Agonistic Behavior in Freshwater Crayfish
The Influence of Intrinsic and Extrinsic Factors on Aggressive Encounters and Dominance

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Aggressive encounters between animals of the same species have been termed “agonistic behavior” in order to differentiate these social interactions from aggression in predator–prey and other nonsocial interactions. Agonistic interactions occur when individuals display and/or fight over resources such as habitats, shelters, mates, and food. These interactions often follow strictly ritualized displays that usually result in nonlethal consequences. The displays may contain auditory, mechanical, visual, and even chemical signals designed to transfer pertinent information such as size or reproductive state of the combatant. The main result of agonistic interactions is the establishment of a dominance relationship that can alter access to resources. Throughout this chapter, I equate the term “winner” in an agonistic encounter with that animal being dominant. In dominance theory, dominance has distinct evolutionary advantages (i.e., increased reproductive fitness; Ellis 1995). In general terms, dominant individuals can acquire more and/or maintain longer control over critical ecological resources, which can result in more matings and higher reproductive success and thereby increased evolutionary fitness. The ability of an individual to possess and control resources within a population is referred to as resource holding potential (RHP; Wilson 1975).

More specifically, selective pressure should be expected on those factors (e.g., RHP) that influence agonistic behaviors during social interactions. To generate a larger theory incorporating both proximate and ultimate mechanisms underlying aggression and its impact on the evolution of behavior, it is necessary to better understand the extrinsic and intrinsic factors, how these factors interact to influence aggression, and how this leads to dominance. In general, we are asking the question, “What makes an animal dominant?” To begin to answer this broad question, a crustacean system, based on the crayfish, has been adopted as a model for social behavior and aggression.

It is important at this juncture to recognize various levels of sociality. Sociality can range from highly organized groups of individuals, such as those that occur in eusocial insects and primate communities, to organisms that exhibit aggressive interactions during brief periods of the year, such as mating periods. Crayfish exhibit agonistic behavior and social dominance in laboratory settings, but given the lack of direct field observations, it is difficult to label crayfish as a highly social organism.

**General Crayfish Ecology**

**Habitat and Burrows**

There are currently more than 500 recognized species of crayfish that inhabit many different freshwater lakes, ponds, streams, rivers, and other aquatic habitats across all continents except Antarctica and Africa (Taylor 2002). Crayfish inhabit areas with all types of substrata, ranging from sandy and muddy substrates to cobble and gravel. Shelters can range from natural assemblages of rocks to constructed burrows in mud or sand. Often these burrows will have a large main entrance and one or two side entrances. For *Orconectes virilis*, one of the species discussed below, home ranges around burrows have been quantified (Hazlett et al. 1974).

Crayfish have been observed fighting over shelters, and the occupant (presumably the owner) usually wins most of these fights (Bergman and Moore 2003). In addition, crayfish have been observed to repeatedly return to burrows even if they are occupied by other crayfish (P.A. Moore and K.C. Fero, personal observations). Some social
interactions in burrows do not result in a fight but consist simply of one crayfish temporarily evicting the other from the burrow. We can conclude from these two observations that it is highly likely that crayfish repeatedly encounter the same individuals and even engage these individuals in agonistic encounters for resources in nature. For the most part, the peak time of this social activity occurs during the night, although limited diurnal activity can be observed. In addition to agonistic behavior over shelters, the majority of nocturnal activity is confined to foraging trips, but social interactions over food resources and mates are not infrequent. During the day, crayfish are often found in shelters with their major chelae pointing out of the shelter, possibly in position to defend a resource over which they claim ownership (P.A. Moore, personal observation).

**Ecological Role in Food Webs**

In most environments, crayfish can play an important role in the structure of the food web. Crayfish are omnivorous, consuming everything from detritus and macrophytes to carrion (Hill and Lodge 1994). Crayfish will also consume benthic macroinvertebrates, and crayfish, in turn, are consumed by fish populations. In some aquatic habitats, crayfish are keystone species based on their central role in food web dynamics (Hill and Lodge 1995). In streams and lakes, crayfish can function as “shredding” organisms that, through foraging, consume and break up terrestrial leaf material, which allows this material to be consumed by other aquatic macroinvertebrates. In addition, adult crayfish can have significant impacts on plant and algal communities in aquatic habitats. The nature of crayfish diets and the exact role that they play in aquatic food webs depend upon the size and age of the crayfish, the distribution of resources available, and the presence and distribution of predators (Lodge and Hill 1994, Momot 1995).

**Sensory Capabilities**

Crayfish have typical sensory capabilities in that they respond to visual, mechanical, and chemical stimuli in their environments. Crayfish have two well-developed compound eyes, with each eye placed on an eyestalk that can be moved independently from the other. Developed as superposition eyes, they are sensitive to low light levels and also exhibit sensitivity to polarized light (Vogt 2002). Crayfish have numerous appendages sensitive to chemical signals, although the majority of behavioral work has focused on the antennae and antennules that originate near the eyestalks. There are additional chemoreceptors on the major chelae, pereopod chelae, telson (i.e., tail), and maxillipeds (Holdich and Reeve 1988). Receptors sensitive to hydrodynamic stimuli are located on the same appendages as the chemoreceptors as well as on individual receptors across the entire body (Thomas 1970).

**Basic Dynamics of Crayfish Fights**

Fighting behavior of clawed decapod crustaceans, and crayfish in particular, has been a valuable addition to the behavioral literature on aggression, social behavior, and
dominance due to the presence of conspicuous visual displays (Bovbjerg 1953) and a basic understanding of the neural circuitry underlying social behavior (Edwards and Kravitz 1997). This large body of work has shown that when two crayfish interact, their meeting leads to agonistic interactions that progressively escalate until one of the opponents withdraws (Bovbjerg 1956). Through these interactions, a dominance relationship is formed. Here I define a dominance relationship as one in which subsequent social interactions between these pairs is highly predictable (Daws et al. 2002).

As a consequence of this dominance relationship, subordinate animals will rarely seek to engage a dominant opponent (Daws et al. 2002). Dominant animals actively reinforce their status upon subordinates through short, low-intensity interactions (all of the descriptions below arise from laboratory studies). These subsequent interactions are often short in duration with lower intensities, where the dominant animal will either display or approach the subordinate, who adopts a submissive posture or repeatedly retreats (Ameyaw-Akumfi 1979). In hermit crabs, the ritualized nature of this dominance relationship may arise from decreased motivation to engage in further aggressive acts by the subordinate, individual recognition of a proven superior opponent, or the detection of an opponent’s relative dominance status (Winston and Jacobson 1978). Whether these three mechanisms (decreased motivation, individual recognition, or status recognition) work in concert or whether one of them is the primary mechanism is unknown. However, all of these mechanisms can affect the outcome of an encounter.

Crayfish agonistic interactions are highly ritualized and can be described by a series of common behaviors of increasing or decreasing levels of aggression (Rubenstein and Hazlett 1974, Zulanutz Schneider et al. 2001; Table 5.1). Although the general description that follows is based on a compilation of the fighting behavior

### Table 5.1. Crayfish ethogram codes (used to score fight intensity levels).

<table>
<thead>
<tr>
<th>Intensity Level</th>
<th>Description</th>
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<tbody>
<tr>
<td>−2</td>
<td>Tailflip away from opponent or fast retreat.</td>
</tr>
<tr>
<td>−1</td>
<td>Retreat by slowly backing away from opponent.</td>
</tr>
<tr>
<td>0</td>
<td>Visually ignore opponent with no response or threat display.</td>
</tr>
<tr>
<td>1</td>
<td>Approach without a threat display, walking slowly toward the opponent.</td>
</tr>
<tr>
<td>2</td>
<td>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.</td>
</tr>
<tr>
<td>3</td>
<td>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.</td>
</tr>
<tr>
<td>4</td>
<td>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.</td>
</tr>
<tr>
<td>5</td>
<td>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.</td>
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of three species of crayfish (Orconectes rusticus, Orconectes virilis, and Procambarus clarkii), they resemble general accounts of fighting in other crayfish species. As with other decapods, when two O. rusticus individuals are introduced into a confined space, a typical fight containing common behavioral patterns results. In general, a temporal sequence of these patterns is evident, with intensities increasing as fights increase in duration (Bruski and Dunham 1987, Daws et al. 2002).

The typical encounter begins with a simple approach of crayfish toward each other (level 1). In this first step of aggression, there are no changes in body posture or limb use (see Table 5.1). Level 2 involves an approach that contains threat displays,

![Figure 5.1 Two form I male Orconectes rusticus crayfish involved in an agonistic encounter. Both males are engaged in open chela combat, which is considered level 3 (see Table 5.1). Notice that the large antennae of the closer animal are in the position to whip the opponent. The lateral and medial antennules of both individuals are carried lower than during nonfighting postures and are placed to maximize detection of urinary signals being released during the encounter. Photo courtesy of Dan Bergman.](image-url)
which consist of heightened body posture and spreading of the chelae (or meral spread). This usually occurs while the crayfish are at some distance apart, typically a couple of body lengths. The next level of aggression occurs when the crayfish use their major chelae in a passive manner with the claws either open or closed (level 3). Crayfish will actively push their opponents back and forth using their chelae but will not actively close the chelae or use them in a grasping fashion (Fig. 5.1). Previous researchers have usually called this boxing or restrained claw use. The greatest proportion of time that crayfish interact is spent at this level of aggression (Zulan dt Schneider et al. 2001, Bergman et al. 2003). Accompanying this boxing are frequent antennal whips, which are rapid downward strikes against the opponent’s carapace with the second antennae.

When combatants increase their level of aggression, they begin grasping their opponent with their chelae (level 4). At this level, chelae are used not only to push opponents but also to flip opponents over or to twist the opponent’s chelae. The most intense fights occur when chelae are used in an unrestrained manner (level 5). This occurs when crayfish use their chelae to actively grasp their opponent’s body parts (typically major chelae) and attempt to damage or remove these appendages. While infrequent, some interactions may result in injuries or lost limbs.

Agonistic interactions are terminated when one of the individuals displays a simple retreat (level –1) or tailflip (level –2) away from the opponent. As a side note, crayfish have multiple types of taillips with different neural mechanisms, and some taillips can be used in an offensive manner during interactions (Herberholz et al. 2001). It is important to note, when documenting fight behavior, the difference between offensive and retreat taillips. Once dominance is established, subsequent encounters remain highly predictable for several hours, days, or weeks, depending upon the exact context (see below).

This foregoing description of the agonistic behaviors indicates the most visually obvious aspects of crayfish interactions. More recently, it has been demonstrated that crayfish spend periods of quiescence during fights, in which olfactory information is exchanged (Bergman et al. 2005; see below).

Factors Influencing Agonistic Behavior and Dominance

What physical, neural, behavioral, and environmental factors make a crayfish dominant? The level of aggression in crayfish can be influenced by many different factors, which include physical size, ownership of resources, previous social history, and even their neurochemistry (Bovbjerg 1956). As an initial approach, it is possible to categorize these factors as either intrinsic or extrinsic. Intrinsic factors are either physiological or physical features inherent to the crayfish. The most obvious of these is physical size of the crayfish or its major chelae (Gherardi et al. 1999). Extrinsic factors include chemical signals from opponents or the value and type of the resource being contested. I recognize that this distinction of extrinsic and intrinsic is somewhat artificial, but it permits grouping of those factors that arise from an individual crayfish (intrinsic) versus those factors that arise from a crayfish’s interactions with their biotic and abiotic environment (extrinsic).
Intrinsic Factors

Body and Major Chela Size

Early studies on agonistic behavior in crayfish focused solely on body size as the most important indicator of dominance in crayfish (Dingle 1983, Edsman and Jonsson 1996). Crayfish do not have a terminal molt; therefore, it is difficult to distinguish the effects of age on aggression from the effects of size. If there are no large-scale differences in chela size between animals (~30% or less difference in size), the crayfish with the larger carapace usually becomes dominant when they fight in pairs. Body size is an excellent predictor of agonistic success (larger animals become dominant in >95% of interactions), if there is a greater than 30% difference in carapace length of the combatants, with all other factors being equal. If the body and chela size difference is less than 10%, then the outcome of the fight becomes random (Pavey and Fielder 1996, Daws et al. 2002).

If carapace size is similar, then weaponry size (major chelae) becomes an important determining factor for dominance (Rutherford et al. 1995). Crayfish with intact chelae that are larger than those of their opponents are more likely to win an agonistic encounter (Schroeder and Huber 2001). In addition to chela size, chela strength is also important. It appears as if dominance in crabs with similar-sized chelae is determined by the strength of the pinching (Sneddon et al. 2000a). During fights, chelae are used as signals of aggression during meral spreads. A meral spread occurs when one crayfish spreads its major chelae, displaying the size of its chelae and body. If viewed from above, the crayfish resembles a Y-shape. The size of the meral spread is thought to be an aggressive signal indicating the size of the crayfish (Zulandt Schneider et al. 1999).

The use of this aggressive signal depends on the physical health of the crayfish. As with most crustaceans (Bliss 1960), appendages are often lost or damaged and can be regrown over a period of time. Male crayfish deprived of one chela have fewer aggressive displays, initiate fewer agonistic encounters, and ultimately rank lower in hierarchies than do crayfish with intact chelae (Gherardi et al. 1999). Once chelae are lost, crayfish increase the frequency of molts. It is during their molt cycle that crustaceans alter their levels of aggression based on changes in hormone levels (Tamm and Cobb 1978). To summarize, in pairwise interactions, crayfish with the larger body or chela size win the majority of encounters and become dominant (Bovbjerg 1956).

Sex

The sex of the individual crayfish is an important factor in determining the outcome of agonistic interactions. Crayfish males are typically dominant over females (Capelli 1975, Peek et al. 1995, Figler et al. 1999). In many species, males have more robust chelae relative to carapace length than do females. Male–male agonistic interactions are more intense than are male–female or female–female interactions (P.A. Moore, personal observations). Since males participate in agonistic encounters with more intensity than do females, it is hypothesized that the size differences between male and female chelae are due to selection for fighting ability (Stein 1976). In aggregations with both sexes present, males occupy the top spots within the hierarchy even if older females are considerably larger. Inter- and intrasex encounters follow similar patterns of aggression, indicating that agonistic interactions are ritualized regardless of the sex.
of the combatants. In many species, females have a smaller ratio of chelae to body size than do males of either reproductive form (Reynolds 2002; see below). Indeed, it may be this difference in weaponry size that accounts for differences in hierarchical position in regard to the sexes. Crayfish can recognize the sex of their opponents through multiple sensory channels (Acquistapace et al. 2002). Although it is clear that males are dominant over females, what remains unclear is whether this social distinction is due to variation in size across the sexes, variation in chela-to-carapace ratio, or some underlying neurochemical/neurohormonal difference between the sexes.

Reproductive State

Similar to the importance of sex in determining aggressive outcomes, the reproductive status of both males and females can alter aggression levels. Adult male crayfish in the family Cambaridae have alternating reproductive morphologies (Berril and Arsenault 1984). These two morphologies are a reproductive form (form I) and nonreproductive form (form II; Fig. 5.2). In northern-hemisphere temperate regions, males will molt from form I to form II in early summer (mid-June) and back to form I in late August to early fall (Crocker and Barr 1968, Berril and Arsenault 1984). Male crayfish have allometric growth during the change from form II to form I. Along with the many physiological changes accompanying this molt, form I males have larger chelae relative to body length than do form II males. The cyclical molting between forms is matched by cyclical changes in chela-to-carapace ratios.

Form I males are dominant over form II males, even when males have similar carapace lengths (Guiasu and Dunham 1998). In a series of carefully planned experiments, these authors concluded that the difference in relative chela size was the factor that determined dominance in interform contests. In addition, form I individuals exhibited a higher level of aggression toward form II individuals. Despite changes in physiology and hormones, there was no difference in overall levels of aggression between the two forms during intraform contests. In some North American habitats, form I and form II individuals can co-occur, and differences in chela size may have profound differences in RHP or resource acquisition in mixed-form populations.

The reproductive status of females can reverse the dominance order between sexes that is outlined above. Female maternal crayfish were more aggressive and won more bouts against males and nonmaternal females than did nonmaternal female crayfish. These results clearly show that the presence of unhatched eggs or first instar larvae increased aggression levels in females (Figler et al. 1995). Changes in aggression or social behavior as a consequence of reproductive status have been observed in other species. This is particularly true for mate guarding (see chapters 7, 10, 16). In summary, reproductive status has the potential to increase aggression in male and female crayfish and alter the outcome of agonistic interactions. Reproductively active males are more aggressive than their nonreproductive counterparts, and maternal females are more aggressive than are males and nonmaternal females.

Previous Social Experience

Another important intrinsic factor that regulates aggression and dominance is the previous social experience of a crayfish. Crayfish without any social interactions for a
period of seven days appear to interact as if they are socially naive (Zulandt Schneider et al. 1999). Otherwise, repeated previous social interactions shape the level of aggression and ultimately can influence the outcome of future interactions (Daws et al. 2002). Previous social experience can have two opposing results: the “winner effect” and the “loser effect.” When a crayfish has a repeated previous winning experience within pairwise encounters, that individual has an increased likelihood of winning the next encounter. Conversely, a crayfish with a repeated previous losing experience has an increased likelihood of losing the next encounter (Daws et al. 2002). This change in the outcome of subsequent interactions is present whether the next encounter is
against familiar or unfamiliar opponents. Winning and losing effects can result from encounters that vary in duration, intensity, and repetition. Interestingly, short-term winner effects can be produced even from a single short encounter that lasts no longer than 30 seconds (Bergman et al. 2003). Stronger and more pronounced winner effects on subsequent social behavior are evident from repeated encounters over extended periods of time (Bergman et al. 2003). The strength and duration of the winner or loser effect probably depends on the subsequent reinforcement through repeated encounters, but the types of encounters necessary to produce specific durations of winner or loser effects have not been systematically studied. The ability of winner and loser effects to alter subsequent social interactions is strong enough to overcome the role of size disparities in opponents that would otherwise serve as an accurate predictor of the outcome (Daws et al. 2002). All of the previous winner effects described above occur only through repeated social encounters.

The impact of winner effects on crayfish social behavior is a time-dependent phenomenon. It appears as if there are two separate processes that underlie winner effects. Winner effects produced from single short interactions (up to 30 seconds) give crayfish an advantage against naive individuals for only 40–60 minutes (Bergman et al. 2003). In fact, the winner effect produced in this manner decays in a linear fashion, with the largest influence appearing within 20 minutes after the first encounter. At 60 minutes, the winner effect is missing, and the crayfish behaves such that the outcome of the subsequent interaction is random or determined by size differences (Bergman et al. 2003).

The mechanisms by which the winner and loser effects arise are not well studied, and there are several theories on how a previous winner’s behavior has changed as a result of a positive outcome in an interaction. Winner and loser effects may be a result of intrinsic changes in the motivation to engage in interactions on the part of the winning or losing crayfish (Copp 1986). Changes in motivation may be tied to short-term or long-term changes in the neurochemistry of winners and losers (see below). In addition, changes in social behavior may alter the way an individual crayfish perceives the fighting ability of an opponent. This may be accomplished by associating specific physical characteristics (e.g., carapace or chela size) with an opponent’s fighting ability. Conversely, an animal may assess its own RHP compared to the population distribution of fighting abilities (Parker 1974) observed when habitat values vary within a natural setting. Changes associated with becoming a winner or loser may be communicated through extrinsic signals (i.e., visual displays, social pheromones; Copp 1986, Zulandt Schneider et al. 2001). The underlying mechanism of winner effects could also include changes in serotonin levels that have been shown to produce both heightened aggressive states and an increase in agonistic behaviors (Huber et al. 2001; see below). If intrinsic causation is responsible for the results of agonistic interactions, an animal that has had a prior winning experience may function as a “successful” fighter and thereby fight more readily in future agonistic interactions. Although the exact mechanism by which winner and loser effects occur is unknown, there is increasing evidence that crustaceans have a social memory and that this memory, either of individuals or encounters, alters subsequent interactions (Hazlett 1969, Johnson 1977, Karavanich and Atema 1998a, Gherardi and Atema 2005).

Winner and loser effects may also result from extrinsic changes, such as changes in the behavior of the winner’s opponent that could be recognized by a conspecific.
Recognition of aggressiveness (dominance) could be accomplished visually (Thorp and Ammerman 1978), through a change in the physiological state of the opponent detected by chemoreception (Zulandt Schneider et al. 1999) or other mechanisms (Rufino and Jones 2001, Obermeier and Schmitz 2003a, 2003b). Changes in aggression and dominance that are due to alterations in previous social experience can occur on much shorter time scales than the other three factors discussed above (size, sex, and reproductive state). This may be due to the underlying neural mechanism associated with previous social experience, which is hypothesized to be due to changes in the neurochemistry of crayfish.

**Neurochemistry**

From a mechanistic perspective, all behaviors ultimately arise as a result of nervous system activity, and consequently, any changes in behavior are likely due to changes in nervous system function. For crayfish, it has been speculated that the behavioral plasticity associated with differences in aggression and dominance influences nervous system neurochemistry. In other words, becoming a dominant or subordinate crayfish alters serotonin neurochemistry. In addition, these changes in neurochemistry affect the subsequent social behavior of the crayfish by altering future levels of aggression and dominance (Yeh et al. 1997). This neurochemistry/behavior loop has the potential to be a positive feedback loop in that dominant crayfish become more aggressive, which in turn can increase their status level. In particular, biogenic amines are thought to underlie changes in aggression and dominance in decapod crustaceans. Biogenic amines are a family of small neuroactive substances that include several behaviorally active compounds. Serotonin, octopamine, norepinephrine, and dopamine have all been strongly implicated in the control of various forms of aggression. Serotonin has received the most attention in regard to its role in aggression and dominance (Edwards and Kravitz 1997, Huber et al. 1997a, 1997b). Despite all of the attention on serotonin, there is evidence that octopamine and dopamine play a role in dominance and aggression in crustaceans (Sneddon et al. 2000b). Shore crabs with higher levels of dopamine and octopamine were more likely to become dominant when paired with size-matched individuals. In addition, the levels of circulating dopamine and octopamine dropped and serotonin increased after dominance was established (Sneddon et al. 2000b). Clearly, more work on other neuromodulators needs to be done to have a fuller understanding of the chemical mechanisms involved in dominance.

The hypothesized role for serotonin in aggression is that changes in social status as a result of previous social interactions alter the function of serotonin within the nervous system of crayfish. In lobsters, crayfish, and other decapod crustaceans, an increase in serotonin levels is closely associated with heightened aggression or dominant behavior (Edwards and Kravitz 1997). Changes in excitability (Krasne et al. 1997) and serotonin receptor subtype populations (Yeh et al. 1996, 1997) have been reported as a consequence of dominance. For example, the role that serotonin plays in neurochemistry is different in dominant individuals than in subordinates (Yeh et al. 1996). Social status has been shown to determine concentrations of neuromodulators in blood, the efficacy of modulators at identified synapses (Yeh et al. 1996, 1997, Krasne et al. 1997), and that of monoamines in different nervous system regions.
In addition, dominance and aggression are thought to be a direct result of serotonin levels or activity within the nervous system. Direct injection of serotonin elicits stereotypical agonistic behaviors (Antonsen and Paul 1997) and produces a posture resembling meral spread (Livingstone et al. 1980). Moreover, increased serotonergic function, through injections, decreases the likelihood of retreat (Huber et al. 1997b, Huber and Delago 1998). Neurons within local circuits controlling taillip, a common retreat behavior (Glanzman and Krasne 1983, 1986), exhibit reduced responsiveness in the presence of this amine (Edwards and Kravitz 1997). This theory can be summarized by stating that serotonergic function alters the “dominance decision point” of agonistic interactions by altering the probability of individuals to taillip in fights (Huber and Delago 1998). Those crayfish with increased serotonergic function are less likely to taillip and thus are more likely to become dominant in social interactions. Some recent work has begun to question whether serotonin injections actually change levels of aggression and dominance within crayfish or if it simply alters some basic functions such as locomotion and behavioral postures that may be interpreted as changes in aggression (Tierney 2001). The exact nature of the connection between serotonin and dominance remains uncertain, but it is clear that serotonin and other neurotransmitters are influenced by aggression and social history, and these chemicals have the potential to influence future social interactions. What is missing in these two hypotheses on the role of serotonin in dominance theory may be the possible role that serotonin plays in influencing chemical communication during social interactions.

Motivational State

Different physiological states of a crayfish, such as hunger and molt stage, can alter levels of aggression and even the outcome of aggressive interactions (Hazlett et al. 1975). Starvation can decrease the potential for survival and thus lead to an increase in motivation to engage in agonistic encounters over valuable resources (Capelli and Hamilton 1984). Crayfish with reduced energy reserves engage more often in aggressive interactions than do those that have been fully fed (Hazlett et al. 1975). In addition, starved crayfish increased their rate of escalation in fights, possibly indicating a willingness to take more risks within a contest. Presumably, these decisions occur through a comparison of the intrinsic state of energy reserves and the assessed value of an extrinsic resource. The motivational state of crayfish is also altered during and shortly after molting (Adams and Moore 2003; J.A. Adams and P.A. Moore, unpublished data). Shortly after molting, crayfish have a soft exoskeleton that renders their major chelae ineffective during contests. In contests involving recently molted and hard-shelled crayfish, molted crayfish display meral spreads more frequently. Although molted individuals had a greater number of displays, these same individuals taillipped more frequently rather than increasing the level of aggression to the point of chela use (Steger and Caldwell 1983; J.A. Adams and P.A. Moore, unpublished data). Although not directly demonstrated for crayfish, these results can be explained within a framework of bluffing and then retreating when the bluff fails to deter an opponent. Molting and aggression are under the influence of hormonal changes that could alter either the neurochemistry or neurophysiology associated with social behavior (Chang et al. 1993). These two intrinsic factors, combined as motivational state, will alter
social behavior and act through changes in the underlying hormonal systems that influence neural functioning, or vice versa.

**Summary of Intrinsic Factors Regulating Dominance**

From the descriptions above, it is apparent that most intrinsic factors studied to date are connected to the physical size of the crayfish. Larger crayfish or those with larger chelae often have advantages in agonistic interactions either through larger aggressive displays (meral spreads) or through greater physical force generated through direct contact. Age, sex, and reproductive status can influence the physical size of the carapace and major chelae. In addition, lost or injured chelae can also influence the dominance status of crayfish in populations. All of these factors may influence the intrinsic neurochemistry of individuals, and in particular, there is evidence that serotonin is involved in the neural pathways that play a role in social behavior. In addition, given the ubiquitous nature of serotonin in the crustacean nervous system, it may be possible that serotonin is also connected to motivation and that changes in aggression due to changes in motivation may be accomplished through alteration of serotonin function. While much evidence shows that serotonin function is altered as a consequence of a crayfish becoming dominant, the connection between serotonin function and future social interactions is not yet clear. It is also possible that serotonin function is altered by extrinsic factors such as chemical or visual communication.

**Extrinsic Factors**

**Chemical Communication**

Decapods rely heavily on olfactory signals during social interactions. Olfaction is important in both the recognition and determination of dominance in crayfish (Zulandt Schneider et al. 1999, 2001, Bergman et al. 2003). Antennules, arguably the most important chemosensory organ of crustaceans, are involved in sending mechanical signals and the reception of chemical signals during fighting (Rutherford et al. 1996), the recognition of sex (Ameyaw-Akumfi and Hazlett 1975, Dunham and Oh 1992, Acquistapace et al. 2002), molt state (Adams and Moore 2003), individuals (Crook et al. 2004; see also chapter 6), and dominance status (Zulandt Schneider et al. 1999, 2001, Gherardi and Daniels 2003). In addition, the presence of urine increases olfactory sampling through antennule flicking during fights (Ameyaw-Akumfi and Hazlett 1975, Rutherford et al. 1996). For lobsters, urine is necessary for recognition during agonistic encounters (Karavanich and Atema 1998b). Crayfish create and control water currents during social interactions to actively send urine to or sample urine from opponents (Bergman et al. 2005). This is also seen in banded shrimp (Hughes 1996) and lobsters (see chapter 6). Urinary signals are excreted through nephropores located at the base of the antennae, and urine is almost exclusively released during social interactions (Fig. 5.3). This urine is a likely source of social pheromones in crayfish (Zulandt Schneider et al. 2001, Bergman et al. 2005) and other crustaceans (Bushmann and Atema 1993, 1996, Breithaupt et al. 1999, Breithaupt and Atema 2000). The role of chemical signals in the social behavior of crayfish can be divided into three areas: the recognition of dominance status, the long-term alteration of social status, and the control and manipulation of chemical information.
Crayfish can recognize an opponent’s social status with their antennae and antennules via chemical signals (Tierney et al. 1984). Chemical information perceived through the antennules alters the fight dynamics of interactions. Removing chemical information from agonistic bouts with crayfish can be accomplished by selectively lesioning the chemoreceptors through osmotic shock or by blocking the release of urine in one of the opponents. When either of these manipulations is performed, agonistic interactions are longer in duration and take longer to escalate to higher levels of aggression (Breithaupt and Eger 2002, Zulandt Schneider et al. 2001). Surprisingly, when crayfish with a winning experience fought against anosmic (unable to smell) naive individuals, the winner effect was eliminated, indicating that chemical signals are involved in the detection of previous social interactions, possibly through recognition of individuals or status (Bergman et al. 2003). The chemical cues involved in this recognition are released in the urine of the crayfish (Zulandt Schneider et al. 1999, 2001). Agonistic battles are longer and reach higher intensity levels when status cues are obstructed (Zulandt Schneider et al. 2001). The presentation of chemosensory cues alone is sufficient to bring about investigative behavior and threat display (Zulandt Schneider et al. 1999). Thus, chemical signals appear to play a role in determining the outcome of social interactions as well as the dynamics of fights themselves.
As well as playing a short-term (hours) role in fight dynamics and outcomes, long-term (days) exposure to social signals can influence subsequent social behavior in crayfish. Crayfish exposed to dominant or subordinate odors adopt a social status that is contrary to the odors to which they were exposed; that is, crayfish exposed to dominant odor become subordinate and vice versa. Crayfish exposed to tank water or odors from naive crayfish do not alter behavior. Thus, previous odor exposure, mediated solely through urinary signals, appears to alter subsequent interactions (Bergman and Moore 2005). The underlying mechanism of changes in social behavior, due to the long-term exposure to social chemicals, could be tied to alteration in the neurochemistry of serotonin (see above).

Finally, since crayfish release urine primarily during social interactions, this strongly suggests that it is a social signal (Breithaupt and Eger 2002, Bergman et al. 2005). Urine release during social interactions shows temporal patterns that are different for dominant and subordinate crayfish (Bergman et al. 2005). In addition, crayfish can create a variety of currents (called information currents) that can either project urine forward or draw an opponent’s urine toward their own antennules (Breithaupt 2001, Bergman et al. 2005). During these periods, crayfish are often not engaged in physical contact, and their antennules are rapidly flicking potentially sampling social odors. Crayfish reengage in physical interactions following these short periods of urine exchange. A detailed analysis of the temporal sequence of urine release, current generation, and subsequent behavioral actions indicates that dominant crayfish have different combinations of these three behaviors compared to subordinate crayfish (Bergman et al. 2005). While it is possible to conclude that urine release and current generation are involved in the social behavior of crayfish and in determining dominance, we do not know whether the chemical composition of the urine, the mechanical signal of information currents, or a combined signal of flow and chemical information determines dominance.

In summary, these studies provide a larger picture of the determinants of agonistic interactions in crayfish. These include extrinsic chemical signals containing a dominant pheromone (Zulandt Schneider et al. 2001, Bergman et al. 2005), control of when and where those signals occur during an agonistic interaction, and long-term alteration of social behavior due to exposure to social pheromones. Given the neurophysiological systems of crayfish, the presence of an open circulatory system, and the presence of a bladder system that stores urine, it may be that these urinary signals are connected to the changes in neurochemistry that either precede or accompany changes in dominance status. Serotonin, its precursors, or metabolites that would be excreted via the urine probably form a biochemically “expensive” metabolite, raising the possibility that it might be used for more interesting purposes than solely as an excretory waste product (Weiger 1997). If indeed the social signals are related to serotonin neurochemistry and since social behavior depends on chemical communication, it is possible that a chemical feedback loop is present. In an interaction, one crayfish would become dominant altering both its behavior and chemical signals. These behavioral and chemical signals would alter the social behavior of the receiving crayfish, making it subordinate. This, in turn, would further reinforce the dominant status of the first crayfish (Bergman and Moore 2005).
Visual Communication

Visual signals also play a role in shaping crayfish aggression, particularly during the initial stages of fighting (Bruski and Dunham 1987). This is most evident during approaches with the meral spread display. Crayfish fighting under different light conditions exhibited changes in their fight dynamics consistent with the notion that visual signals are important during agonistic interactions. Crayfish performed visually mediated behaviors under conditions where light was not limited. In particular, behaviors such as tailflipping or retreat were performed by subordinate animals when dominant animals approached or displayed (Bruski and Dunham 1987). In darkened conditions, these behaviors were less evident, suggesting that visually localizing the presence of a dominant crayfish is important for subordinates. Other behaviors mediated through tactile or chemical information were not significantly altered by changes in light conditions. 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 effect 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.

Mechanical Communication

The final sensory system that plays a role in determining dominance in crayfish is mechanoreception. Given the large role that the physical size of major chelae and antennal whips play during agonistic bouts, it is clear that mechanical information is used during these interactions (Smith and Dunham 1996). In addition, information currents are used during agonistic interactions (Breithaupt 2001), but differently by dominant and subordinate crayfish (Bergman et al. 2005). Compared to the wealth of literature on visual and chemical signals, relatively little is known about the use of mechanical information in agonistic bouts. It is unclear what kind of information is exchanged during antennal whips, chela grasps, and information currents. For example, is the size or strength of an opponent transmitted through force and pressure generated by chelae or by the strength of information currents? Or is this just a mechanism used for physically manipulating the opponent or controlling chemical information? Clearly, more work needs to be done with mechanical signals to understand their role in the social behavior of crayfish.

Resources

Environmental resources are a central part of the RHP theories of dominance and social behavior (Parker 1974). These theories state that the ultimate consequence of dominance is differential access to critical resources like mating territory, mating opportunities, food, or shelters. If true, the perceived value of the resource should influence the level of aggression and the outcome of social interactions. Other crustaceans are more gregarious and exhibit some level of resource sharing, most notably, shelters
(Eggleston and Lipcius 1992, Bushmann and Atema 1997, Duffy et al. 2002). Often dominant crustaceans will control access to shelters or other environments. Dominant lobsters have been observed periodically “evicting” subordinates from their shelters, presumably to reinforce their social status (O’Neill and Cobb 1979, Karnofsky et al. 1989a, 1989b). There is evidence that social crustaceans are attracted to common shelters through chemical signals and that these signals may be related to social status (Nevitt et al. 2000). Unlike these examples, most crayfish do not share shelters and are solitary burrowers (chapter 15).

The presence of food and shelters increases the level of aggression among different crayfish species (Capelli and Hamilton 1984, Usio et al. 2001). Crayfish that perceive “ownership” of the resource are often more likely to increase aggression and to defend their ownership of the resource more vigorously than the intruder crayfish (Peeke et al. 1995). These owner crayfish have a higher probability of winning these encounters and defending their territories or resources (Ranta and Lindstrom 1992, Vorburger and Ribi 1999). In natural settings, agonistic encounters are more intense and last longer on those resources that are considered more valuable. In fights observed in the field (Bergman and Moore 2003), the presence of shelters results in longer and more intense fights than those involving available food resources, such as macrophytes or detritus patches. Furthermore, fights on detritus patches exhibited higher overall intensities and ended with more tailflips away from an opponent than when on macrophyte beds. Because of the differing availability of shelters, detritus patches, and macrophyte beds, Bergman and Moore (2003) concluded that fight intensity and duration were correlated with resource availability. In summary, fighting intensity and levels of aggression are elevated when fights occur over valuable resources. Therefore, the perceived value of the resource to the combatant determines the overall intensity of the fight and influences the outcome of agonistic interactions.

A Comparison of Aggression in Other Crustaceans and Arthropods

A striking similarity in aggressive behavior exists between the American lobster, *Homarus americanus*, and crayfish (for review, see Atema and Voigt 1995; see also chapter 6). Lobster encounters often begin with a meral spread and increase in stepwise fashion to higher intensities of more active chela use. In fact, use of chelae appears to be a common feature in agonistic encounters among several decapod crustaceans. Prawns (Barki et al. 1997), fiddler crabs (Rosenberg 1997), stomatopods (Caldwell 1992), and snapping shrimp (Hughes 1996) actively use and display chelae during agonistic encounters. In all of these cases, larger chelae are often advantageous in the encounters and help confer dominance. This is the case whether the chelae are used actively, such as in grasping or ripping, or in displays. Interestingly, it has been argued that recently molted stomatopods will display their chelae in order to bluff their dominance status or level of aggression (Steger and Caldwell 1983). Although this action has not been documented in crayfish, the concept of bluffing or dishonest signals may be applicable. Finally, snapping shrimp also use their chelae in determination of dominance. Snapping shrimp generate a mechanical signal upon closing their major chelae, and the magnitude of this current is correlated with the size of the chelae (Schmitz and Herberholz 1998; see also chapter 4). Information contained within these signals is used in the determination of dominance.
In addition to these visual and mechanical displays, other crustaceans use chemical signals to transfer information during agonistic encounters. Lobsters will generate information currents that are used to propel water toward or away from the animal during agonistic encounters (Atema and Voigt 1995; see also chapter 6). It is thought that urine is released into these currents and the signals contained within the urine are used in either status recognition or individual recognition. Indeed, stomatopods use chemical signals for individual recognition, and this may modify subsequent social interactions (Caldwell 1979, 1985). Snapping shrimp also produce a series of different currents used to deliver chemical signals during agonistic encounters (Herberholz and Schmitz 2001). In contrast to the many instances where aquatic crustaceans use chemical signals in aggression, terrestrial arthropods appear to be remiss in this category of chemical signals. The terrestrial arthropods have numerous social chemicals used for aggregation, nest recognition, mating, and other social situations (Cardé and Millar 2004), yet despite this diversity of social chemical signals, very few are used for aggression and dominance. Probably the best understood example is the cockroach dominance pheromone, which actually confers dominance on the individual (Moore et al. 1997).

**Summary and Future Directions for Research**

Fighting success and dominance in crayfish depend on a variety of extrinsic and intrinsic factors (Fig. 5.4). Several intrinsic factors improve the chances of a crayfish becoming dominant, such as physical size (Ranta and Lindström 1992, Daws et al. 2002), larger weapons (Garvey and Stein 1993, Rutherford et al. 1995), the reproductive form (Guiasu and Dunham 1998), previous social experience (Daws et al. 2002), and changes in serotonin function (Huber and Delago 1998). Extrinsic factors that lead to increased dominance include status pheromones in the environment (Bergman et al. 2005), appropriate visual and mechanical signals (Bruski and Dunham 1987, Smith and Dunham 1996), and ownership of valuable resources (Peeke et al. 1995). Despite all this work, relatively little is known about the evolutionary consequences (in terms of overall fitness) of dominance in crayfish (see chapter 7). Presumably, they are similar to those in rock shrimp, where females prefer dominant males over subordinates (Diaz and Thiel 2003). It is unknown whether dominance confers other advantages. While it is fairly easy to list the types of factors that influence aggression and dominance relationships between crayfish, many questions regarding both the proximate and ultimate level of causation and consequences of aggressive behavior remain unanswered.

With a plethora of factors that influence aggression and dominance in crayfish, it is unknown how these factors interact together to produce dominance. Although we are unlikely to identify a single most important factor that determines dominance, it may be possible to investigate how the factors outlined in this chapter interact with each other to make crayfish more or less aggressive and, as a consequence, dominant or subordinate. For example, is it possible that dominance pheromones can make a smaller individual dominant over larger individuals? How much of a winning experience is necessary to establish an individual as dominant over an extended period of time? How effectively can extrinsic factors, such as resource value and ownership, override the influence of intrinsic factors, such as size or serotonin levels? From a
proximate point of view, it is important to establish the relative strengths of intrinsic and extrinsic factors in determining social dominance and levels of aggression.

Most of the studies reviewed in this chapter have been conducted in laboratory settings under controlled conditions. While this allows the establishment of what factors play a role in influencing dominance and aggression, their importance in natural settings is unknown. Researchers have established that crayfish have the capability of individual or status recognition in the lab, but it is uncertain whether this occurs or can occur in natural settings. Crayfish are very mobile in nature, and the role of repeated encounters with the same individual is not well documented. The role of visual, chemical, and mechanical signals in natural habitats needs to be addressed. Crayfish habitats include fast-running streams that can be muddy or swampy, which may limit the effective distances of visual and chemical signals. Many species are nocturnal, which may further limit the usefulness of visual signals. More field studies are needed to establish that the factors that influence aggression and dominance in the lab also influence aggression and dominance in natural settings.

Finally, from an ultimate perspective, the evolutionary consequence of aggression and dominance is assumed to be tied to reproductive success or increased RHP. This assumption needs to be tested in both laboratory and natural settings. Do dominant crayfish get more matings? Do dominant crayfish with more matings have a higher reproductive output? What is the role of female choice and dominance among males? Do females select mates based on hierarchy position, physical size, or a mating
pheromone that may be linked to a dominance pheromone? What is the role of genetics in dominance? Are there genetic differences among crayfish in serotonin levels or the types of dominance pheromones produced? In general, all of these questions are designed to determine the evolutionary advantage of being dominant. Only through a multidisciplinary and multilevel approach is it possible to address the question that started this chapter: “What makes a crayfish dominant?”

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