

# Chapter 16

## Deception in Visual and Chemical Communication in Crustaceans

John H. Christy and Dan Rittschof

**Abstract** Deception in animal communication occurs when one animal causes another to respond to a condition that does not exist or to fail to respond to one that does. Signals that bluff produce the first kind of error, behavior that hides causes the second, and both are common in visual communication by crustaceans. In contrast, crustacean chemical communication may usually be honest because the communicative chemicals typically are byproducts of the biochemical mechanisms by which crustaceans are built and operate. These cues, which often are released in urine, reliably reveal an individual's identity, sex, reproductive state, and condition. There are, however, opportunities for deception by bluffing and by hiding in the chemical channel. Bluffing may occur when dominance relationships are learned and individuals recognize each other. Subordinates may avoid known dominants even after the condition of the dominant has declined and it is no longer able to win a fight with the subordinate. Frequent probing by subordinates should check such bluffing. Hiding in the chemical channel may occur in escalated fights in which one animal fails to chemically announce its intent to strike and wins by delivering a blind-side punch to an unprepared opponent. Receptive female crabs and lobsters may also withhold cues of their receptivity to avoid courtship by some males, yet direct the same cues to preferred potential mates. In species with multiple male morphs, we speculate that subordinate males may hide from dominants by withholding male odors or mimicking female odors. In species with internal fertilization we also suggest that male seminal fluids may contain chemicals that affect female reproductive processes and bias the rate the male's sperm fertilize the female's eggs. Detecting deception in chemical communication will be very challenging, but we encourage crustacean researchers to keep this possibility in mind when examining signaling behavior via chemicals.

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## 16.1 Introduction

Deception is common between species (e.g., mimicry), but, primates excepted, it seems to be rare between individuals of the same species even though the interests of signalers and receivers usually differ (Searcy and Nowicki 2005). Ironically, I (JC) first encountered apparently deceptive behavior in an animal after I stopped studying howler monkeys and began observing fiddler crabs. Over the past 3 decades, I have discovered several cases of visual deception in fiddler crab communication perhaps because the profound differences in our nervous systems make it easy for me to detect deception that goes unnoticed by the crabs. These discoveries are not unique; visual deception appears to be more common in crustaceans than in any other nonprimate taxon. In contrast, the second author's (DR) studies suggest that crustacean chemical communication usually is honest because the chemicals are often byproducts of basic physiological processes and cannot be faked. Here we combine our different research backgrounds and perspectives to explore how crustaceans might deceive using chemicals. We review visual deception by bluffing, hiding, and mimicry, speculate freely on the possible existence of these modes of deception in the chemical channel, and offer a few tentative examples. First, we define some terms.

## 16.2 Definitions

Although consensus definitions for common terms and concepts used in animal communication research are close at hand (Searcy and Nowicki 2005), disagreement remains.

### 16.2.1 *Signals and Cues*

A signal is a feature of an individual's phenotype that evolves because it elicits a response from other organisms that increase the signaler's fitness (after Hasson 1994). Maynard Smith and Harper (2003) and Scott-Phillips' (2008) definitions of signaling require that the response also evolves because it increases the receiver's fitness. Unfortunately, this requirement disqualifies as signals all deceptive traits that elicit costly responses that decrease the receiver's fitness (Hasson 1994; Wiley 1994) and classifies them as coercion instead (e.g., Scott-Phillips 2008). We also do not require that deceptive signals be variants of signals that are honest on average (Johnstone and Grafen 1993), though sometimes they are (see Table 16.1). In order to accommodate deception by hiding and mimicry, we find it necessary to allow some signals to elicit costly responses that do not benefit receivers (see also Hebets and Papaj 2005).

**Table 16.1** Deception in crustacean visual communication

Context	Species	Signal/behavior	Kind of deceit	Mechanism	References
Aggression	<i>Alpheus heterochaelis</i> snapping shrimp, males	Display large snapping claw	Bluffing RHP	Claw size increases with body size which determines RHP. Small males with relatively large claws bluff RHP when they signal and they bluff most often in encounters they are sure to lose if they escalate to fighting	Hughes (1996, 2000)
	<i>Pagurus bernhardus</i> , hermit crab, males	Present or extend larger (right) claw	Bluffing aggressive intent	When males approach each other, one or both extend their chelae toward the other crab. Larger (body size) males usually win fights for shells. Both small and large males with relatively large claws tend to display more often. About 3% of the time chela displays are not backed up with future aggression. Claw size residuals do not predict winners in escalated fights for shells	Laidre (2009) and Arnott and Elwood (2010)
	<i>Cherax dispar</i> Australian slender crayfish, males	Display large chelae	Bluffing strength	Males with the more powerful chelae win fights, but most encounters are resolved without fighting. Winners usually have larger but not stronger chelae; hence they bluff strength. Male large chelae deliver forces about half those of females and they vary widely in strength	Wilson et al. (2007, 2009)
	<i>Uca annulipes</i> , <i>Uca mjobergi</i> and related species, fiddler crab, males	Wave and threaten with large claw	Bluffing strength	Large males with relatively large claws win fights. Males assess opponents visually and avoid larger males. When males lose their large claws they grow (regenerate) new ones that are long,	Jennions and Backwell (1996), Backwell et al. (2000), and Lailvaux et al. (2009)

(continued)

Table 16.1 (continued)

Context	Species	Signal/behavior	Kind of deceit	Mechanism	References
				thin, and weak compared to their original claws. Opponents avoid fighting males with long weak claws as often as those with long strong ones. Hence, regenerated claws bluff strength.	
	<i>Neogonodactylus bredini</i> , mantis shrimp, both sexes	Display merus of large maxilliped	Bluffing strength	Just before molting, individuals frequently challenge their neighbors using the meral spread display. Immediately after molting they are too weak to fight, but nevertheless use the display and bluff their ability to strike	Caldwell (1986) and Adams and Caldwell (1990)
	<i>Uca pugilator</i> , <i>Uca beebei</i> , <i>Uca rapax</i> fiddler crabs, both sexes	Furtive approach and motionless crouch	Hiding (perceptual) of self	A crab without a burrow crouches low and motionless several centimeters from a resident's burrow and the resident stops interacting with it. When the resident moves away from the burrow the crouching crab dashes into the burrow before the resident can return to defend it	Christy (1980) and B. Greenspan, personal communication
	<i>Uca arcuata</i> , <i>U. beebei</i> , <i>Uca capricornis</i> , <i>Uca formosensis</i> , fiddler crabs, both sexes but typically females	Chimneys	Hiding (physical) of the burrow entrance	Crabs build a cylinder of mud centered on their burrow entrance. Burrows with mud chimneys are less frequently found by crabs seeking new burrows than are burrows without chimneys. In <i>U. beebei</i> chimneys are taller than the eyes of intruders thus making the burrow opening impossible to see. Chimneys built by male <i>U.</i>	Wada and Murata (2000), J. Christy unpublished, Slatyer et al. 2008, and Shih et al. 2005

<p><i>formosensis</i> may hide the male from rivals as he expands the burrow after attracting a mate</p>					
<p>Males with long, thin, weak regenerated claws lose fights, but they court females by claw waving as do males with robust original-form claws that win fights. Females are as attracted to males with regenerated claws as they are to males with original claws</p>	<p>Bluffing condition</p>	<p>Wave large claw</p>	<p>Courtship</p>	<p><i>Uca annulipes</i> (and possibly its sister species, <i>U. lactea</i>, <i>U. perplexa</i>, <i>U. mjobergi</i>) fiddler crab, males</p>	<p>Backwell et al. (2000)</p>
<p>Crabs without burrows orient to and hide against objects on the surface to reduce their predation risk. Females leave their burrows and search for mates by visiting several courting males at their burrows before they choose one. Males sometimes build structures at the entrances to their burrows. Females are more attracted to burrows with than without structures and this preference increases with perceived predation risk. The preference reduces females' predation risk and incidentally biases mate choice in favor of males with structures</p>	<p>Mimicry, sensory trap</p>	<p>Sand hoods, mud pillars</p>	<p><i>Uca terpsichores</i>, <i>U. beebei</i> and perhaps other structure-building species; fiddler crabs, males</p>	<p>Christy (2007) (review)</p>	
<p>As a mate searching female leaves the burrow of a male she has visited but not mated, the male, with claw held low, moves quickly away, stops, raises his claw high and runs back to</p>	<p>Mimicry, sensory trap</p>	<p>Startling male displays</p>	<p><i>U. terpsichores</i>, <i>U. beebei</i>, <i>U. pugilator</i>, fiddler crabs, males</p>	<p>Christy and Salmon (1991) and J. Christy unpublished</p>	

(continued)

**Table 16.1** (continued)

Context	Species	Signal/behavior	Kind of deceit	Mechanism	References
				<p>his burrow. This may startle the female into the burrow whereupon the male follows and the pair may mate. <i>U. terpsichores</i> males with sand hoods may instead move behind them, climb over the top and jump down in front of the burrow startling the female into the burrow. These rapid, elevated male movements present stimuli that are similar to those usually associated with predatory birds perhaps explaining why they startle females</p>	

A cue also is a feature of an individual's phenotype (or the environment) to which other organisms respond. Receivers benefit when they respond to cues and their response can be either beneficial or harmful to the cue bearer. For example, tracks and odors left by a passing social group of prey could be used by lost group members to relocate the group or by predators to find a meal. Unlike signals, cues do not evolve because the responses to them increase the fitness of the cue bearer (Hasson 1994). Cues can be traits with noncommunicative functions, byproducts of those traits, or nonfunctional features of the phenotype (e.g., tracks in the above example). However, once cues elicit responses that affect the fitness of the cue bearer, they may be elaborated as signals if they are beneficial or they may be lost from the phenotype if they are costly and these costs are not balanced by benefits in other contexts.

### ***16.2.2 Honesty and Deception***

Maynard Smith and Harper's (2003) definition of signaling (see above and Wyatt, Chap. 2) requires that receivers benefit from their response in the signaling context and reliable delivery of such benefits constitutes honesty. There has been much debate about what ensures signal reliability (Harper 2006). It is now generally agreed that the costs of signal development, production, or maintenance and those imposed by skeptical receivers when they probe to detect deception ensure signal reliability (Searcy and Nowicki 2005). However, receivers can make errors in honest signaling systems when they have problems either detecting signals due to noise (Johnstone and Grafen 1992; Wiley 1994) or interpreting them when signalers vary in both the costs and benefits of signaling at a given level (Johnstone and Grafen 1993). The former errors are mistakes caused by the environment and are not the result of deception. The later errors provide the opportunity for deception as illustrated by some crustacean visual threat displays (e.g., snapping shrimp and hermit crabs, Table 16.1).

Although deception is familiar to us all, there is no widely accepted definition of deceiving by humans (Mahon 2007). The difficulties include specifying the intentions of the deceiver, what both parties do and do not believe, and how they come to hold those beliefs. Fortunately, a biological definition of deception is easier to write because the intentions and beliefs of animals are unknowable and are excluded from the definition. The following definition combines elements of those by Mitchell (1986) and Mahon (2007).

To deceive is to act or appear in a way that causes another organism to respond appropriate to condition  $x$ , when  $x$  is not the case, or to fail to respond appropriate to condition  $x$ , when  $x$  is the case.

Thus, there are two broad classes of deception that differ according to the kind of error a receiver makes. Receivers make an error of the first kind when they falsely respond to signals that bluff or mimic and they make an error of the second kind

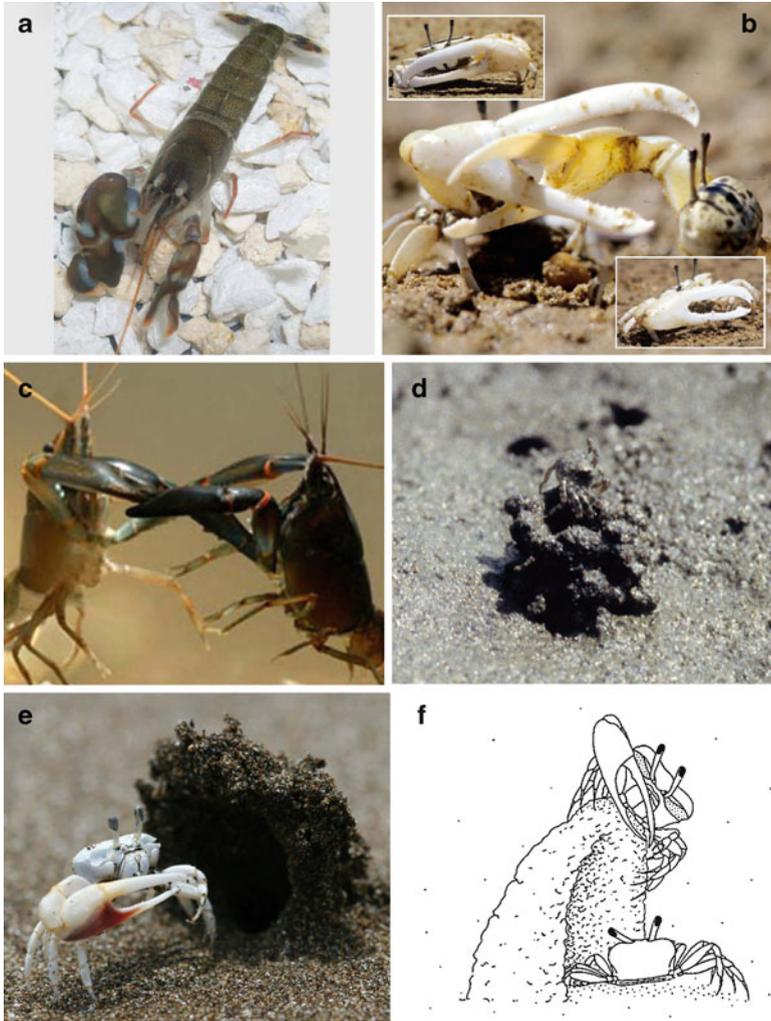
when they fail to respond to behavior that hides a trait of interest; we present cases of each below. These two kinds of errors are analogous to statistical type one (false alarms) and type two (missed opportunities) errors (Hasson 1994; Wiley 1994). The first results in a cost to the receiver because its response is inappropriate and the second because its lack of response results in lost potential benefits. We exclude from deception cases in which an animal forcefully interferes with the ability of another to respond; an animal that wins a fight by blinding its opponent is using coercion, not deception. Next, we present examples of visual deception by bluffing, mimicry, and hiding by crustaceans during fighting and courtship, the two social contexts in which the interests of sender and receiver seldom coincide.

## 16.3 Visual Deception

### 16.3.1 Aggression

Equipped with hard exoskeletons and multiple appendages allowing specialization, crustaceans have evolved a diversity of powerful weapons (Emlen 2008), many of which can deliver fatal blows. When death is a possible outcome of a fight, it is in the mutual interest of opponents to use displays to assess their relative RHP (Resource Holding Potential) without exchanging blows; the weaker withdraws and avoids injury and the stronger wastes little time in an interaction it is sure to win. Not surprisingly, aggression between crustaceans typically begins with displays allowing assessment of weapons. These displays can include pushing and rubbing and other relatively nonforceful tactile components (chemical cues of sex or status are often present as well). The honesty of such threat displays should be maintained by escalated fights in which individuals that bluff RHP by displaying large but weak weapons suffer costly losses. Nevertheless, there are four examples of apparent bluffing of RHP or strength by crustaceans via weapon display and one example of bluffing aggressive intent (Table 16.1, Fig. 16.1).

In an especially perspicacious study of aggressive displays and fighting in snapping shrimp, Hughes (1996, 2000) (Table 16.1, Fig. 16.1a) showed that individuals with signals (chela) that are larger than average for their competitive ability (determined by body size) will appear to be better competitors than they are. Some receivers may avoid fighting an individual with a large signal residual even though they might win. As predicted, Hughes (2000) found that smaller individuals with positive signal residuals, those with the most to gain by exaggerating their body size, were more likely to display aggressively, effectively bluffing their competitive ability, yet they were not more likely to win when receivers probed the deception and contests escalated to fights. This approach to detecting deception in an otherwise honest signaling system is useful only when signal residuals do not affect fighting ability (e.g., Briffa 2006). It has been used to detect bluffing of aggressive intent in hermit crabs (Arnott and Elwood 2010) and the evidence



**Fig. 16.1** Visual deception in crustaceans. Bluffing RHP wherein the size of the weapon may not reliably indicate strength: (a) *Alpheus heterochaelis*; (b) *Uca perplexa*; (c) *Cherax dispar*. Hiding burrow entrance and self: (d) female *Uca beebei* and her chimney. Sensory traps based on responses selected by predation: (e) *Uca tersichores* male and his hood; (f) *U. tersichores* male running over his hood and startling a female into his burrow (Image credits: (a) Melissa Hughes; (b, d, and e) John Christy; (c) Anthony O'Toole courtesy of Robbie Wilson; (f) drawn by Donna Conlon)

generally supports low levels of deception in this context (Laidre 2009). However, in many crabs, clawed lobsters, and crayfish, individuals with relatively large claws are better competitors (Table 16.1, Fig. 16.1b, c), in which case Hughes' signal residual analysis is inappropriate. Examples in Table 16.1 ("bluffing strength")

show how threat signals that are honest on average can be corrupted when variation in the traits (muscle mass and cuticle strength) likely to affect RHP are not apparent to the viewer. Such variation may be caused by individual differences in nutrition, molt stage (Fig. 16.2), or even history of weapon loss and regeneration as in fiddler crabs (Fig. 16.1b). The crustacean exoskeleton coupled with the visual display and use of lethal weapons may predispose these animals to bluffing RHP.

There are two cases of deception by hiding during fiddler crab aggression, one by use of a furtive behavior, the other by concealment. I (JC) first saw furtive behavior (July 1974, Table 16.1) in male sand fiddler crabs *Uca pugilator* (Christy 1980) and subsequently in both sexes of several other species, most notably *Uca beebei*. Most remarkable is the ability of the crouching crab to determine when the resident is sufficiently far from its burrow to make the dash worthwhile and to orient to the burrow entrance it may not see (Zeil and Layne 2002).

The second example shows how fiddler crabs that are burrow residents sometimes build chimneys around their burrows that conceal both the burrow entrance and themselves (Table 16.1, Fig. 16.1d). Chimney building is known in at least 22 of the 97 recognized species of fiddler crabs (Rosenberg 2001; 21 species listed by Shih et al. 2005, plus *U. beebei*; J. Christy, unpublished). There is considerable variation in the sex, reproductive status, and sizes of crabs that build chimneys, how they are built, their shape, and how often and when they are built. Chimneys may have additional, and perhaps, multiple functions (e.g., for defense; Salmon 1987).



**Fig. 16.2** Stomatopods *Neogonodactylus bredini* recognize each other by odor. They may bluff their dominance over another individual when they molt or when other physiological changes not reflected in their individual odor decrease their RHP (Image by Roy Caldwell)

### 16.3.2 Courtship

Male decapods use their weapons to signal during courtship. Berglund et al. (1996) pointed out that the crucible of combat should ensure that weapons honestly indicate RHP and that RHP should reliably indicate male condition and viability. Hence, females that choose mates by assessing their weapons may mate with males in good condition. However, when males bluff RHP with large but weak weapons, they may also bluff their mate quality. Indeed, this appears to be the case in *U. annulipes* (Table 16.1).

Two sensory traps, a mode of signaling based on mimicry (Christy 1995), have been discovered in the courtship of the fiddler crab *Uca terpsichores* and a few other species (Table 16.1). A sensory trap operates during courtship when a signal or display elicits a response from a receiver that increases the chance the signaler will mate, but that has not evolved for mate choice (Christy 1995). The first case, the subject of over a decade of field research, was summarized recently by Christy (2007). The female response to the male signal, a structure the male builds at the opening of his burrow (Fig. 16.1e), is selected by predation, increases in strength with predation risk (Kim et al. 2007, 2009), and incidentally results in mate choice. The female's response results in a direct immediate benefit (reduced risk of predation), but it also may be costly if it results in choice of a mate that is different from her choice had the sensory trap signal not been used (Bradbury and Vehrencamp 2000). However, males that are in better condition are more likely to build structures (Backwell et al. 1995; Kim et al. 2010). Hence, females that mate with structure builders may benefit provided that female fitness increases with the condition of their mate. If so, then females that are caught in this sensory trap may doubly benefit and we leave it to the reader to decide whether this "white lie" qualifies as deception (Christy 1997).

The second sensory trap in fiddler crab courtship was discovered in *U. pugilator* (Christy 1980; Christy and Salmon 1991) and has subsequently been seen in *U. terpsichores* and *U. beebei*. When a female that is searching for a mate stops at a male's burrow and begins to leave, the male usually courts the female with claw waving. However, just as the female begins to depart, males sometimes execute two displays that include rapid movement of their large claw or entire body above the female's visual horizon (Table 16.1, Fig. 16.1f). Such looming stimuli elicit a startle response (Layne 1998); the females dash back to the burrow as if they have detected an approaching predator. Hence, the deception relies on females' mistaken responses to displaying males as if they were predators.

## 16.4 Chemical Communication with Cues, not Signals

As chapters by Duffy and Thiel (2007) attest, crustaceans respond to chemicals that originate from conspecifics during hatching, settlement, maternal care, and family

interactions, while seeking and interacting with mates and when competing for food and shelter. Some of these chemicals have not been modified for communication and therefore fit the definition of a cue rather than a signal (see below). Few chemicals used in social interactions have been identified. In contrast, studies of chemical communication by crustaceans have produced detailed descriptions of signaling behavior and the structures used to deliver and receive chemicals.

Peptides mediate hatching, settlement and, in hermit crabs, shell-seeking behavior. Research on these peptides spans 5 decades and has produced over 100 publications (summarized in Rittschof and Cohen 2004). The peptides result from hydrolysis of structural proteins by trypsin-like serine proteases. These proteases are endogenous to the source or are produced by bacteria that feed on the proteins or by the digestive enzymes of predators of gastropod shell occupants, or as part of coagulation processes (Matsumura et al. 2000; Dickinson et al. 2009). Hence, the production of the active chemical is routinely a predictable byproduct of an important activity and is not under direct control of the source as would be expected of most signals. As is typical of cues but not signals, the peptides and proteins are active at very low concentrations (e.g.,  $10^{-7}$  to  $\ll 10^{-11}$  M for natural cues from eggs that stimulate larval release behavior in females) and they do not stimulate greater responses at higher concentrations. Many features of peptide-based chemical interactions in crustaceans and other phyla support the view that the active chemicals are cues of interest to responders, that they evolved before the responses to them, and that they have not been modified as signals. Substituted amino sugars mediate behavioral interactions in some crustaceans (Rittschof and Cohen 2004); since these molecules too are byproducts of the basic chemical pathways by which crustaceans and other aquatic organisms are built and manage hygiene, they are cues.

It is not known whether chemical social signaling in crustaceans uses cues or chemicals that are specifically modified as signals. The recent identification of the first crustacean sex pheromone (Hardege and Terschak, Chap. 19) supports the former view. The chemical is uridine diphosphate (UDP) which is a byproduct of the final step in chitin synthesis. Interestingly, as expected of a conserved cue but not a highly evolved signal, UDP elicits male sexual behavior in several unrelated crabs (Bublitz et al. 2008). Lacking evidence to the contrary, we therefore speculate that chemical signaling in crustaceans may typically be accomplished by modulated production, release, and delivery of chemical cues. If this is correct, then one way that deception in this channel, if it exists, could be achieved is through changes in the behaviors used to release and direct otherwise genuine cues to receivers.

### ***16.4.1 Bluffing Dominance***

Many benthic crustaceans live at high densities in self-made or natural refuges for which they compete intensely. Dominance relationships are established through fighting and may often be maintained through individual recognition (IR) based on chemical cues (Table 16.2). IR occurs when receivers perceive and recognize others

**Table 16.2** Possible mechanisms of deception in crustacean chemical communication

Context	Kind of deceit	Mechanism	Possible examples
Aggression	Bluffing individual dominant status	Individuals recognize each other by odor. When an animal fights and loses, it associates the odor of the winner with its dominant status. When the individuals again meet, the subordinate recognizes the dominant by odor and defers to it even if the fighting ability of the dominant has declined making it likely to lose if the animals fought again	Gonodactylid stomatopods, Caldwell (1986) and Adams and Caldwell (1990) <i>Homarus americanus</i> , Karavanich and Atema (1998) <i>Pagurus bernhardus</i> , Hazlett (1969) <i>Pagurus longicarpus</i> , Gherardi et al. (2005)
	Hiding RHP to deliver a “blind side” winning punch	Dominant males tend to release more urine more often in fights and urine release tends to be coincident with aggressive acts. However, when fights escalate, the variance in urine release by dominants increases in <i>H. americanus</i> , fights are just as likely to reach the highest levels whether or not males release urine in <i>Astacus leptodactylus</i> and, at the highest levels of fights, dominant <i>Orconectes rusticus</i> cease directing urine toward opponents. Hence, when fights escalate dominant males may deliver winning forceful aggressive acts without producing urine or directing it toward opponents and chemically signaling their aggressive intent	<i>H. americanus</i> , Breithaupt and Atema (2000) <i>A. leptodactylus</i> , Breithaupt and Eger (2002) <i>O. rusticus</i> , Bergman et al. (2005)
	Hiding sexual receptivity but not sex	Male stomatopods <i>N. bredini</i> can detect females by odor, but not their state of receptivity. Around the time of the full moon, female <i>N. bredini</i> that are not sexually receptive exploit the tendency of males to admit females to their cavities for mating. Such females gain access to males' cavities and prevent the males from re-entering about twice as often as do sexually receptive females	<i>N. bredini</i> , Caldwell (1986), Mead and Caldwell, Chap. 11
Courtship	Hiding sexual receptivity	Sexually active males detect females and their state of	<i>H. americanus</i> , Atema and Steinbach (2007)

(continued)

**Table 16.2** (continued)

Context	Kind of deceit	Mechanism	Possible examples
		sexual receptivity by odors in their urine. During mate sampling and assessment females control the release of their urine and its transmission in currents toward or away from males. In this manner they can hide from and thus reject some males and reveal their sex and status to others they prefer as mates	<i>Carcinus maenas</i> , Bamber and Naylor (1996) <i>Callinectes sapidus</i> , Jivoff and Hines (1998)

by their uniquely distinctive cues and respond in a manner appropriate to the identified individual (Caldwell 1986; Sherman et al. 1997). IR mediates dominance when an individual that has fought and lost learns to associate unique cues with the winner. Although the response “defer to dominant” may be a class-level response, it is elicited because the dominant is identified individually (Mead and Caldwell, Chap. 11; Aggio and Derby, Chap. 12; Wyatt, Chap. 2).

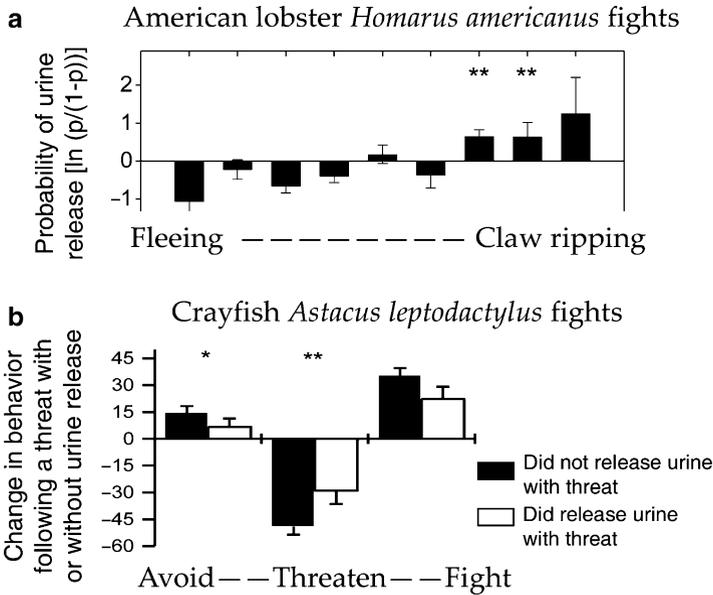
We suggest that dominance relationships that are mediated by IR are vulnerable to bluffing because the cue used for IR and the property of the individual that allows it to dominate another are not immutably linked (Caldwell 1986). Presumably, IR cues are individually distinctive body odors that are unrelated to condition or other traits that affect RHP. Indeed, lack of such relationships would be advantageous because IR could mediate a variety of interactions based on other learned qualities and physiological states. Thus, an individual’s identity will remain constant, while some of the factors that affect its transitory physiological or condition-dependent qualities vary (However, a change in body odor when an individual molts would reveal a temporary reduction in RHP). If an individual’s RHP declines after the individual has established its dominance over another, the weakened individual can use its IR cues to bluff dominance until the subordinate calls the bluff. This situation is analogous to bluffing RHP with weapons made of exoskeleton that do not decrease in size with a loss in condition or muscle mass. Experiments in which an individual’s RHP is decreased by forced exercise or starvation could be used to explore bluffing dominance by IR. Under natural conditions, the decay in the relationship between IR and dominance, as measured by the extinction of the subordinate’s submissive deference when the two meet, should relate to the average reduction in individuals’ RHP with time and, consequently, a reduction in the costs to the subordinate of probing the relationship. The bluff should be effective and used for a time determined by the rate of decay of condition and the decrease in the costs of probing. If bluffing dominance by IR is common, subordinates should “forget” their status sooner rather than later or use other cues to detect a reduction in RHP (e.g., coincident with molting). Under experimental laboratory conditions, American lobsters ceased to recognize individuals that beat them in fights after about 1 week, even though when they challenged the dominant they lost again (7 cases,

Karavanich and Atema 1998). Subordinates may “forget” and probe sooner than dominants lose their relative RHP. We emphasize that the use of IR to bluff may be possible when the relationship between IR cues and class membership is arbitrary, learned, and ephemeral. Hence, bluffing may occur in other relationships based on IR chemical cues and learned temporary states that affect social interactions.

### 16.4.2 Hiding RHP

Chemicals that mediate social interactions in decapod crustaceans often are present in urine, with highly controlled directed release (Atema and Steinbach 2007). Urine contains metabolites that are potential cues of an individual’s identity, membership in a social or biological class, physiological or motivational status, and diet or future behavior (Atema and Steinbach 2007). Here we explore urinary signaling during fighting in lobsters and crayfish and during sexual interactions in lobsters and crabs. Our intent is to identify situations in which it might be to the sender’s advantage to withhold the chemical. We then present possible evidence of chemical “hiding” (Table 16.2).

Homarid (clawed) lobsters and crayfish that are not familiar with each other interact aggressively when they meet and these interactions often escalate to fights in which individuals may be injured or (rarely) killed. Fights typically escalate following a patterned progression of exchange of visual, tactile, and chemical cues. The relationships between fight outcome and the release of urine have been explored on fine temporal scales during symmetrical interactions between male *Homarus americanus* (Breithaupt and Atema 2000), *Astacus leptodactylus* (Breithaupt and Eger 2002), and *Orconectes rusticus* (Bergman et al. 2005). Lobsters and the crayfish *O. rusticus* release urine as opponents approach and meet, and winners are more likely to release urine than are losers. In *A. leptodactylus* winners also tend to release urine more often than do losers, but significant urine release occurs only after the animals begin to fight. In all species, urine release is associated with offensive behaviors and it increases significantly, especially by dominants, as interactions escalate. In lobsters the probability that a male releases urine at a given level in a fight is strongly positively associated with the probability that it has released urine up to 30 s before. Hence, urine release both precedes and accompanies offensive acts as one would expect of a threat. However, at the highest level of aggression (claw ripping) in lobsters there is no significant increase in urine release compared to the level at which they begin to interact but cannot touch each other (Breithaupt and Atema 2000). Examination of the data (Fig. 16.3a) suggests this is a consequence of high variance in urine release at the highest level of escalation. Similarly, male *A. leptodactylus* are just as likely to escalate to a physical fight following a threat at a distance whether or not they released urine when they gave the threat (Breithaupt and Eger 2002 (Fig. 16.3b). Yet, in escalated fights receivers decrease their subsequent aggression and respond with defensive acts only if an opponent’s offensive behavior is accompanied by the release of urine (see



**Fig. 16.3** Lobsters and crayfish may hide chemical cues of aggression in escalated fights: (a) the high standard error of the mean probability (log odds  $\pm$  SEM) of urine release by male lobsters *Homarus americanus* at the highest level of combat suggests winners sometimes stopped releasing urine which otherwise reliably predicts aggressive intent (urine release both immediately precedes and accompanies aggressive acts); probability is measured as  $\ln(p/(1-p))$ ; categories of aggression range from defense (fleeing) to forceful offensive acts (claw ripping) (b) fighting male crayfish *Astacus leptodactylus* are more likely to exhibit defensive behavior if their opponent releases urine when it acts aggressively (Breithaupt and Eger 2002). However, about half the time, fights escalate to the highest levels of aggression following threats in which males do not release urine and this may reduce the chance opponents will mount effective defenses. (a) Adapted with permission from Journal of Experimental Biology after Breithaupt and Eger (2002), and (b) modified after Breithaupt and Atema (2000) with kind permission from T. Breithaupt and Springer Science + Business Media

Fig. 13.5 in Breithaupt, Chap. 13; Breithaupt and Eger 2002). Finally, when crayfish grab each others' claws, dominant *O. rusticus* tend to produce less urine and to generate posterior currents sending the urine away from opponents just before the end of a fight. The temporal patterns of fighting and urine release in these crustaceans suggest that males may sometimes attempt to catch opponents off guard and deliver a "blind-side punch" by withholding urine or directing it away before they deliver a highly aggressive and winning act. The advantage of such cheating, measured by an increase in the probability of a win, comes from the failure of the opponent to respond effectively to the blow due to the lack of the threat that usually precedes it. Such cheating would persist only if it was attempted infrequently.

Fights may also be won by withholding cues not of RHP, but of sexual receptivity in the stomatopod *Neogonodactylus bredini* (Table 16.2; Mead and Caldwell, Chap. 11). During peak mating periods males come out of their cavities (where these

mantis shrimp mate) and allow females to enter whether or not the female is receptive. Evidently, males chemically detect the sex, but not the reproductive status of the female. Once in the cavity, a nonreceptive female can use her positional advantage to exclude the male. However, it is not clear whether nonreceptive females more often seek cavities during peak mating periods as would be expected if there is selection to deceive males into relinquishing their burrows.

### 16.4.3 Hiding Sex

Clawed lobsters and many species of crabs and shrimps usually mate a short time after the female molts. Depending on species, either or both sexes may seek the other by following chemical cues (Table 16.2). For example, female *H. americanus* approach dominant males in dens and these males make their presence, dominance, and probably individual identity known by broadcasting cues in urine. Once at a preferred male's den, both sexes direct jets of urine at each other, presumably for mutual mate assessment (Atema and Steinbach 2007). In the blue crab *Callinectes sapidus* females also locate males using chemical cues (Bushman 1999; Kamio et al. 2008). Sexually active males take up a relatively fixed position and dribble seminal fluid. They direct cues toward females by paddling their last walking legs which they hold high above the posterior edge of their carapace (Jivoff and Hines 1998; Kamio et al. 2008; Kamio and Derby, Chap. 20). Receptive premolt females move until they come close to a dribbling male whereupon they release urine which contains cues that inhibit feeding and elicit cradling by the male (D. Rittschof, unpublished) and guarding (Jivoff and Hines 1998). Using restrained males in aquaria, Bamber and Naylor (1997) showed that sexually receptive female green crabs *C. maenas* play an active role in courtship and mate choice by soliciting guarding or copulation. These observations strongly suggest that female lobsters and crabs seek out and discriminate among potential mates using chemical and perhaps other cues and that they indicate their selection by sending chemical cues preferentially to their future partner. Females may thereby increase the net benefits of being guarded by minimizing the costs of overly long guarding by typically always eager males (Jivoff and Hines 1998). Indeed, males are far less selective than are females: in the lab they court, guard, and attempt to mate with sponges (Kamio et al. 2000), stones (Bublitz et al. 2008), and even other males (Hardege et al. 2002) that are treated with chemical cues from sexually attractive females. In the field male blue crabs *C. sapidus* also sometimes carry smaller males (D. Rittschof, unpublished). Hence, by withholding chemical cues of sexual receptivity, female crabs and lobsters can avoid certain males as mates. Their lack of signaling can be interpreted as a form of perceptual hiding, analogous to the motionless crouch of a fiddler crab that prevents its visual detection by a burrow resident.

We close with two highly speculative suggestions for other modes of chemical deception and manipulation in crustaceans. First, in species with polymorphic

males of graded social status, such as the shrimps *Rhynchocinetes typus* (Correa et al. 2000) and *Macrobrachium rosenbergii* (Kuris et al. 1987), sexual access to females and fertilization success usually is strongly biased toward the dominant morph (Ra'anana and Sagi 1985; Correa et al. 2003). In this context selection may favor female-like morphology, behavior, and chemical cues in subordinate classes. By mimicking females in several sensory modalities, subordinates may be able to remain near to dominants and gain occasional uncontested access to females that the dominant male defends. Chemical mimicry of females by subordinate males is not without precedent in arthropods; the passive winged morphs of males of the ant *Cardiocondyla obscurior* use sexual mimicry to gain sexual access to emerging reproductive females without having to fight aggressive wingless males (Cremer et al. 2008).

Second, in *Drosophila* and a number of other insects (Arnqvist and Rowe 2005), male seminal fluid is a cocktail of chemicals that induces a large range of physiological and behavioral responses in females that increase male reproductive success. Decapods typically pass sperm and seminal products to females as external spermatophores or as a viscous fluid stored in the spermathecae (Sainte-Marie 2007). Females may store seminal fluid briefly, or until they oviposit following a molt, or for life depending on species and life history. Storage of seminal fluids in the female creates the opportunity for selection to favor the incorporation of chemicals in seminal fluid that manipulate female sexual receptivity. As emphasized by Sainte-Marie (2007), there is a dearth of information on male gametic strategies in decapods (and other crustaceans).

## 16.5 Looking Forward

Deception in crustacean chemical communication has not yet been detected. This mode of communication may most often involve the transfer of cues that are byproducts of essential biochemical processes and that cannot be faked. Yet, we see no reason, based on first principals, why deception via the withholding and directed release of such cues should be rare. But we also acknowledge that detecting such deception will be very difficult. Techniques to monitor and visualize the production and release of chemicals by senders and the detection of and responses to them by receivers under both seminatural and experimental conditions have just begun to be used to study signaling in aggressive contexts in lobsters and crayfish.

**Acknowledgments** We thank Martin Thiel and Thomas Breithaupt for their guidance, helpful criticism, and especially their patience. J. Christy thanks Pat Backwell for freely sharing ideas and for her expert assistance in field studies of visual deception in fiddler crabs. D. Rittschof thanks Sarah McCall, Zach Darnell, Kelly Darnell, and Ruth McDowell for the quality time in the field with sexually receptive blue crabs.

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