*) has seen up to 22 *Neogonodactylus bredini* inhabiting cavities in the same rock over at least several consecutive days. By comparison, *Hemisquilla californiensis* and *Squilla empusa* live at a much lower density, with distances on the order of meters separating their burrows in the sand and mud (Reaka and Manning 1981; Staaterman et al. 2011; Mead and Minshall 2012). The lower concentration of shelters and the less stringent competition for space may imply fewer aggressive encounters with other individuals. However, at least some *H. californiensis* routinely forage tens of meters away from their burrows (Caldwell, *pers. obs.*) and thus have a greater change of encountering conspecifics, so this calculus is not clear.

The moderate permanence exhibited by the *N. bredini* sharing a rock is probably another requirement for individual recognition. In the laboratory, the behavioral changes that indicate individual recognition seem to persist about four weeks after the initial exposure (Caldwell 1991). In *N. bredini*, at least, this timing correlates with their reproductive periodicity: female receptivity and male-female pairing is timed with the full moon, and brooding lasts nearly the whole of the following month. Although it hasn't been formally tested, the permanence of the individual recognition is likely to vary with mating pattern. *Lysiosquillina,* for example, pair for decades. If separated after several years of sharing a burrow, the recognition would be predicted to continue for much longer than in *N. bredini*.

Behavioral Complexity and Flexibility

One of the hallmarks of the Stomatopoda is their complex array of behaviors, especially regarding aggressive contests over habitat and mating rituals. The behaviors are simultaneously complex and flexible, enabling them to adapt to the particular social and environmental context of the current manifestation of the behavior. This flexibility is relevant to individual recognition, because it enables them to respond differently to different individuals and context combinations. This plasticity of response is probably due in part to the incredible "dexterity" of their appendages, especially their maxillipeds. These appendages allow for an almost infinite variety of behaviors involved in grooming, burrow excavation and maintenance, current production, food searching and manipulation, displays, courtship, egg mass handling, and other essential functions.

Other appendages used in signaling displays include the antennules, antennal scales, and the raptorial appendages. One common behavioral display with a variety of functions is the meral spread. In this posture, all maxillipeds, antennules, and antennule scales are extended laterally and held statically. Meral spreads can play at least three roles including antipredator defense, intraspecific defense (such as cavity defense), and courtship. The extent and intent of the meral spread varies among groups. The antipredator meral spread, shown by all stomatopods, tends to be the most dramatic. Meral spreads used during conspecific fights are smaller and are directed specifically at the opponent. Meral spreads used during courtship tend to include maxilliped whirling, which probably acts to conduct chemical information as well as serving as an additional facet of the display (Caldwell and Dingle 1976). Because these displays are used as a measure of aggressiveness, their mode of use in an animal's behavior during an encounter is an important indicator of recognition. Other aspects of the meral spread, especially the meral spots on the raptorial appendages, may be important in species recognition, territoriality, and other aspects of social recognition (Caldwell and Dingle 1975). For example, nearly all stomatopods exhibit the same color of meral spots in males and females of a species (*Neogonodactylus oerstedii* is an exception), and different species tend to have different color spots.

Additional factors leading to behavioral flexibility include the fine sensory acuity experienced by many mantis shrimp, and of course the constant threat of damage if signals are misinterpreted.

While most mantis shrimp are inquisitive and adept at manipulating their environment, the pattern differentiating smashers and spearers is evident. Smashers consistently show more complex types of agonistic interactions than spearers. For example, smashers show 12–15 different categories of acts, with more frequent displays, while spearers show 6–10 categories of acts, with less frequent displays (Caldwell and Dingle 1975).

The next section of this chapter deals with individual recognition using chemical cues, which is the best-studied form of individual recognition among mantis shrimp. This will be followed by a brief treatment of the role of visual cues in individual recognition, and a short section on the potential for individual recognition using audial cues among mantis shrimp. We will then discuss multimodality and the dominant role of chemical cues.

Individual Recognition Using Chemical Cues

Chemical Senses and Olfactory Apparatus

Chemical sensing can be separated into olfaction ("smell") and distributed chemoreception (Schmidt and Mellon 2011). Olfaction tends to refer to a distant source, while the distributed chemoreceptive sensilla are in physical contact with the stimulus, but the functions can overlap.

Any chemical component to individual recognition is likely to rely on odors from distant sources, and thus would be considered an aspect of olfaction. Ablation experiments suggest that the portions of the mantis shrimp olfactory apparatus responsible for individual recognition are the unimodal chemosensory sensilla (aesthetascs) located on their antennules (Fig. 2.2a) (Mead and Caldwell 2011). These aethetascs are located on the distal portion of the dorsolateral flagellum (Fig. 2.2b) (Hallberg et al. 1992; Mead and Weatherby 2002; Derby et al. 2003). Aesthetascs are long, slender, thinly cuticularized structures inserted into the flagellum at an angle of 40–60° in rows of three (Mead et al. 1999; Mead and

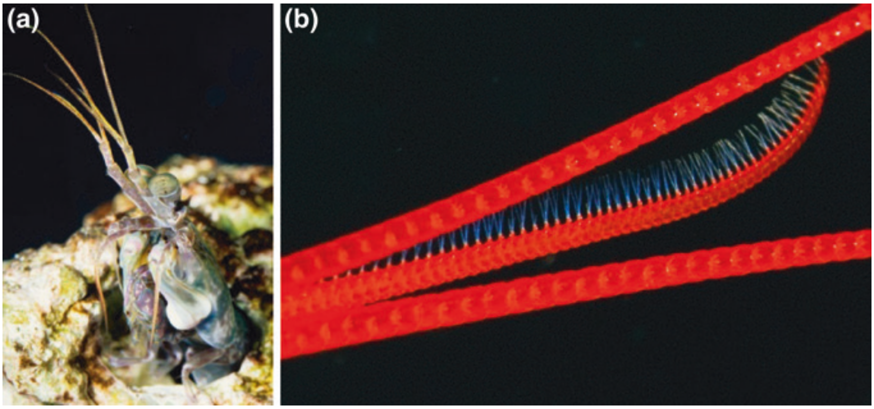

Fig. 2.2 Olfaction. **a** Antennules from *Haptosquilla bangai.* **b** Close-up of an antennule from a male *Odontodactylus scyllarus*, showing aesthetascs

Weatherby 2002). Their length and diameter depend on size and species, varying from 10 µm in diameter and 200 µm length in an 8 mm telson-rostrum length *Gonodactylaceus falcatus* to 32 µm in diameter and 550 µm length in a 157 mm telson-rostrum length *H. californiensis* (Mead and Caldwell 2011). They are innervated by bipolar olfactory receptor neurons (ORNs); there are 12–20 ORNs per aesthetasc in *G. falcatus* (Mead and Weatherby 2002). These chemosensory neurons project proximally to the ipsilateral olfactory lobe, which is organized into spherical glomeruli (Derby et al. 2003).

Chemically Mediated Individual Recognition

Mantis shrimp use chemically mediated individual recognition in a variety of circumstances, including contests over burrows, and in various reproductive behaviors. In no case is the identity of the chemical cues is known, or is the exact mode of delivery. However, there are some likely candidates. When *Haptosquilla* females defend their burrows, they position their telson in the entrance of the cavity and fan their pleopods to push jets of water out of the entrance. Caldwell (*pers. obs.*) has seen fecal pellets included in these jets. *S. empusa* also create currents using their pleopods when disturbed (Mead and Minshall 2012), but no fecal material was observed in this species. Dye studies indicated that female *N. bredini* defending their cavities against approaching males generated currents by whirling their maxillipeds (Caldwell 1992). These currents are thought to carry chemical cues, perhaps in the form of urine as in crayfish (Breithaupt 2001) and lobsters (Aggio and Derby 2011).

Individual Recognition in Aggressive Contests Over Burrows

The first experiments investigating individual recognition in stomatopods were performed using paired aggressive contests over artificial shelter cavities, in the small tropical mantis shrimp species *Neogonodactylus festae.* In the initial study, Caldwell (1979) placed *N. festae* into artificial cavities. After fifteen minutes, a second stomatopod matched for size and sex was introduced into the test arena. The resident and intruder fought for ownership of the cavity, with the resident almost always winning due to positional advantage. The fight was stopped once dominance was established (usually within five minutes). Fifteen minutes later, the intruder was replaced in the test apparatus, which had been cleaned and refilled with seawater, with an artificial cavity that had been filled with one of three types of water. The three test fluids were: “clean” water that had never contained a stomatopod, “stranger” water from the container of a stomatopod of the same size and sex that the intruder had never encountered, or “known victorious resident” water taken from the previously victorious resident’s container removed prior to the encounter between them. This testing procedure was repeated over three days, each intruder encountering all three odors, with a randomized order of presentation. While intruders all quickly approached the empty cavities, their behavior was markedly different depending on the source of the water. If there was no odor of another stomatopod, the intruders took no defensive action and entered the cavity within a minute or two. If the cavity contained the odor of another stomatopod with which the intruder had no experience, the intruders entered cautiously, often inserting their armored telson into the entrance as if expecting an attack from the phantom resident. If the cavity contained the odor of the previously encountered resident that had defeated the intruder earlier, most approached the entrance, sampled the odor diffusing from the cavity with their antennules, and immediately fled the area. When exposed to the water containing the odor of a stranger, 50 % entered within 4 min, and all entered by 13 min. However, only 41 % ever entered the cavity containing the odor of the animal that had previously defeated them during the course of the 15 min test.

This experiment opened a new avenue of research for Caldwell and colleagues, but there were some concerns that the results represented intruders responding differently to broader classes of animals such as “known” versus “unknown” opponents, rather than recognizing individuals. To test for this possibility, a different design was needed where the intruder encountered at least two opponents over a short period of time and then reacted differently to them. In this new scenario (Caldwell 1985), intruders were first matched against either a resident that was 5 % longer and could successfully defend its cavity or against a 20 % shorter resident that the intruder could evict. Thirty minutes later, the intruder was matched against the other type of resident. The residents were the same sex as the intruder and the order of presentation was randomized. Thirty minutes later, the intruder was tested using the odor of one of the residents it had just fought and 30 min after that it was tested against the odor of the other resident. The results of these rematches were that intruders quickly entered cavities spiked with the odor of an animal that they had evicted (median time = 19 s), but delayed entering cavities with odor from animals that had successfully defended the cavity in an earlier bout (median time = 324 s; Caldwell 1985). Since the same intruders failed to respond differentially to odors of larger and smaller unfamiliar conspecifics, it is unlikely that odors providing information on size alone served as the basis for the difference in time to enter the cavity. The response to odor was based on previous experience, suggesting individual recognition.

In addition to conspecific individual recognition, experiments with the stomatopod species *Neogonodactylus zacae* and *N. bahiahondensis* suggest that mantis shrimp are able to use chemical cues to discriminate between different individuals of sympatric species as well (Caldwell 1982). In the competition for cavities, what is important is the fighting ability of resident, not its species.

Chemically mediated recognition can even occur across distantly related species that compete for cavities. *N. bredini* and the octopus *Octopus joubini* fight viciously over quality living quarters. *N. bredini* previously exposed to *O. joubini* show greater delay when approaching test cavities containing octopus odor than odor-free cavities (Caldwell and Lamp 1981). Naïve *N. bredini* do not show this response. There is no evidence that the stomatopods are recognizing individual octopus, so this appears to be a form of social recognition rather than individual recognition.

Chemically Mediated Individual Recognition and Reproduction

Since cavities and burrows are as essential for reproduction as for shelter from predation, the potential for aggressive contests over mating space and mating partners is high. Reproductive pressure can add impetus to the already strong impulse to defend space. One can imagine the extra selective pressure to develop individual recognition and thus avoid unnecessary damage.

Individual recognition can have different purposes, depending on the reproductive mode of the species. Mating systems range from life-long monogamy in some lysiosquillids to multiple sequential matings in many neogonodactylids to rampant promiscuity in *Pseudosquilla ciliata* (Caldwell 1987). The following examples detail species with three different mating habits. In each case, the role of individual recognition via odor seems critical, but for different reasons.

All known species of *Lysiosquillina* are spearers that make large (up to 10 m) burrows in soft sediment (Christy and Salmon 1991). Adults are nearly always found in pairs. They have reduced armor and are thus very vulnerable outside of their burrow. Although there is typically plenty of the sandy substrate preferred for excavating burrows, so that there is little of the competition for space experienced by gonodactylids, burrow construction represents a large investment. One of the most costly components is the considerable amount of mucus required to stabilize the burrow walls. The biological cost of the mucus prevents adult *L. sulcata* from being able to construct a new burrow if evicted from their old one (Caldwell 1991). Together, the large investment in burrow construction and the vulnerability to predation are thought to have led to long-term monogamy (Christy and Salmon 1991). Their nocturnal nature, coupled with their dull body color, greater turbidity, and lower light levels of their preferred habitats may have created an additional evolutionary pressure for individual recognition mediated by chemical cues. The use of chemical cues to support mate recognition and monogamy is often seen in crustaceans (e.g. *Hymenocera picta*, Wickler 1973; Wickler and Seibt 1981). Thus, in *Lysiosquillina*, individual recognition facilitates the pair bond.

Individual chemical recognition acts to facilitate reproduction in the opposite way in *P. ciliata,* widely distributed stomatopods found in a variety of habitats. Females will copulate at any stage in their reproductive cycle and have been observed to mate with several different males in one day. Females are extremely aggressive when pursuing mates, often harassing males until they copulate. Mating occurs in the open and the participants separate immediately after coupling. Interestingly, animals that have mated with each other will not remate within the same pair for several hours but they will copulate with a new partner within a few minutes (Hatziolos and Caldwell 1983). This reluctance to pair with a previous mate may be because males are thought to be sperm-limited, and a single copulation is sufficient to fertilize a brood of eggs (Hatziolos and Caldwell 1983). It appears that some form of individual recognition is occurring, this time to avoid the original mate.

Individual chemical recognition plays a different role in *N. bredini.* In this species, males and females are solitary and defend their own cavities except for when they are reproductively active (Shuster and Caldwell 1989). A few days before each full moon, mating pairs form in cavities, which the males guard (Caldwell 1991). Once the female spawns, the male leaves. Caldwell (1992) studied twenty-five mated pairs that produced egg masses. Fourteen days after the male left the breeding cavity, Caldwell (1992) compared the interaction between the female (placed in a new cavity) to the original male and to a stranger male. The males were also tested as intruders against brooding females that they had not previously encountered. Aggressive acts (meral spread threat, lunge, strike; see Caldwell 1979 for precise definition) occurred only 12 % of the time when the original male was introduced to his brooding mate, but 76 % of the time when a stranger male was introduced. Contests between animals that had not previously been paired escalated more rapidly. The reduced aggression displayed by previously paired males was not due to a general holding back in the presence of brooding females or eggs: they attempted to evict "stranger" brooding females. Also, males did not escalate contests when encountering former mates whose eggs had been removed, perhaps because she could be storing his sperm. Thus individual recognition keeps a male from threatening his own current or future offspring (Caldwell 1992).

Other species that experience competition for cavities, high search costs, and guarding of females by males, such as other neogonodactylids and the squillid *Meiosquilla*, are thought to have similar mating systems, and thus perhaps may also rely on individual recognition to modulate aggression.

In an interesting twist, *N. bredini* are able to distinguish males from females by odor, but can't decode the reproductive status of females (Caldwell 1986a).

The females use this to their advantage. Females with ripe ovaries not currently in a pair may go looking for a male. If the moon is full, the male usually admits the female without hesitation. She evicts the male 15 % of the time if she is reproductive, but 33 % of the time if she is non-reproductive (Caldwell 1986a). The males appear to be trading their cavity for the chance to mate. By broadcasting her sex but not signaling her reproductive status, a female increases her overall chances (i.e. not just when she is receptive, but throughout her reproductive cycle) of gaining access to a cavity.

To summarize, individual recognition may serve to promote a variety of functions, but appears to be most common in species that experience high competition for burrows, have costly burrows, or rely on individual recognition to promote reproduction, either by maintaining pair bonding, by facilitating the identification of new partners, or by protecting a reproductive investment.

The Role of Visual Cues in Individual Recognition

Visual System

Mantis shrimp possess appositional compound eyes segmented into three lobes consisting of two peripheral hemispheres separated by a midband of specialized ommatidia (Marshall and Land 1993). This arrangement enables each eye to act as an independent, trinocular rangefinder, since the stomatopod can image the same location in space with three spatially separate areas of the eye (Marshall 1988). They possess a diverse and complex array of photoreceptors capable of perceiving light intensity, color, and polarization (Marshall et al. 2007). They have at least 16 types of visual pigments that are sensitive to wavelengths of light from UV to the near infrared (Marshall et al. 2007). The opsins that respond to UV in *N. oerstedii* appear to interact with four optical filters that extend and diversify the wavelengths to which the animal can respond (Bok et al. 2014). Because the receptors that mediate color vision are arranged linearly, stomatopods have to scan objects of interest (Cronin et al. 2006). Recent discoveries suggest that mantis shrimp use a novel temporal scanning pattern across the photoreceptors, rather than using the color channels comparatively, as in humans and many other animals (Thoen et al. 2014). This approach may allow for particularly rapid decision-making based on visual input, facilitating behavioral flexibility.

An abundance of visual pigments is probably very useful in underwater environments, which tend to be low contrast (Cronin et al. 2006). Even if the original function was probably related to orientation and predation, color vision is extremely important in mantis shrimp behavioral displays (Cronin et al. 2006). As evidence, many of the coral-dwelling gonodactylids show bright, contrasting, species-specific color markings on raptorial appendages, walking legs, antennal scales, antennules, maxillipeds, pleopods, and uropods. Often the long setae framing the antennal scales, pleopods, and uropods are a different bright color than the supporting appendage (Reaka and Manning 1981). In addition to bright

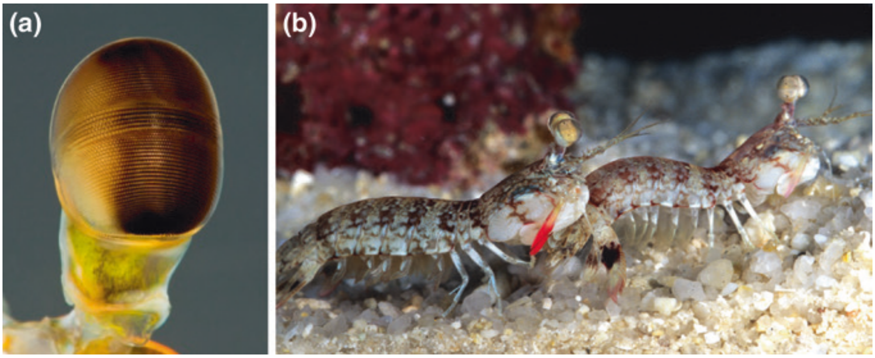

Fig. 2.3 Vision. **a** Eye of a *Hemisquilla californiensis* juvenile male. **b** Male and female *Odontodactylus latirostris*. The photo was taken with a polarizing filter showing that the male antennal scales are polarized, the female scales are not

colors on appendages, some smashers reveal contrasting meral spots on the raptorial appendages (Reaka and Manning 1981). Contrasting colors on appendages are important in transmitting agonistic intent, and may signal species and sex (Cheroske and Cronin 2005).

Some stomatopods have patches on their antennal scales, maxillipeds or uropod scales that structurally polarize light (Cronin et al. 2003). Stomatopods appear to recognize polarized-light features of a visual stimulus (Marshall et al. 1999) suggesting that mantis shrimps use light polarization analogously to color. Among the taxa that have the ability to polarize light, potential polarized light signals appear to become more common with increased habitat depth (Cronin et al. 2003). These signals, in addition to augmenting color patterns, may provide a private line of communication. The use of polarized signals is more prevalent among the smashers than among the spearers. A few species, such as *Haptosquilla trispinosa*, show dimorphic polarization, promoting sex recognition (Chiou et al. 2011). These signals are usually on the antennal scales and uropods (Fig. 2.3).

Smashers tend to be diurnal and to live in clear water, while spearers are more commonly nocturnal, or live in turbid environments with soft substrates. While coral-dwelling smashers have the acute vision described above, spearer eyes are better adapted for the detection of prey at short distances in dim light.

Individual Recognition Using Visual Cues

Individual recognition can rely on visual cues. Experiments were performed in which a focal *Haptosquilla glyptocercus* was allowed to observe one of two other conspecifics matched by sex and size but with different coloration (Cronin et al. 2006). This initial observation lasted an hour. The animal was then allowed to view either the originally observed conspecific again, or the other, novel size and sex matched but differently colored, conspecific. These tests showed that 83 % were more attentive to novel animals, measured as percent time poised with eyestalks beyond the entrance of its burrow. Since the focal animal was isolated from all but visual cues, this suggests the important of visual cues in differentiating animals. This type of visual identification of individuals would be expected to occur in species, like *H. glyptocercus*, that exist in many color morphs and occur in high densities with many burrows in close proximity in open habitat. *P. ciliata* would be another candidate.

Another piece of evidence suggesting the importance of visual cues is the role of bluffing. Bluffing is when stomatopods engage in an aggressive display without being willing and/or able to fight. For example, molting or newly molted *N. bredini* will continue to produce intense meral spread threat displays during cavity defense, even though their soft exoskeleton makes striking impossible. *N. bredini* bluff when facing smaller intruders, who are likely to be deterred by the (false) threat (Adams and Caldwell 1990). The newly molted residents tend to flee when the intruder is larger than they are, or if the bluffing leads to escalation rather than deterrence. The strategy appears to work: residents that do bluff were more likely to retain their cavities and less likely to sustain injury than animals that neither fled nor threatened (Adams and Caldwell 1990). Mantis shrimp appear to pave the way for future bluffing success by performing extra meral spread threat displays in the days leading up to their molt (Caldwell 1986b). This strategy only works if animals learn to recognize their neighbors, and are attentive to visual (as well as to chemical) displays.

The Social Roles of Auditory Cues

Auditory Sensory System

No true pressure-sensitive ear-like structures have been found in any crustaceans yet studied, and crustaceans have no air-filled cavities. As a result, crustaceans are not thought to be able to detect far-field, or pressure, component of sound (Breithaupt and Tautz 1990; Popper et al. 2001). Therefore, any response to sound has to be to the near-field, or particle displacement, component of sound (Breithaupt and Tautz 1990). Stomatopods do not appear to have any specialized structures, but they do have distributed surface setae and internal proprioceptors that are likely to respond to vibrational displacements in the water (Staaterman et al. 2011). In mantis shrimp, these mechanoreceptors are mostly simple, smooth, tapered setae varying from 50 to 2000 μm long (Schram et al. 2013). Experiments in copepods indicate that the smaller setae are more sensitive to higher frequency signals while the longer setae respond more to low frequency stimuli (Fields et al. 2002). Mantis shrimp setae appear to be in an appropriate size range for the detection of environmentally and socially relevant acoustic and hydrodynamic signals (Schram et al. 2013).

Auditory Cues and Behavior

Two sounds known to be made my mantis shrimp include the rumble made by *H. californiensis*, and the click made when stomatopods strike their raptorial appendages against another animal's carapace or against a hard surface.

H. californiensis males (and possibly females) produce a low-frequency rumble by vibrating their posterior mandibular remoter muscles (Patek and Caldwell 2006). The vibration may mark territory or attract females (Staaterman et al. 2011). These sounds may contain information about size and sex (Caldwell, *pers. obs.*). These rumbles have a dominant frequency of 167 Hz, with a range of 53–257 Hz (Staaterman et al. 2011). The near-field vibrational component of sound travels five times farther in sea water than in air. Therefore, the *Hemisquilla* rumble is probably perceptible at least nine meters from the source, making it likely that other mantis shrimp living in nearby burrows can detect these stimuli (Staaterman et al. 2011). *Lysiosquillina* make a similar rumble, but it has not been investigated. There is no evidence that rumbles are used in individual recognition.

Clicks can occur at various points during aggressive contests over shelters. A resident may strike the lip or wall of the cavity, producing a loud warning click. Or, a resident may strike the intruder, or vice versa. Sometimes, the winner of a contest will strike the substrate in a "victory display," reinforcing the win (Caldwell 1987). Researchers collecting data can hear the click, even if it occurs within the burrow. Both smashers and spearers use clicks. There is no evidence that clicks are used in individual recognition, but it is possible that clicks convey information about animal size in addition to serving as a general warning (Taylor and Patek 2010). Although not explicitly tested, it seems likely that molt stage might affect some of the properties of the strike signal as well.

Multimodal Signals Enhance Communication

The fierce competition for burrow space experienced by many mantis shrimp, combined with the potentially lethal weapons at their disposal, places a premium on rapid, accurate information that can reduce the risk involved in assessing and fighting other stomatopods and other dangerous competitors. Multimodal communication may enhance the information content or signal accuracy (Hebets and Rundus 2011).

One example of the importance of two sensory modalities is in the intersection of stomatopod visual and olfactory systems. Visual signaling plays a large role in gonodactylids, which are active in the daytime, are brightly colored, live in clear water in fairly high light areas, and have excellent vision. Even so, their sense of smell is likely to provide cues that may contain more (and possibly more reliable) information than visual cues (Christy and Rittshof 2011). Furthermore, for an animal anxious to probe the unseen occupant of a cavity, odor provides a channel of reliable information without requiring potentially dangerous intimate contact.

This is important because the hidden cavity resident can easily see intruders in the open and can at least assess the size and vigor of their opponent, and because possession of a shelter poses a distinct positional advantage. Thus, olfactory information can help to assuage the often asymmetrical transfer of information inherent in the visual system of cavity-dwellers.

The integration of sensory systems may be especially critical when environmental conditions favor one modality over another. For example, visual information can be compromised by low light levels (at night or in turbid environments), extraneous light in the environment, or the animal's position in its cavity or burrow. Recent work indicates that stomatopods increase their antennular flicking under low light conditions, presumably relying more on olfactory cues and less on visual cues under these circumstances (Cheroske et al. 2009).

In a potentially synergistic interweaving of vision and sound, *H. californiensis* may be able to see a visual analog of the carapace vibration created during rumbling. As described above, *H. californiensis* produce a low-frequency rumble by vibrating their posterior mandibular remoter muscles (Patek and Caldwell 2006). The males also have linearly polarized red patches along the sides of their carapace, merus, and proximal portions of their antennules. The muscles thought to drive the acoustic signaling are very near the carapace color patches. The flexing and relaxing of the carapace at 20–60 Hz could lead to a rapidly alternating pattern of polarization. Gonodactylids, including *H. californiensis,* are capable of detecting polarization (Cronin et al. 2000). If the flicker fusion frequency of ommatidia of *H. californiensis* is faster than 20–60 Hz, then *H. californiensis* should be able to detect changes in the patch polarization, reinforcing and possibly extending the acoustic signal. If individual males vibrate at characteristic frequencies, this could serve to assist individual recognition.

As indicated by the "victory display" strike of *N. bredini*'s raptorial appendage on the substrate after evicting an opponent, sound cues can reinforce the chemical signals also being sent. Obviously, there are many ways that signals can be combined to increase signal fidelity and avoid potentially lethal combat, and this is likely to be a fruitful area for future research.

Summary

Individual recognition occurs in only a subset of stomatopods, but for them, it plays several important roles. Often, these roles revolve around control of shelters. Contests over shelters can be critical for survival, as defensible cavities of the appropriate size are limited, are almost always already occupied, and predation risks outside shelters are high. By identifying and remembering specific individuals, and adjusting their behavior in consequence, mantis shrimp can more accurately decide whether or not to engage in a particular aggressive contest over a shelter. Through rapid identification of specific cavity residents who lost in previous contests, would-be intruders can choose their battles and increase their chances of success while minimizing injury. By recognizing their pair-bonded mate, *Lysiosquillina* avoid fighting every time they return to their shared burrow. In general, avoiding aggressive contests with previous mates (at least during the current breeding cycle) keeps would-be intruders from destroying their genetic legacy. Alternatively, avoiding previous mates altogether and constantly seeking new ones is another approach to reproductive success!

The pressure to develop individual recognition, and the resultant ability, varies among stomatopod groups. Species facing the greatest competition for cavities, the greatest replacement cost, and/or the most vulnerability outside the shelter are most likely to improve their lot via individual recognition. The amount of repeated contact with a limited number of individuals over a period of time is also a factor. The capacity for individual recognition relies on the ability to differentiate individuals via multiple sensory cues, learning and memory, and behavioral flexibility. As these capabilities vary among stomatopod groups, so does the ability to recognize individuals.

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