Chapter 12
Chemical Communication in Lobsters

Juan Aggio and Charles D. Derby

Abstract Lobsters are fascinating animals that use chemicals as messages regarding their sexual status, their standing in a social hierarchy, and whether they affiliate with or avoid conspecifics. This, plus their economic importance, makes them important models for the study of intraspecific chemical communication. Our chapter is an overview of these processes, including the types of interactions between lobsters influenced by chemicals, how those interactions are affected by chemicals, and how these chemicals are detected. Since "lobster" refers to a common body plan rather than a taxonomic group and thus includes animals of differing phylogenetic relatedness and lifestyles – most notably clawed lobsters, spiny lobsters, and slipper lobsters, their use of chemicals in intraspecific interactions is diverse. Whenever possible, we compare the different groups of lobsters, though the amount of data available for relevant behaviors varies with the lifestyle of lobsters. Clawed lobsters use urinary chemicals processed by the olfactory pathway to identify previous opponents and maintain a stable social order, which is important because only the most dominant males will mate. After a hierarchy has been established by fighting, subsequent rematches are shorter and less violent, with urinary chemicals playing a key role in this process. Mate choice and mating behavior are also mediated by urinary olfactory cues. These behaviors are disrupted when one of the animals either has a compromised olfactory sense or is not allowed to release urine. Although there is less available data, the picture seems similar in spiny lobsters, with females using urinary chemicals from males as one of the cues in mate selection. Both spiny and slipper lobsters form dominance hierarchies, but little is known about how they are influenced by chemical signals. Conversely, spiny lobsters have been extensively studied regarding the mechanisms of aggregation and avoidance. Aggregation is mediated by urine-borne chemicals and avoidance is mediated by blood-borne chemicals, both processed by the olfactory system. Molecular identification of these compounds will be critical in allowing researchers to study the neural processing of intraspecific chemicals.

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12.1   Introduction

12.1.1   Why Study Lobsters?

Because of their abundance, size, tastiness, and accessibility, lobsters are appreciated by all who enjoy a good seafood meal, are important in the fisheries of many countries, and are well known by most people throughout the world. Lobsters are also well known to scientists because they have been frequently used as models for the study of, among other things, the chemical senses, including the role of chemicals in mediating intraspecific behavior. Much is known about how lobsters use their chemical senses to find or avoid each other, recognize individuals, mate, and battle. Unfortunately, the chemical identities of most of the compounds driving these behaviors are unknown, which has limited the types of studies that can be done and our current understanding of lobsters' chemical ecology. Nevertheless, chemical communication among lobsters is a fascinating topic that is being investigated in many laboratories worldwide.

In this chapter, we review the ways whereby lobsters chemically communicate with each other and the contexts in which they do it. We make a distinction between different types of chemicals. Based on the terminology of Wyatt (Chap. 2), we use "semiochemicals" as chemicals involved in animal interactions and "pheromones" as a subset of semiochemicals used in intraspecific contexts. We also use "cues" as chemicals that benefit the receiver and not necessarily the sender, with a prime example being alarm cues released in the blood of injured conspecifics.

12.1.2   Is There Such a Thing as a Lobster?

The word "lobster" evokes in most people a precise image: a large, bottom-living, long-tailed marine crustacean. Depending on the geographical location, that image might include big claws. However, to those who study crustacean systematics, lobsters do not exist as a single taxonomic group. Lobster is a polyphyletic group and usually refers to three disparate clades of crustaceans – clawed lobsters, spiny lobsters, and slipper lobsters – although the name lobster is even applied to a group of hermit crabs, the squat lobsters. As seen in Fig. 12.1 (Dixon et al. 2003), clawed lobsters are members of the Homarida and are in reality closely related to crayfish, while spiny lobsters and slipper lobsters are members of the Achelata and are closer to hermit crabs and true crabs. In fact, a common ancestor to both clawed and clawless lobsters is also a common ancestor of, among others, crayfish, hermit crabs, and true crabs.

In spite of this, and because of historical reasons, even in academic publications such as this volume, the word "lobster" is widely used, and we will not be the exception. But be warned: we will use "clawed lobster," "spiny lobster," and
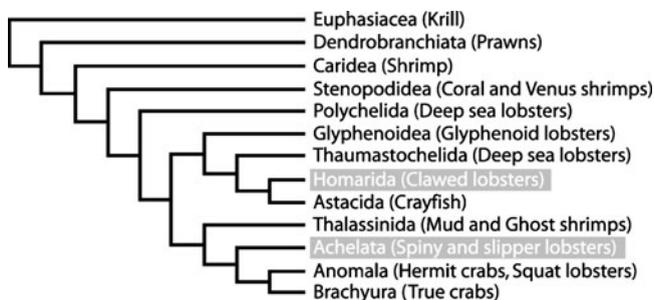
Fig. 12.1 Phylogeny of decapod crustaceans, showing that lobster is not a monophyletic grouping, but rather a body form. The clades representing the lobsters that we discuss in this chapter – clawed, spiny and slipper lobsters – are *shaded* in this figure. Clawed lobsters are more closely related to freshwater crayfishes than spiny and slipper lobsters, which are more closely related to true and hermit crabs, the latter in a group (Anomala) that includes animals also referred to as lobsters. Reproduced with modifications from Dixon et al. (2003). Copyright 2003 by Koninklijke Brill NV, Leiden, The Netherlands

"slipper lobster" when we want to refer specifically to one type, and we will use lobster when we make no distinction.

Significant to our considerations is that the different lobster types vary in their lifestyles, and this has enormous consequences on the types of information they exchange. This results in an unbalanced amount of information about different species, with most of what is known about agonistic and sexual semiochemicals coming from studies of clawed lobsters, and most of what is known about aggregation and sheltering semiochemicals from studies of spiny lobsters. Nevertheless, we will attempt to compare these two groups wherever possible.

12.2 Emission and Reception of Semiochemicals

Urine is often the source of semiochemicals. This is true for sheltering and dominance cues in the spiny lobster *Panulirus argus* (Horner et al. 2006), dominance cues and sex pheromones in the clawed lobster *Homarus americanus* (Atema and Voigt 1995; Bushmann and Atema 1997; Breithaupt and Atema 2000), dominance cues in the clawed lobster *Nephrops norvegicus* (Katoh et al. 2008), and sex pheromones in the spiny lobster *Jasus edwardsii* (Raethke et al. 2004). This seems to be a very general principle, at least within the decapods, with urine as a source of sex pheromones in blue crabs and other true crabs (Gleeson 1980; Kamio 2009) (Hardege and Terschak, Chap. 19; Kamio and Derby, Chap. 20) and crayfish (Breithaupt, Chap. 13). In some publications, the experimental design does not allow for precise identification of the site of origin of the chemical cues, but urine cannot be ruled out as a source. Other sources of semiochemicals are possible. For example, female sex pheromones of freshwater prawns are released from the sternal

gland (Kamiguchi 1972a, 1972b), and alarm cues are found in the hemolymph of spiny lobsters (Shabani et al. 2008), crabs (Ferner et al. 2005), and crayfish (Hazlett 1994).

Receptors for semiochemicals of lobsters and many other decapod crustaceans are typically restricted to a very limited set of sensors. These are olfactory sensory neurons contained in specialized setae called aesthetascs, localized in the lateral flagellum of the first antenna or antennule (Fig. 12.2). Ablation experiments show the necessity of aesthetascs for the response of lobsters to different types of semiochemicals (Johnson and Atema 2005; Horner et al. 2008; Shabani et al. 2008). The chemosensory neurons innervating the aesthetascs project their axons exclusively to the olfactory lobes, and thus are considered olfactory, while the other setae contain both chemo- and mechanoreceptors that project to the lateral and medial antennular neuropils (Schmidt and Ache 1996a, 1996b) (Schmidt and Mellon, Chap. 7). Many studies showed that receptor sites for semiochemicals are located in the first antenna without showing them to be in aesthetascs (e.g., Raethke et al. 2004; Skog 2009). Detectors of semiochemicals of crayfish have been
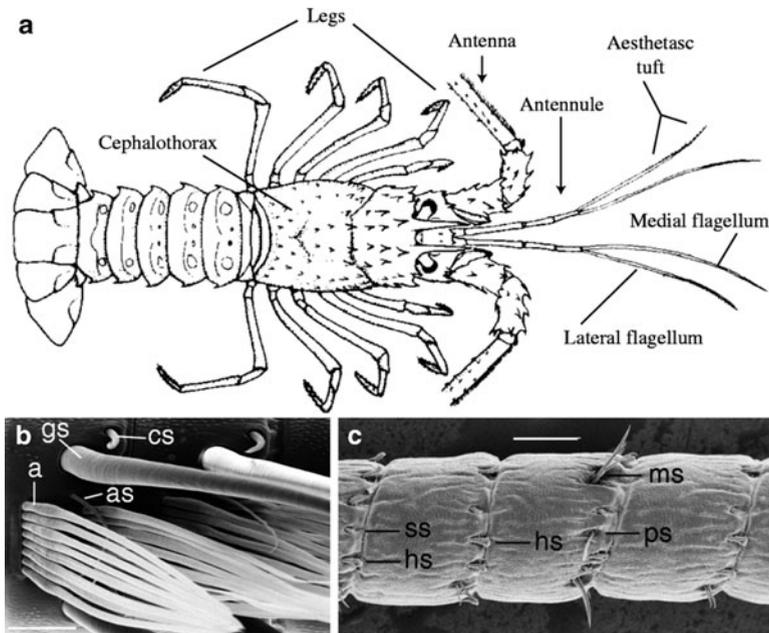

Fig. 12.2 Chemosensors of spiny lobsters. (**a**) Chemosensors are found on all appendages and body surfaces. (**b, c**) The antennules are covered with different types of chemosensilla, including several in the aesthetasc tuft: aesthetasc sensilla (a), guard sensilla (gs), companion sensilla (cs), asymmetric sensilla (as); and those outside the tuft: setuled sensilla (ss), hooded sensilla (hs), plumose (ps), and simple sensilla (ms). The aesthetascs however are the only sensilla that house exclusively chemoreceptors (the others also contain mechanoreceptors). The aesthetascs contain olfactory receptor neurons that mediate responses to intraspecific signals and cues. Reproduced from Steullet et al. (2001) with permission from The Journal of Experimental Biology

located on the first antennae (Tierney et al. 1984; Dunham and Oh 1992) and chelae (Belanger and Moore 2006, 2009).

12.3 Sexual Signals

In sexual communication, the different lifestyles of clawed, spiny, and slipper lobsters have profound effects on the nature of the semiochemicals and the amount of information available to us. Relative to one another, clawed lobsters tend to live solitarily and to not aggregate except when mating, while spiny lobsters tend to have very active social lives year round. Perhaps because of this, the amount of information on sexual communication in spiny lobsters tends to be much less than in clawed ones. Much of our understanding about the role of chemical communication in the sexual behavior of lobsters originated in the laboratory of Jelle Atema and pertains to the American lobster, *H. americanus*. We also have some knowledge of mating signals in the closely related European lobster, *Homarus gammarus*, and also in a spiny lobster, *J. edwardsii*. No information is available on slipper lobsters. Because clawed lobsters are solitary and aggressive towards one another, courtship must include a means to diminish aggression. For this reason, we first describe events leading to and following copulation in clawed lobsters, focusing on what the majority of the available literature supports. Then we briefly discuss data that contradict these results, and lastly we discuss what is currently known in spiny lobsters.

As a broad generalization, mating in *H. americanus* takes place as follows: a female searches for a male, preferably dominant, gains access to his shelter, molts, mates, and eventually leaves his shelter, so that the male may mate again with another female (Cowan and Atema 1990; Atema and Voigt 1995; Atema and Steinbach 2007). Intermolt females also mate, and it is believed that this is caused by lack of enough sperm to fertilize eggs, a situation that may be due to less than ideal mating (Gosselin et al. 2005; Waddy and Aiken 1990). Courtship is strongly influenced by urinary chemical signals, detected by antennular chemoreceptors. Bushmann and Atema (2000) showed that if the release of male urine is blocked, females tend to approach shelters less and, once there, they spend less time attempting to enter them. Because releasing urine from empty shelters does not restore these behaviors, Bushmann and Atema concluded that other sources of chemical information must exist. The response of the male to the female's attempt to enter is highly dependent on his ability to detect the female's urine. If females are prevented from releasing urine, then males still allow females to enter the shelter, but in the face of male aggressive behavior, the number of matings is greatly reduced (Bushmann and Atema 1997).

Two studies on clawed lobsters are inconsistent with the above scenario and with each other (Cowan 1991; Skog 2009). Cowan (1991) reported that the antennules of females, but not males are required for normal mating behavior in *H. americanus*, while Skog (2009) found that male antennules are necessary for normal mating in

H. gammarus. Differences in the findings of these studies might be due to the use of different species, but further studies are needed to resolve this question.

Another contradicting point of view was advanced by Snyder et al. (1993), based on studies of *H. americanus*. These authors reported that blocking urine release had no effect on intra- or intersexual behavior. Once again, although it is possible that there are additional, redundant sources of pheromones such as have been shown in crabs (Bushmann 1999), an alternative explanation is a methodological one – the methods of blocking urine release were different in these studies and the method of Snyder et al. (1993) may not have been completely successful.

In spiny lobsters, which are gregarious, most of the available data do not deal strictly with mating but with aggregation, and we treat this subject elsewhere in this chapter. However, Raethke et al. (2004) addressed the importance of chemical communication in mating of *J. edwardsii* by investigating the role of urine in mate selection by females. Large females normally choose large males, probably to ensure an adequate supply of sperm. In a clever experiment, Raethke and collaborators "reversed" the urines of a small and a large male so that the small male's urine was released close to the big one's nephropores (the site of release of urine) and vice versa. This resulted in the females choosing the large and small males with equal probability, indicating that although urine alone is not sufficient to attract a female, it plays an important role. When they investigated the effect of ablation of the antennules of either males or females on courtship and mating, they found no significant effects, but a tendency to a delayed mating in both experimental conditions, with a slightly greater effect when the ablation was performed in males.

In addition, mating behavior in both spiny and slipper lobsters seems to be simpler and faster than in clawed lobsters, a fact that further hinders our ability to collect data (Lipcius et al. 1983). In their 11-month study, Barshaw and Spanier (1994) failed to observe mating between slipper lobsters.

Overall, results from clawed lobsters paint a picture that urinary chemical cues released by males and detected by females are necessary for the initial location of males by females. Then, when the animals are near each other, females release urinary chemicals that are detected by males, and this drives subsequent behavior. In spiny lobsters, females have been shown to approach tethered males (Raethke et al. 2004), and males have been observed to search for females in the field (Lipcius et al. 1983). More data are needed to establish the precise sequence of events leading to mating in spiny lobsters.

12.4 Individual Recognition and Social Status

The structures of groups of clawed, spiny, and slipper lobsters in the field are, at first sight, very different. However, there are similarities in their use of chemical communication in social interactions: clawed and spiny lobsters establish dominance hierarchies that are maintained, at least partially, via urinary chemical cues.

In clawed lobsters, the hierarchy is very clear and important because normally only the dominant male will mate (Karnofsky and Price 1989). In the wild and in semi-naturalistic aquaria, shelter sharing can occur in juvenile lobsters (Cowan et al. 2001), and networks of relationships can be established and can persist relatively unchanged over time (Karnofsky and Price 1989). The structure of the hierarchy is based on the outcomes of individual fights (Karavanich and Atema 1998a, 1998b). When the size disparity between two animals is large, fights tend to be short, with the smaller animal retreating and assuming the subordinate role (Karnofsky and Price 1989). But when animals are of similar size, fights can be so long and violent that one or both animals may be injured (Karnofsky and Price 1989; Huber and Kravitz 1995). Figure 12.3a–f depicts a battle between two juvenile American lobsters illustrating several of the behavioral patterns displayed. Although the first fight among two individuals may escalate to dangerous levels of violence, subsequent ones are much shorter and milder. For example, Karavanich and Atema (1998a; 1998b) showed that the average duration of two consecutive fights between the same animals drops from 450 to 50 s; concurrently, the behavior of the loser is aggressive on the first fight, but exclusively submissive on the second (Fig. 12.3g). This, of course, explains the short duration of the match.

Thus, when two clawed lobsters that have previously battled meet again, each one knows its place. The question then becomes: How is this accomplished? A series of elegant experiments by Karavanich and Atema (1998a, 1998b) showed that animals are capable of individual recognition that is mediated by the olfactory system detecting compounds in urine. Karavanich and Atema first asked if animals can recognize individuals or an overall dominance status. These two hypotheses have very different predictions, which the authors tested. If animals recognize individuals, then a second fight will only be short and non-violent if the two animals have met before and dominance has been established. If the second hypothesis is true, a "loser" will always retreat from a "winner," even if they have never met before. Karavanich and Atema created "winners" and "losers" by allowing pairs to fight once and then either repeated the same fight (as a control) or paired winners and losers that had not fought each other. As expected, control second fights were short and non-violent. However, when the "loser" had never been exposed to the "winner" in the pair, it did not retreat and actually won in 3 of 10 fights (Karavanich and Atema 1998a). These results support the hypothesis that American lobsters can recognize individuals.

To elucidate the mechanism underlying this recognition, Atema and colleagues (Karavanich and Atema 1998b; Johnson and Atema 2005) staged fights to establish dominance and then re-staged them after manipulating the release of urine or antennular aesthetasc sensilla. They found that ablating the antennular lateral flagella eliminated the dominance that was established in the first fight, and that a similar result was obtained by blocking urine release. Thus, the chemical signals used for individual recognition are in the urine released during the fight and are detected by the olfactory pathway.

The social hierarchy of spiny lobsters in naturalistic conditions is more difficult to observe than in clawed lobsters because many species of spiny lobsters are far
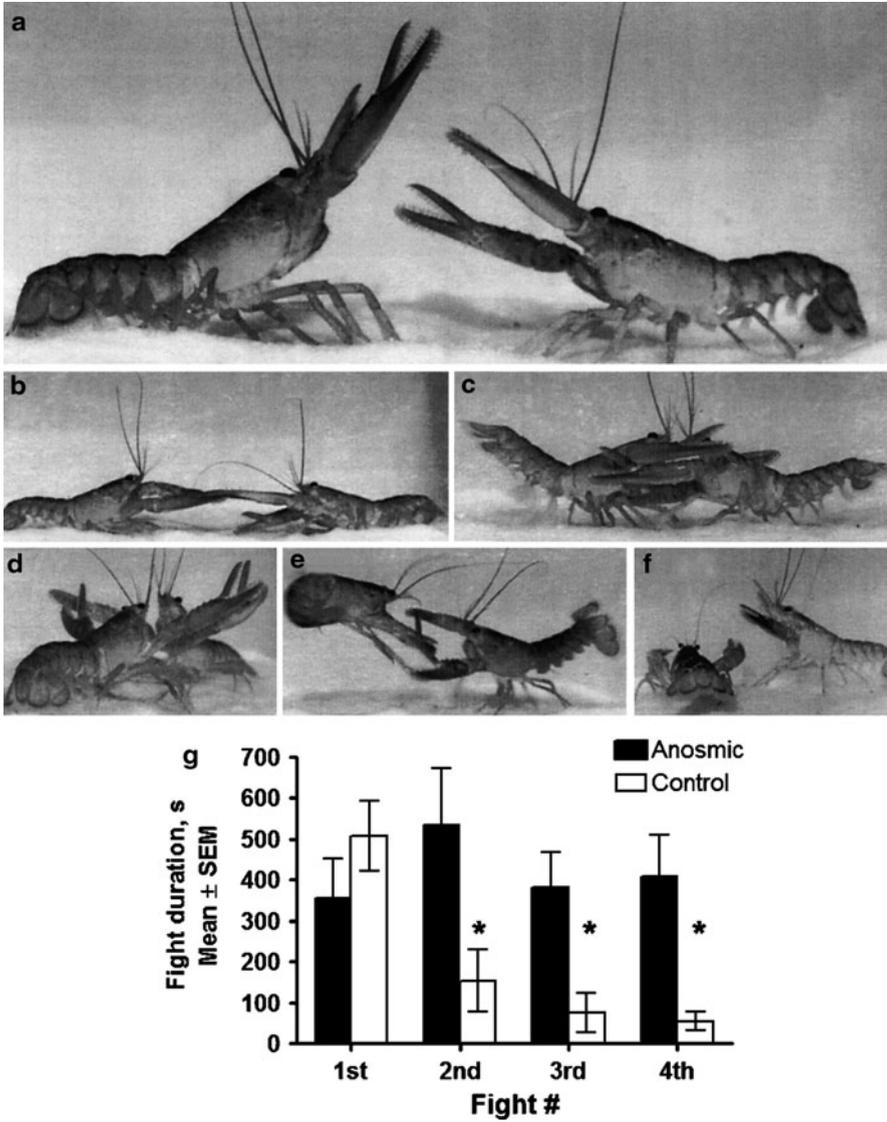
Fig. 12.3 *Top*: Fighting in juvenile American lobsters. After a fight that includes behaviors such as meral spread (**a**), wrestling (**b–d**), and tailflip by one animal (*left* in **e**), the victor (animal on *right* in **e** and **f**) assumes a dominant posture while the vanquished assumes a submissive posture. From Huber and Kravitz (1995) and used with permission. *Bottom*: Successive fights between lobsters become progressively shorter, but only if animals retain their olfactory capabilities. From Karavanich and Atema (1998b). Copyright 1998 by Koninklijke Brill NV, Leiden, The Netherlands

more gregarious and usually share communal shelters. Individual spiny lobsters will compete for food and shelter, displaying aggressive and submissive behaviors (Fielder 1965; Berrill 1975, 1976). When shelters are a limiting factor, they are occupied by dominant individuals that will, if necessary, evict lower-ranked ones (Fielder 1965). In *P. argus*, a highly gregarious species, juveniles introduced into a shelter-containing aquarium will at first exhibit very little aggressive behavior, and consequently shelter density is high; with time, aggressive behavior increases and consequently there is less shelter sharing. Berrill (1975) speculates that stress due to novel surroundings reduces aggression, but that it subsequently resumes as individuals become accustomed and shelter sharing becomes less likely. A similar situation is found in *Panulirus longipes* (Berrill 1976). The solitary species of spiny lobsters are probably more aggressive, but they have received far less attention than the gregarious species (Childress 2007).

Unfortunately, very little is known about chemical communication during social behavior of spiny lobsters, other than aggregation cues (see below). Shabani et al. (2009) showed that in *P. argus* as in clawed lobsters, urine is important in reducing the levels of aggression. Urine release is context- and individual-specific; dominant animals increase urine release when engaged in interactions, while subordinate animals do not (see Fig. 12.4 for an artist's depiction and Fig. 12.5 for original data). Also in *P. argus*, as in clawed lobsters, blocking urine release results in an increase in the number and duration of agonistic encounters. This effect is reversed by reintroducing the urine of one of the combatants into the aquarium. Finally, the aesthetascs are responsible for the responses to urine: solitary spiny lobsters with their olfactory system intact respond to conspecific urine with avoidance behaviors, but when their aesthetascs are ablated they respond with appetitive behaviors, no

Fig. 12.4 Artist's drawing of a pair of Caribbean spiny lobsters engaged in agonistic interaction. The dominant animal (*right*) releases more urine, which in this in drawing is depicted as a white plume, than the subordinate animal (*left*), whose urine is indicated as a smaller black plume. Urine from dominants reduces the level of aggression in subordinates. Drawing by Jorge A. Varela Ramos
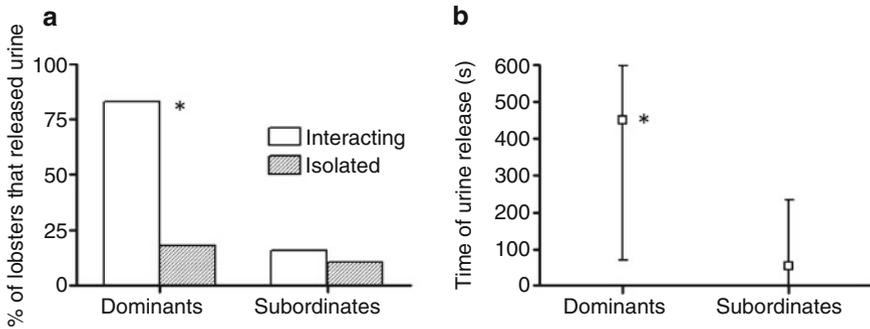
Fig. 12.5 Social interactions and urine release in Caribbean spiny lobster. Dominant animals are more likely to release urine than subordinates (**a**), and dominants release more urine than subordinates (**b**). Adapted from Shabani et al. (2009) with permission from The Journal of Experimental Biology

doubt due to the many other compounds found in urine. It should be noted, however, that spiny lobster urine can also attract conspecifics (Horner et al. 2006), and differences in results may be due to an interaction between the chemical stimulus and the experimental conditions.

Although much less is known about slipper lobsters, one species (the Mediterranean slipper lobster, *Scyllarides latus*) is known to establish and maintain an almost linear dominance hierarchy in semi-naturalistic conditions (Barshaw and Spanier 1994). Interestingly, females were reported to interact more often than males, which were not observed to engage in intrasexual agonistic encounters (Barshaw and Spanier 1994).

Thus, clawed, spiny, and slipper lobsters exhibit similar behaviors; they all engage in agonistic encounters that result in the establishment of a dominance hierarchy, and urine is involved in maintaining it without the need for further, possibly dangerous, combat. Hierarchy maintenance through individual recognition is not restricted to lobsters, as it is also found in mantis shrimp (Mead and Caldwell, Chap. 11) and hermit crabs (Gherardi and Tricarico, Chap. 15).

12.5 Aggregation and Avoidance

As seen above, clawed, spiny, and slipper lobsters have very different lifestyles, and this influences how chemicals are used in their behavioral interactions. Clawed lobsters lead mostly solitary lives and do not cohabitate except when mating, a process controlled by sex pheromones (Atema and Cobb 1980). Some spiny lobsters and slipper lobsters, on the other hand, share communal shelters (Berry 1971; Berrill 1975; Cobb 1981; Zimmer-Faust et al. 1985; Spanier and Almog-Shtayer 1992) (Fig. 12.6a), a behavior that improves survival against predation (Eggleston et al. 1990; Mintz et al. 1994; Weiss et al. 2008). These aggregations are
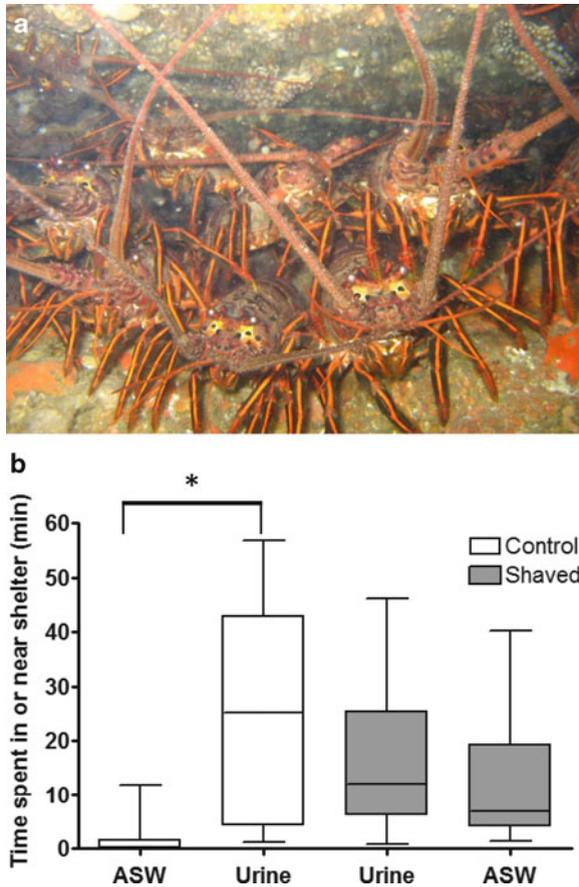
Fig. 12.6 Aggregation and shelter sharing in spiny lobsters. (**a**) California spiny lobsters in a shelter, using their second antennae to protect the entrance to the shelter from predators. From C. White and used with permission. (**b**) Caribbean spiny lobsters are attracted to shelters emanating conspecific urine but only if their aesthetascs are intact. Adapted from Horner et al. (2008) with permission from Springer

chemically mediated, as demonstrated in field and laboratory experiments in which individual animals are given a choice between a control shelter and one from which conspecific chemicals emanate. Conspecific chemicals are attractive, and shelters that emanate them are consistently chosen by higher numbers of animals than predicted by chance alone (Zimmer-Faust et al. 1985; Zimmer-Faust and Spanier 1987, Nevitt et al. 2000).

Although some spiny lobsters and slipper lobsters aggregate, many factors influence this behavior. For example, the introduction of a predator causes *P. argus* individuals to change the preferred shelter size (Eggleston and Lipcius 1992). When there is no predation risk, small spiny lobsters choose either small- or

medium-sized shelters whereas medium-sized spiny lobsters prefer medium or big shelters. Upon introduction of a predator, all spiny lobsters prefer medium-sized shelters, presumably because they provide more protection for medium-sized spiny lobsters, while these in turn protect smaller ones (Eggleston and Lipcius 1992). Small (<15 mm carapace length) individuals tend to be solitary, but after they reach 15 mm they begin to aggregate (Marx and Herrnkind 1985; Childress and Herrn-kind 1996; Ratchford and Eggleston 1998; Childress 2007). Interestingly, even small individuals release a chemical attractant, but in such small quantities that a relatively high number of animals may be needed to produce enough to have behavioral effects in naturalistic conditions (Ratchford and Eggleston 1998). In *J. edwardsii*, large males do not aggregate year round, but disperse during mating season and try to attract females with which they cohabit exclusively in order to mate (MacDiarmid 1994). This indicates an interaction between aggregation and sexual cues.

Another factor influencing aggregation in spiny lobsters is time of day, because these nocturnal animals forage alone and return to their shelter at dawn (Zimmer-Faust et al. 1985; Weiss et al. 2008). Ratchford and Eggleston (2000) demonstrated that this change is due to the discontinuous production of the chemical cue responsible for aggregation. Having the donor and experimental animals at different subjective times, they were able to prove that the aggregation cue is only released at dawn. The chemical cues mediating aggregation of spiny lobsters are in the urine and detected by aesthetasc chemoreceptors (Horner et al. 2006, 2008) (Fig. 12.6b). Nothing is known about whether chemical cues mediate other types of aggregation, such as the long migratory queues observed in the field.

Finally, once again, studies on slipper lobsters are rare. Barshaw and Spanier (1994) report that *S. latus* aggregates in the daytime, but there is no information regarding what, if any, chemicals influence this behavior. As with spiny lobsters, gregariousness does not seem to be a universal characteristic of this group. Morin and MacDonald (1984) report that in Hawaii the congeneric species *Scyllarides haanii* and *Scyllarides squammosus* have different lifestyles, the former being solitary and the latter gregarious.

For spiny lobsters, as with other animals, avoiding danger and possibly injury and death by staying away from predators is an adaptive strategy (Hay, Chap. 3; Hazlett, Chap. 18). Each stage of an event of predation will result in the release of chemicals that contain information about the event – chemicals from the predator, disturbance or injury-related chemicals from the prey, and finally chemicals released from food during the act of consumption (Wisenden 2000).

Many species of animals, including lobsters, detect and react appropriately to chemicals from predators. For example, Wahle (1992) showed that American lobsters exposed to chemicals from a predatory fish spend significantly more time in their shelters than control animals, and Horner et al. (2006) showed that *P. argus* tends to avoid the scent of a predatory octopus. Hermit crabs are even able to discriminate between predatory and herbivorous crabs by their scent alone (Rosen et al. 2009), although we know of no comparable lobster-specific data.

   Disturbance and injury-related chemicals can also influence lobster behavior. Disturbance cues are released by animals that are harassed or disturbed, while the injury-related cues passively leak into the environment due to the damage produced by the predator. Avoidance of injured or freshly dead conspecific has been shown for *Panulirus interruptus* (Zimmer-Faust et al. 1985), *Panulirus cygnus* (Hancock 1974), and *P. argus* (Parsons and Eggleston 2005; Briones-Fourzán et al. 2006). Interestingly, *Panulirus guttatus* does not seem to avoid the scent of injured or freshly killed conspecifics (Briones-Fourzán et al. 2006), providing us with an example of different lifestyles resulting in different modes of chemical communication. Briones-Fourzán et al. (2008) performed a series of experiments specifically designed to compare *P. guttatus* and *P. argus*, which are syntopic species. They confirm that *P. argus* avoids shelters emanating the scent of a freshly killed conspecific and show that they also avoid shelters emanating freshly killed *P. guttatus* scent. In contrast, *P. guttatus* is indifferent to the smell of freshly killed individuals of either species; it selects a den that emanates its scent with the same probability as a control. The authors interpret these results in view of the two species' different lifestyles. They propose that a *P. argus* individual returning to its reef after foraging will gain an advantage by avoiding alarm cues. The fact that the alarm cues may not originate from a member of its own species is not relevant in this scenario because the predator could very well attack the returning spiny lobster too. In the case of *P. guttatus*, there is less advantage in avoiding alarm cues because *P. guttatus* is solitary and only forages very close to its den entrance (Briones-Fourzán et al. 2008). These closely related species also share many predator defense mechanisms, but vary widely in the performance of them, adding support to the idea that their different lifestyles result in different ways of dealing with predation risk (Briones-Fourzán et al. 2006).

   Briones-Fourzán (2009) reanalyzed data discussed above by differentiating between lethally and non-lethally injured (one or more autotomized limbs) animals. This analysis shows that *P. argus* only avoids the scent emanating from lethally injured conspecifics, a result that agrees with results from Parsons and Eggleston (2005). For *P. guttatus*, Briones-Fourzán further distinguished between experiments carried out in the spring, which is the peak mating season, and late summer. This new analysis shows that in the spring, when these animals are most gregarious, both intact and slightly-injured animals are attractive to conspecifics.

   Hemolymph is the source of alarm cues in *P. argus*; it causes conspecifics to spend more time inside their shelters and counters the effect of food-related chemical cues (Shabani et al. 2008). Alarm cues are detected by aesthetasc chemoreceptors. Spiny lobsters with ablated aesthetascs do not respond to hemolymph with an alarm response; indeed, spiny lobsters without an olfactory sense respond to hemolymph as if it were an appetitive cue and advance towards its source (Shabani et al. 2009). This is due to the fact that hemolymph contains many food-associated compounds that spiny lobsters detect through their non-olfactory antennular chemoreceptors (Steullet et al. 2001, 2002; Schmidt and Mellon, Chap. 7). Interestingly, hemolymph from *P. interruptus* or blue crabs (*Callinectes sapidus*) did not

produce the same responses in *P. argus*: they responded with mixed alarm and appetitive behaviors to hemolymph from the California spiny lobster *P. interruptus*, but only with appetitive behaviors to the hemolymph of blue crabs, indicating that phylogeny is more important than sympatry (Shabani et al. 2008). This result is at odds with the one reported by Briones-Fourzán et al. (2008), an effect that might be due to two possible reasons. In the first place, the two studies did not measure the same variable: Briones-Fourzán and her colleagues left the spiny lobsters overnight in a Y-maze and recorded the shelter choice the next morning, whereas Shabani and colleagues evaluated the immediate effect of introducing hemolymph into the aquarium that held a spiny lobster. Another and to us much more interesting explanation rests with the difference in the stimuli used: Shabani et al. (2008) used hemolymph and Briones-Fourzán et al. (2008) used dead animals. Another layer of complexity is added by the fact that injured conspecifics are aversive for a limited time period after injury (Ferner et al. 2005), and so in the case of overnight experiments using dead specimens as stimuli, the actual stimulus may be changing over time.

Our knowledge of avoidance behaviors in clawed lobsters is virtually nonexistent, mainly because there is very little aggregation to begin with. So once again, we find that the extent to which a particular behavior is exhibited (or studied!) depends on an animal's lifestyle. Gregarious spiny lobsters have been extensively used by researchers interested in the nature and mode of action of the chemicals mediating aggregation, while non-gregarious spiny lobsters and clawed lobsters have been largely ignored except in the special and altogether different case in which individuals gather for reproductive purposes. For the same reasons, avoidance and its mechanisms have been studied most extensively in gregarious spiny lobsters. Fortunately, there is an exception to this rule, and Briones-Fourzán and her collaborators (2006) explicitly compared sympatric gregarious and non-gregarious spiny lobsters and found that only the former avoided dead conspecifics.

12.6 Recognition of Diseased Animals

An interesting special case of conspecific avoidance is that *P. argus* is able to detect and avoid conspecifics infected with a lethal virus (Behringer et al. 2006, 2008). When given the choice, these highly social animals avoid shelters occupied by diseased individuals and prefer empty ones, the opposite of what happens when the shelter is occupied by a healthy conspecific. In addition, diseased individuals are avoided before they become infectious, a necessary condition if the avoidance is to reduce the spread of the disease among the population. Although the experimental design does not allow determination if the animals base their decisions on chemical cues, it would be very interesting to evaluate the possibility that they are able to detect the disease from a "safe" distance using their chemical senses, and to elucidate if those signals originate from the host or the virus.

12.7   Summary and Conclusions

We have attempted to give a brief overview of intraspecific chemical communication between lobsters. Lobsters communicate through chemical compounds that are predominantly but not exclusively located in their urine. Other lobsters detect these compounds with olfactory sensory neurons, located in the aesthetasc sensilla on their antennules. As far as is known, this is true for mating in spiny and clawed lobsters, aggregation in spiny lobsters, and social hierarchy establishment and maintenance in spiny and clawed lobsters. Alarm cues, which are in the hemolymph and leak from an injured animal, have some degree of species specificity. These chemical cues can also be detected by the olfactory pathway. One very obvious gap in our knowledge and stumbling block to our progress is that we do not know the chemical identities of these semiochemicals.

12.8   Future Directions

Our review shows that the greatest future contributions to our understanding of the comparative study of chemical communication in lobsters would come from focusing on two areas. The first is to identify the molecules producing these behaviors. With these identified compounds, we will be able to more accurately pinpoint their sources in living animals and perform carefully controlled behavioral experiments. Additionally, this knowledge will allow us to perform physiological experiments to shed light on where and how these important signals are processed. The second area of emphasis is to study the role of chemical communication in mediating the behavior of species that have received less attention. This includes mating, individual recognition, and recognition and avoidance of diseased individuals in spiny lobsters, attraction in clawed lobsters, and just about any aspect of chemical communication in slipper lobsters.

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