UNIVERSITY OF GRONINGEN

Fight or Flight

Crustacean decision-making on the edge of a claw

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Contents

1. Introduction

1.1 Animal hierarchies

Hierarchical animals have what is known a 'pecking order'. Animals at the top of the hierarchy aggressively dominate those lower down the ranks in order to retain access to resources such as food, mates, or a safe places to sleep (Maynard Smith and Price, 1973). This "struggle for life" is most important within a species itself as members of the same species rival for the same resources. Aggression between conspecifics is something that appears among a great amount of species within the animal kingdom.

Patterns of animal conflict within the species reveal important insights into the evolution of behavior and the influence of behavior on relationships that develop in a social group. Pair-wise interactions have been observed to promote social hierarchies within groups of animals where individuals with successful agonistic behaviors often achieve dominance (Huntingford and Turner, 1987). These behaviors, which include aggression, threats, displays, and fighting, give insight in competition over resources, such as food or mates. These behaviors may vary depending of a variety of factors.

The decisions that animals make whether they engage in an agonistic encounter are defined by the tradeoff between the costs and benefits of agonistic behaviors. When initially developed, game theory (Maynard-Smith 1982), the study of optimal strategies during pairwise conflict, was grounded in the false assumption that animals engaged in conflict had the same amount of fighting ability. Modifications, however, have provided increased focus on the differences between the fighting capabilities of animals and raised questions about their evolutionary development. These differences are believed to determine the outcomes of fights, their intensity, and animal decisions to submit or continue fighting. The influence of aggression, threats, and fighting on the strategies of individuals that engage in antagonistic behaviors has proven to be important in establishing social hierarchies (Adamo and Hanlon, 1996).

The differences between individuals have been categorized into three types of interactions:

1. Resource-holding potential (RHP)(Moore 2007): Animals that are better able to defend resources often win without much physical contact.
2. Resource value: Animals more invested in a resource are likely to invest more in the fight despite potential for incurring higher costs (Priem and Butler, 2001).
3. Intruder retreats: When participants are of equal fighting ability and competing for a certain territory, the resident of the territory is likely to end as the victor because he values the territory more. If one participant believes he is the resident of the territory, he will win more often when the opponent is weaker or food is scarce. However, if both believe they are the true territory holder, the one with the greater need for food, and therefore, one that values the resource more, is most likely to win (Jennions and Backwell, 1996).

1.2 Fitness

As expected, the individual who emerges triumphant is rewarded with the dominant status as he has shown his physical superiority. However, the costs for the loser, which include loss of reproductive opportunities and quality of food, can hinder the individual's fitness (Bergman and Moore, 2003). In order to minimize these losses, animals generally retreat from fighting or displaying fighting ability unless there are obvious cues indicating victory. These often involve characteristics that provide an advantage during agonistic behavior, such as size of body, displays (fig. 1).

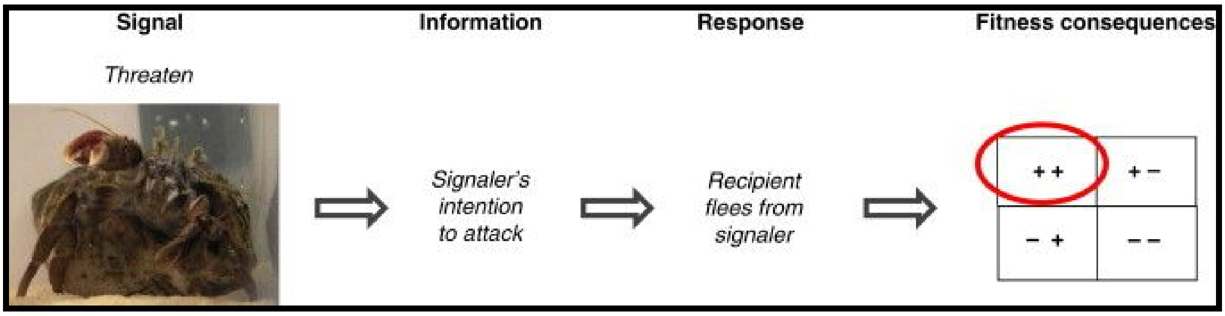

Figure 1. Signals can be defined in a four-part definition: acts or structures produced by signalers, which evolved for the purpose of sending information to recipients, such that the information elicits a response in recipients, and the response results in fitness consequences that, on average, are positive for both the signaler and the recipient (Laidre and A. Johnstone 2013).

There are many examples of species that display fighting behavior between conspecifics. Some species have a clear sign of status that makes agonistic behavior unneeded. White crowned sparrows for example have white feathers during the wintering period and the amount of white feathers on their crown determines their status (Laubach, Zachary M., et al 2013)(Fig. 2).

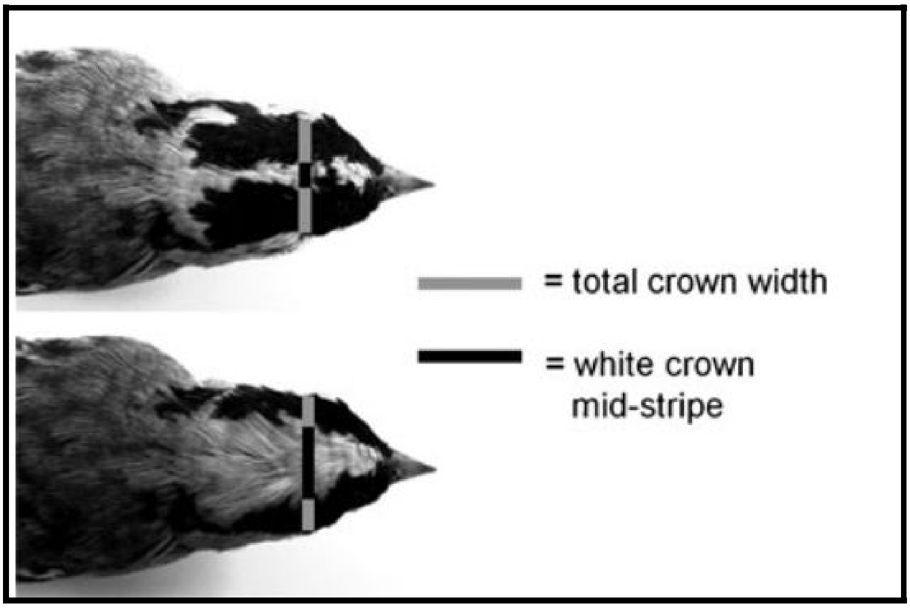

Figure 2. Mountain white-crowned sparrow (*Zonotrichia leucophrys oriantha*) crown morphology. Crownwhite is defined as the fraction (in percent) of the black bar divided by the total gray bar (Laubach, et al. 2013).

1.3 Crustaceans

Some animal species however do not maintain a social hierarchy without a fight or threats of fighting behavior. An example of one group of species which has gathered a lot of interest in the literature on aggression are crustaceans (Moore, 2007). The reason for this is interest that crustacea display a broad array of visual displays and they also possess potential lethal weapons with their claws (Moore, 2007)(Ayres-Peres et al 2015). With these claws they can deal a great amount of damage to each other when it comes to a fight between conspecifics (Fig. 3). The claws can for example be used to rip off legs and claws. To avoid or reduce injury communication plays a key role in these species. By communicating social status crustaceans can make a decision whether to escalate a fight. They have to choose between “fight or flight”.

With this thesis i want to shed light on how this decision is made. To do this i will try to answer the following questions:

How does communication between conspecifics takes place?
Are the communication signals used honest or can they be manipulated?
What are the effects of the decision to “fight or flight” on an individual's fitness.

I will try to answer these questions by researching the way communication of social position affects the decision to “fight or flight” in the case of conspecific interactions between crustacean species. The thesis will mostly center around crayfish and lobster species.

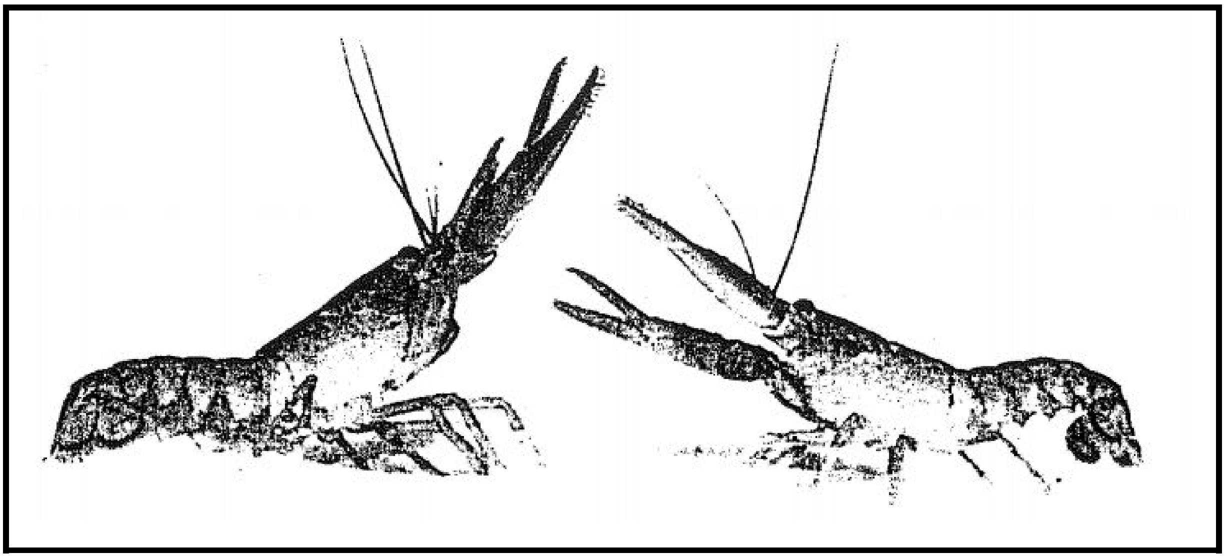

Figure 3. Agonistic interaction between two European lobsters (*Homarus americanus*) (Huber and Kravitz, 1995).

2. Agonistic encounters

Agonistic behavior is defined as aggressive encounters between individuals of the same species (Moore, 2007). Most of the encounters between two conspecifics commence with ritualized threatening behaviors. These acts can change the behavior of another animal without any direct physical contact. When the encounter moves further than these energetically cheap movements they are followed by more energetic behaviors. These include physical contact, such as wrestling and pushing, that do not cause any injury yet but which can escalate to high-energetic behaviors that can be very dangerous.

The ritualized behaviors displayed by crustacean species have many forms (Fig. 4). They however often do resemble each other when the species are ecologically similar (habitat preference, diet, trophic web position) (Ayres-Peres et al 2015). Crayfish and lobsters are a good example of this. The species have a similar morphology. Their behavioral traits, such as using rocks and crevices are also similar. They also defend their shelters and there is a link between the quality of their shelter and their hierarchical status. (Atema & Steinbach, 2007).

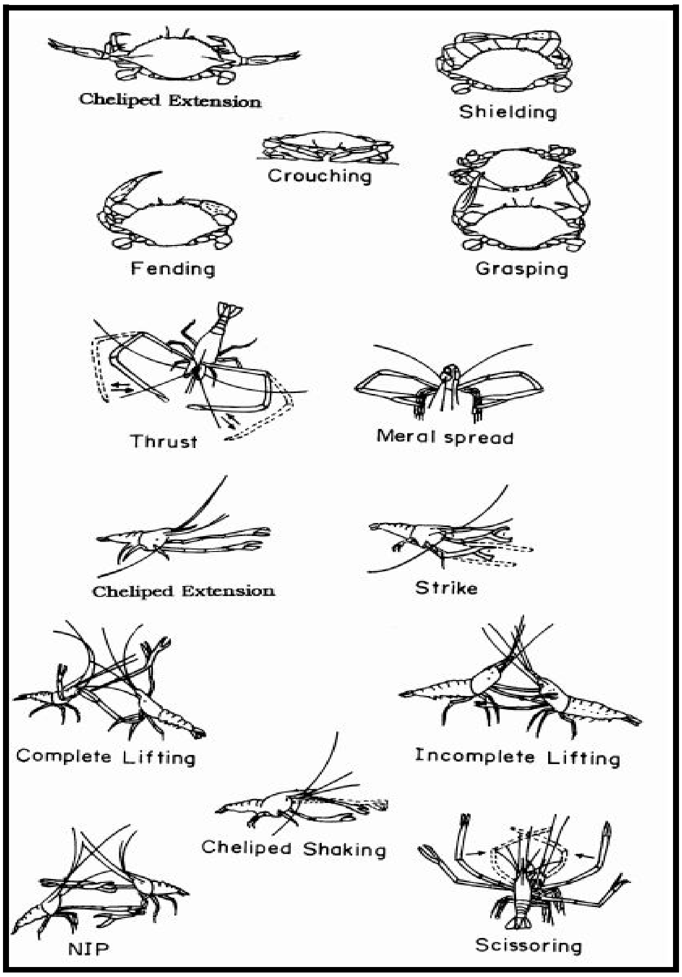

Figure 4. Overview of different agonistic behaviors of crustaceans (Ayres-Peres et al 2015) .

Crayfish respond to visual, chemical and mechanical input of their environment. They have two compound-eyes, with each eye located on an eyestalk (fig. 5) that can be moved independently from the other (Moore 2007). These eyes are developed as superposition eyes which are sensitive to low light conditions and to polarized light (Muller, 1973). Crayfish have a large amount of appendages that are sensitive to chemical signals. There are additional chemoreceptors on the major chelae, telson and maxillipeds (feeding appendages). Receptors sensitive to hydrodynamic stimuli are located on the same appendages as the chemoreceptors as well as on individual receptors across the entire body (Moore 2007).

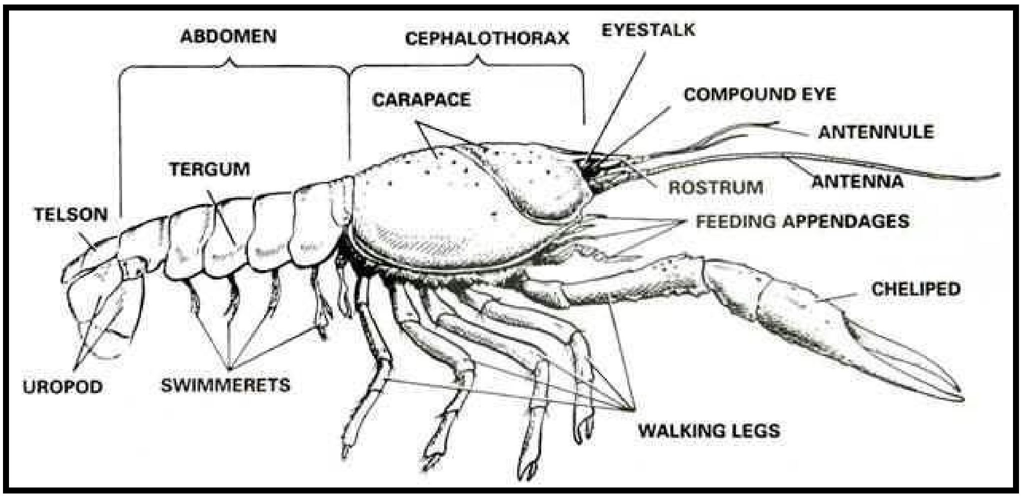

Figure 5. Schematic overview of crayfish morphology.

The following description is a summary of the agonistic behavior of three species of crayfish (*Orconectes rusticus, Orconectes virilis*, and *Procambarus clarkii*). These behaviors are common within other crayfish species and give a good overview of a general agonistic encounter between crayfish individuals. The intensity levels (IL) are scored using the codes in table 1. The intensity levels are based on visual observations of agonistic encounters of these species (Moore 2007).

A normal engagement starts with two crayfish that approach each other (IL 1). During this start of the engagement the crayfish approach each other without any change of their body stance and no further movements of their extremities. After this stage the aggressiveness is taken up a notch and includes an approach with threat displays where the crayfish raise their bodies and spread their chelae (claws)(IL 2). This display is called the meral spread. During these displays the crayfish are most of the time a few body lengths away from each other. When the crayfish start using their major chelae open or closed to physically manipulate each other the next intensity level is reached (IL 3). During this stage the chelae are used to push but not to grab. This behavior is also called boxing or restrained claw use. This intensity level is the where the most time is spent during aggressive agonistic encounters. While engaging with their chelae the crayfish also whip their opponent with their antennae. Their second antennae are slashed against the carapace of the opponent. If the dispute is not yet resolved the aggressiveness escalates to the next level (IL 4). At this level the chelae are not only used for pushing but the crayfish start to flip their opponent over and they try to twist the opponent's chelae. The highest level of aggressiveness is reached when the crayfish go all out with their chelae use (IL 5). The crayfish then use their chelae to actively grab the limbs of their opponents in an attempt to damage or remove them. This does not happen very often but this can result in the loss of limbs. Agonistic encounters can be ended when one of the contestants retreats from the fight (IL -1). A tail flip can also be used to make a fast escape. Tail flips are not only used in a defensive matter. Crayfish have multiple types of tail flips that have different underlying neurological innervations and which can also be used in an attacking way (Herberholz et al. 2001).

The given description of agonistic behaviors between crayfish only describe the interactions that are clearly visible. But before and during this behavior communication takes place in different forms between the participants which will be considered in the following chapter.

Table 1. Crayfish ethogram codes (used to score fight intensity levels) (Schneider et al. 2001).

Intensity Level	Description
-2	Tail flip away from opponent or fast retreat
-1	Retreat by slowly backing away from opponent.
0	Visually ignore opponent with no response or threat display
1	Approach without a threat display, walking slowly toward the opponent
2	Approach with meral spread threat display with the major chelae; antennal (2nd antennae) whips are present, often with maxillipeds creating currents. Antennules (1st antennae) often are seen flicking
3	Initial major chela use by boxing, pushing, and/or touching with closed chelae. Chelae are not used to grasp but can be opened and pushed. Antennal whips are more vigorous. Antennule (1st antennae) flicking is not seen
4	Active major chela use by grabbing and/or holding opponent. Crayfish will try to turn opponents over or physically manipulate them, generating force through active major chela use
5	Unrestrained fighting by pulling at opponent's claws or body parts. Opponents try to pull or tear legs, antennae, or major chelae off of individuals.

3. Factors influencing agonistic behavior

3.1 Intrinsic and extrinsic factors

What are the behavioral, physical and environmental factors that are important for establishing dominance? Aggression level in crustaceans can be changed by a lot of different factors such as: physical size, previous interactions and ownership of resources. These factors can be categorized as intrinsic and extrinsic factors. Inherent physiological or morphological features are intrinsic factors. An example of this is physical size or the size of the major chelae. Signals from agonists or the value of the resource that is contested are examples of extrinsic factors.

3.2 Intrinsic factors

Size gives an advantage in agonistic encounters. Larger crayfish for example have more success either through larger aggressive displays (meral spreads) or due to the greater amount of sheer physical force in their main chelae (Jennions and Backwell, P.R., 1996). The physical size of the carapace and major chelae is dependent on Age, sex, and reproductive status. As loss of chelae is not uncommon this can also affect the dominance status of crayfish within a population (Moore 2007). Sex is also an important intrinsic factor in determining the winner of an aggressive encounter. Males are typically more dominant than females. The males have in many crayfish species larger chelae in relation to carapace size than females. Reproductive state of males and females can also alter aggression levels. Males that are reproductively active are more aggressive than nonreproductive males and maternal females are more aggressive than males and nonmaternal females (Moore 2007).

Previous social encounters also regulate aggression and dominance. The effect of previous agonistic encounters can have two different results. The so called “winner effect” and the “loser effect” (Daws et al. 2002). When a crayfish is victorious in an encounter that individual has an increased chance of winning the next encounter. When a crayfish is on the losing side however the losing experience increases the chance of losing a consequent encounter.

Furthermore different physiological states such as molt stage and hunger can affect the levels of aggression and the outcome of agonistic encounters. Starvation decreases the survival chances which can lead to an increase of aggression when two conspecifics fight over an important resource. During these fights the rate of escalation is increased which shows that starving animals are more willing to take greater risks (Moore 2007).

3.3 extrinsic factors

3.3.1 Visual communication

Communication through visual signal plays a large role in determining the amount of aggression that is displayed in crayfish. This is most important during the initial stages of the fight where both contestants approach each other and try to impress their enemy with their claws using a meral spread display (Bruski and Dunham 1987). However, visual communication is highly dependant on the surrounding environment as both contestants must be able to see their opponent to communicate (Gherardi et al 2010). Changes in in fight dynamics do occur when crayfish fight under different lighting conditions, which shows that visual signals are an important part of agonistic encounters. In situations where light was not limited crayfish showed behaviors that were induced by visual displays (Bruski and Dunham 1987). Most evident are behaviors such as retreating and tail flips that are performed by subordinate animals when confronted with an approach or display of a dominant animal. With lower light levels these behaviors appear less often which suggests that visual displays are important for subordinate animals to locate a present dominant animal. The lower light levels do not have a significant effect on behaviors that are influenced by mechanical or chemical communication (Moore 2007).

Interestingly, it appears as if visual signals and chemical signals may play different roles in agonistic interactions. Changes in visual information appear to alter fight dynamics, such as the number and type of behaviors or level of aggression, whereas changes in chemical information do not seem to affect these fight dynamics. Conversely, chemical signals appear to play a larger role in determining or communicating the outcome of fights, whereas it is unclear if visual signals are necessary for determining the outcome as opposed to the dynamics of fights.

3.3.2 Chemical communication

Vision plays an important role in communication as stated in the previous section. However when water clarity is reduced crustaceans have to rely on additional communication pathways such as olfactory signals. Social interactions between decapod crustaceans are strongly mediated by communication using the olfactory system or the "sense of smell". The use of olfactory signals is important in recognition of of conspecifics and determining which animal is dominant in crayfish and lobsters (Moore et al. 2005)(Skog 2008). The sense of smell is located in the antennules (Fig. 5). These are the most chemosensory organs in crustaceans and are used for sending and receiving chemical signals during agonistic encounters. These organs also send and receive chemical information that is used to determine sex, molt state, dominance and to recognize individuals of other animals (Moore et al. 2005).

Urine plays a key role as a chemical signal mechanism in crustaceans (Atema and Steinbach 2007). The urine is excreted from the nephropores that are located near the lower side of the antennae (Fig. 6 and 7). Lobsters and crayfish use urine for recognition (Breithaupt et al. 2002). They actively create and direct water currents to send urine to their opponents and to receive their urine (Atema and Voigt 1995) (Fig. 7). The function of chemical communication with olfactory signals consists of three elements: recognition of dominance, influence on temporal alteration of dominance status and the manipulation of chemical signals (Moore and Bergman 2005).

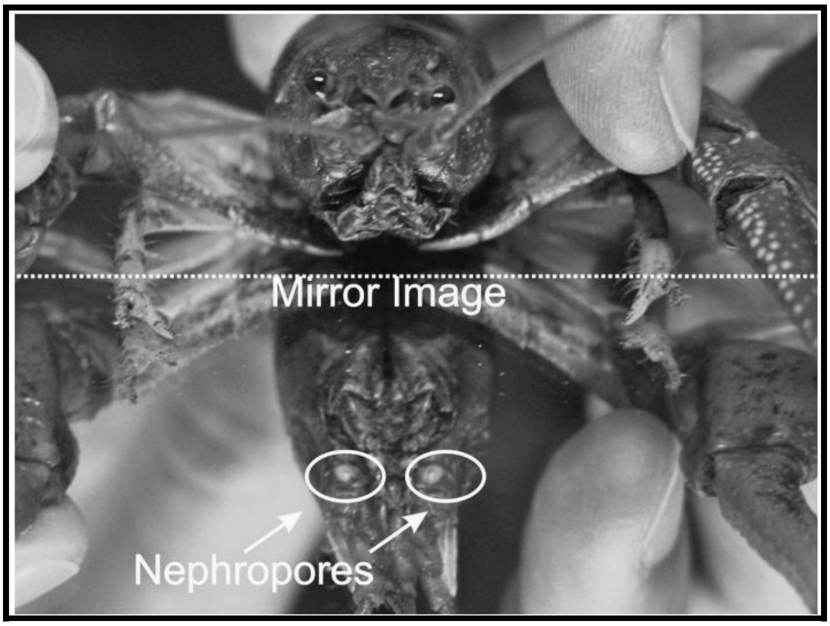

Figure 6. Anterior view (with mirror reflection) of a male form *Orconectes rusticus* crayfish with major chelae held out. Circles show the location of the nephropores that release urine during social interactions. Urine is released as the crayfish controls flow currents that direct the urine outward.

Dominance status can be recognized by crayfish when they perceive chemical signals of their counterpart through the antennules. This alters the dynamics of the fight during agonistic interactions (Moore 2007). When the communication signals are blocked by either lesioning the chemoreceptors or blocking the release of urine, the agonistic interactions take more time and escalate more slowly in aggression level (Moore 2007). The “winner effect” is also affected when chemical signaling is blocked. When a winner of a fight is paired with an individual that is not able to smell his opponent the winner effect is cancelled which indicates that chemical signals are integral in detecting previous social encounters by recognition of dominance status (Moore 2007). The presence of chemical signals alone is enough to start investigative behavior and threat display. Crayfish react to chemical signals alone and alter their behavior when they receive dominant or subordinate signals. When they smell dominant signals they become subordinate and the the other way around. So these signals affect social interactions in short-term as well as in long-term (hours and days) and influence outcome and or fight dynamics (Moore and Bergman 2005). Urine is mainly released when there are social interactions and the release shows different patterns of dispersion. Subordinate and dominant animals differ in their temporal patterns of urine release and they can also direct the urine to or from the antennules by creating currents (Atema and Voigt, 1995) (fig. 7)The release and direction of urine is very likely to play an important role in determining dominance. It is however still unclear whether the chemical makeup of urine, the mechanical signal of information currents or a combination of these determines dominance (Atema and Steinbach 2007).

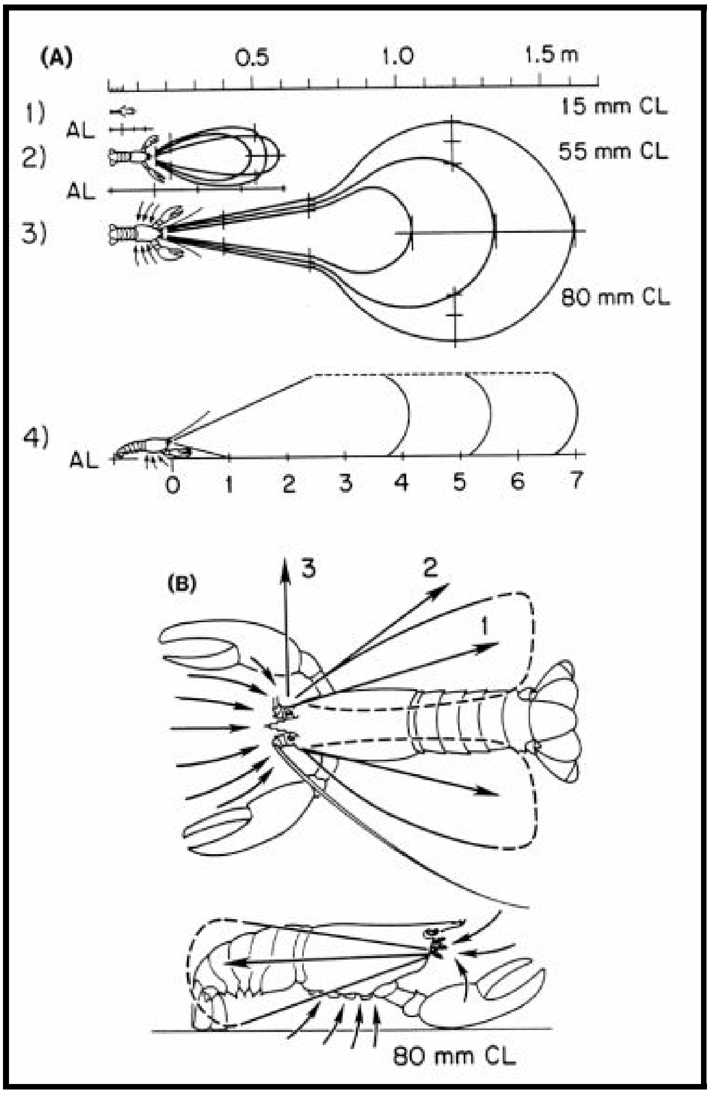

Figure 7. Information currents of the American lobster, Homarus americanus. (A) Forward gill currents with mean and standard deviations; top view of three different-sized animals (1-3). Side view of mature animal (4) - broken line indicates that vertical expansion of plume is limited here by horizontal stratification of water. Arrows indicate water uptake into gill chamber. (B) Exopodite ‘fan’ current. Direction 1 is commonly observed; directions 2 and 3 occur occasionally. Small arrows show water flow drawn toward the lobster. (Atema and Voigt, 1995).

3.3.3 Mechanical communication

The third way information is communicated between crustaceans is by use of mechanoreception. As crustaceans use their chelae and whip their antennae during agonistic encounters it is clear that this is used to communicate during social interactions. Information currents are also used during agonistic interactions (Breithaupt et al. 2002). Compared to visual and chemical communication there is not a lot known about the information that is transferred this way during agonistic encounters and with information currents. Does for example the power transmitted during the grasping of chelae or the whipping of the antennae give an indication of strength? Or is this transmitted using chemical signalling? More research on mechanical signals has to be done to get an idea of its role in communication during social behavior in crustaceans.

4. Honesty and deception

Between species deception is something that occurs abundantly. Some species for example mimic another species to protect themselves from predators (Kikuchi and Pfennig 2010) (fig. 7). But within species deception is less common. Crustaceans are in possession of powerful weapons (chelae) that can deliver fatal blows. This means it is in the interest of both opponents that they use displays to measure each other's resource holding potential (RHP). This minimizes the costs that come with a fight. However when one of the two pretends to have a high potential RHP and the other one retreats without a fight this opens up the potential to bluff with potential RHP (Adams 1990) (Christy and Rittschof 2010). The question rises whether these signals are evolutionary stable. There is selection on the receiver to distinguish reliable from unreliable cues which may cause the signals that are easily bluffed to fall in disuse (Adams 1990). However, this is not always the case and under certain conditions unreliable signals can exist in signalling systems and be maintained in frequencies greater than initially theorised. Empirical evidence of such signals has been identified in several species of crustaceans via this mismatch of signal size and underlying quality (Bywater et al. 2015)(Christy and Rittschof 2010).

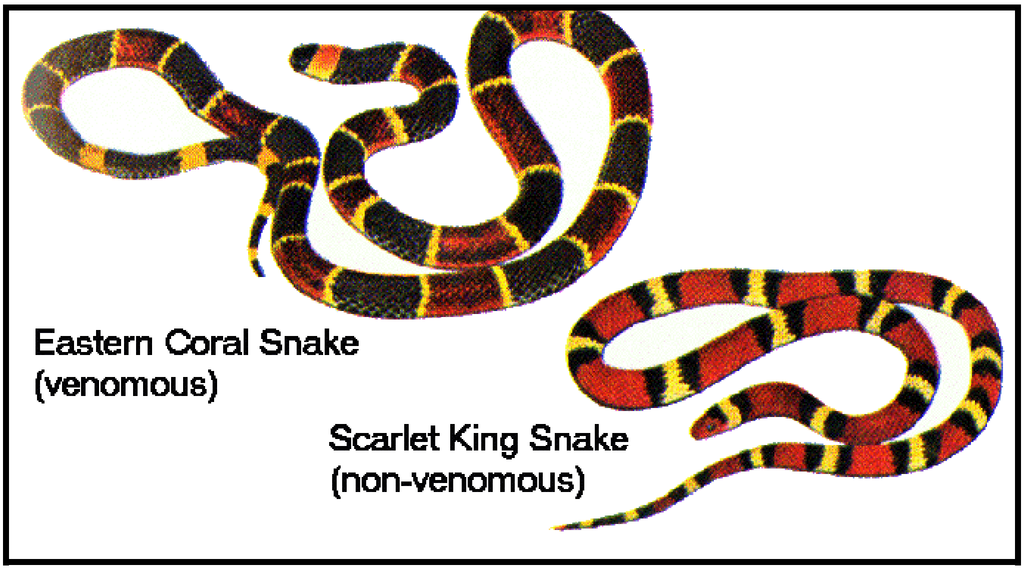

Fig 7. The scarlet king snake (*Lampropeltis elapsoides*) mimics the poisonous eastern coral snake (*Micrurus fulvius*).

Biological definition of deception:

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 (Christy and Rittschof 2010).

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 do not respond to behavior that hides a trait. Bluffin RHP does occur in crustacean species. With the snapping shrimp (*alpheus heterochaelis*) (Fig. 8) for example the claw size increases with their body size and this determines RHP. Small males that have large claws in comparison to their body size bluff RHP during threat displays (Adams 1990). This bluffing behavior occurs most often when the smaller male is sure to lose the fight with their larger opponent. Another example is with the fiddler crab species *uca annulipes* and *uca mjobergi* (Christy and Rittschof 2010)(Bywater et al. 2015)(Fig.8). With these species the large males with their relatively large chelae win the most agonistic encounters. The males assess each other visually and they avoid the bigger males. When they lose their large chelae new ones are grown. These regenerated new chelae however are long, thin and weak compared to their original chelae. During agonistic encounters opponents avoid fighting the males with these regenerated long thin chelae as much as they avoid males with strong original chelae. So this generated weak chelae bluffs strength.

As discussed before dominance hierarchies are established by fighting and are sometimes maintained by the recognition of individuals using chemical cues. The recognition occurs when the chemical signals of an specific individual are recognized by another individual and they respond appropriately. This i seen with the "winner effect" where an individual that has fought and lost, associates his loss with the winner's chemical cues. If dominance relationships are mediated by recognition of individuals only this opens the possibility of bluffing (Christy and Rittschof 2010). When an individual is dominant over a subordinate animal and the dominant animal's RHP decreases the individual with it's decreased RHP can bluff with its individual chemical cues until this bluff is called. When this bluffing using recognition of individuals is common the subordinate animals should start to call these bluffs more often. 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 (Karavanich and Atema, 1998). This type of bluffing in crustaceans with chemical communication has not yet been detected because too little is known about chemical communication signals.

Fig. 8 The fiddler crab species *uca annulipes* (upper left) and *uca mjobergi* (upper right). the snapping shrimp *alpheus heterochaelis* (bottom).

5. Discussion

At the start of this thesis I wanted to know the answers to a few questions regarding the decision that crustacean species make when they are involved in conspecific agonistic encounters.

- How does communication within species take place?
- Are these communication signals honest or can they be manipulated?

The decision to "Fight or flight" within crustacean species is a decision which has many factors that have to be taken in account such as communication of social status. Communication during these encounters depends mainly on visual and chemical communication as discussed. And it appears as if visual signals and chemical signals may play different roles in agonistic interactions. Changes in visual information appear to alter fight dynamics, such as the number and type of behaviors or level of aggression, whereas changes in chemical information do not seem to affect these fight dynamics. Conversely, chemical signals appear to play a larger role in determining or communicating the outcome of fights, whereas it is unclear if visual signals are necessary for determining the outcome as opposed to the dynamics of fights. The signals that are used in these types of communication are not always honest as is seen in the ways certain crustacean species use visual bluffs. With chemical communication the signals are honest as bluffing with these signals has not yet been detected. This does not mean that dishonesty can not take place.

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