Chapter 2: Literature Review

I. Intrinsic and Extrinsic Factors

Many factors have been shown to affect aggression in agonistic interactions between crayfish. These factors include, size, sex, hunger states, social experience, resource availability, and shelter presence (Bergman & Moore, 2003; Davis & Huber, 2007). These same factors that influence aggression between crayfish, such as size, sex, resource presence, and social experience contribute greatly to the outcome of agonistic interactions and have been shown to be accurate predictors of dominance (Davis & Huber, 2007). Even increased habitat complexity seems to have an effect and reduces aggressive encounters between crayfish as well as providing shelters (Baird et al., 2006; Corkum & Cronin, 2004; Patullo et al., 2009). These factors are divided into what are known as intrinsic factors and extrinsic factors.

Intrinsic factors are dependent on the individual crayfish and extrinsic factors are more dependent on the environment. Intrinsic factors mainly pertain to the physical and physiological aspects of the crayfish such as sex, carapace size, chelae size, social experience, neurochemistry, and physiological state (Bergman et al., 2003; Bovbjerg, 1956; Daws, Grills, Konzen, & Moore, 2002; Hazlett et al., 1975; Rutherford, Dunham, & Allison, 1995). Extrinsic factors include chemical signaling, visual signaling, mechanical signaling, and resources (Bergman et al., 2003; Bergman, Martin, & Moore, 2005; Bergman & Moore, 2003; Bruski & Dunham, 1987; Capelli & Hamilton, 1984). Resources include food, shelter, and mates.

II. Intrinsic Factors

Carapace and Chela Size

Size is one of the strongest determinants of whether an individual is likely to achieve dominance (Davis & Huber, 2007; Hazlett et al., 1975). If the carapace length and chela size difference is less than 10% the outcome of the interaction is random (Daws et al., 2002; Pavey & Fielder, 1996). If the difference is greater than 10%, the larger crayfish generally becomes dominant. Crayfish with larger chelae, when carapace length is similar, also tend to become dominant (Rutherford et al., 1995). During agonistic interactions, crayfish use their chela as a signal of aggression during meral spreads (Bruski & Dunham, 1987). During meral spread, a crayfish will spread its major chelae, displaying carapace size and chelae size. If crayfish continue to escalate their interactions after meral spread their interaction may lead to more intense use of chelae (Lisa Schroeder & Huber, 2001). While fighting they may continue to assess their opponent to reduce the risk of injury. Male crayfish lacking 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).

Sex

Another important intrinsic factor that determines aggression and dominance is the sex of the crayfish. Male crayfish are typically dominant over females but maternal females have been shown to have increased aggression leading to higher placement in social hierarchies when compared to nonmaternal females (Figter, Finkelstein, Twum, & Peeke, 1995; Peeke, Sippel, & Figler, 1995). Generally, males will have larger carapace length and chelae size when compared to females. In social communities of crayfish, males are typically on the top of the hierarchy even if older females are larger. This is again most likely due to the overall size differences between males and females although there may be other unknown underlying factors contributing to this as well.

Previous Social Experience

Previous social experience is also a determinant of an individual's success in agonistic interactions. Crayfish lacking social interaction for seven days appear to interact as if they are socially naïve (R. A. Schneider, Zulandt, Schneider, S, & Moore, 1999). Repeated previous social interactions contribute to the level of aggression and influences the outcome of future interactions (Bergman et al., 2003; Daws et al., 2002). Individuals that experience a win during an agonistic interaction are more likely to win the next encounter against familiar and naïve opponents. This increased tendency of winning is called the "winner effect." The opposite of this effect also applies for the loser. The loser of the encounter is more likely to lose the next encounter. This is termed the "loser effect." Winner and loser effects influence on subsequent interactions is strong enough to overcome size differences in opponents that would otherwise accurately predict the outcome (Daws et al., 2002).

These winning and losing effects can result after a single encounter that varies in duration, intensity, and repetition. Short term effects were produced from a single short encounter lasting no longer than 30 seconds (Bergman et al., 2003). The effects were strengthened with repeated encounters over extended periods of time. These effects are dependent on reinforcement through repeated encounters as the effect was observed to decrease after an hour (Bergman et al., 2003). The largest influence appeared within the first 20 minutes after the first encounter. In an experiment performed by Hsu and Wolf on the winner and loser effects of *Rivulus marmoratus*, the effect lasted for at least 48 hours (1999).

The mechanism of the winner and loser effect is not clear and there are a few theories in regard to an individual's change in behavior. It does not appear as if these changes are due to long-term intrinsic physiologic changes as the effect could be demonstrated after a single encounter of 30 seconds (Bergman et al., 2003). The change could also be related to motivation to engage in interactions. Changes in motivation and behavior could be related to changes in the neurochemistry of the individuals as the effects are short-term. Short-term neurochemical changes would be consistent with the short-term changes in behavior which could also be reinforced through repeated encounters. These effects may also alter how a crayfish perceives the fighting ability of its opponent or itself, influencing their interaction. This was not observed in the study performed by Bergman et al. as there was no significant change in the length of interactions or time to reach different intensity levels (2003). This again seems to indicate the change is more likely related to a neurochemical change.

Neurochemistry

It has been speculated that the behavioral differences in aggression and dominance influences nervous systems neurochemistry. Biogenic amines have been shown to influence behavior of decapod crustaceans. These include serotonin, octopamine, norepinephrine, and dopamine (Bergman et al., 2003; Edwards & Kravitz, 1997; Yeh, Fricke, & Edwards, 1996; Yeh, Musolf, & Edwards, 1997). It is thought that changes in social status as a result of previous social interactions alter the function of serotonin in the nervous system of crayfish. These changes in neurochemistry in turn affect social behavior by altering levels or aggression and dominance (Yeh et al., 1997). Increased serotonin levels are closely associated with increased aggression or dominant behaviors (Edwards & Kravitz, 1997). Changes in serotonin receptor excitability have been observed as a consequence of achieving dominance (Yeh et al., 1996, 1997). Serotonin was shown to react differently in subordinate and dominate individuals. Increased serotonergic function through injections decreased the likelihood of retreat in crayfish (Huber, Smith, Delago, Isaksson, & Kravitz, 1997). Neurons associated with the tailflip mechanism for retreat exhibit reduced responsiveness in the presence of serotonin (Edwards & Kravitz, 1997). Thus, those with increased serotonergic function are more likely to become dominant in agonistic interactions.

Motivational state

Different physiological states such as hunger also alter the level of aggression and outcomes of agonistic interactions in crayfish (Hazlett et al., 1975). Starvation decreases the potential for survival leading to an increase in motivation to engage in agonistic encounters over valuable resources (Capelli & Hamilton, 1984). Hazelett et al. found that starved crayfish engaged in more aggressive interactions than crayfish that were fully fed (1975). Starved crayfish also had an increased rate of escalation of interactions, possibly indicating their willingness to take more risks involved in agonistic interactions.

III. Extrinsic Factors

Chemical communication

Communication is used by crayfish during agonistic interactions to provide information to conspecifics about an individual’s social status. Information is transferred during interactions using various methods involving visual, chemical, and mechanical signals to communicate. Decapods, such as crayfish, rely heavily on olfactory signals during social interactions. Olfaction is important for recognition and determination of dominance in crayfish (Bergman et al., 2003; R. A. Z. Schneider, Huber, & Moore, 2001; R. A. Schneider et al., 1999). Crayfish create and control water currents during social interactions to actively send urine or to sample urine from opponents (Bergman et al., 2005). Urine is released through nephropores and is almost exclusively released during social interactions. Urine likely contains social pheromones in crayfish (Bergman et al., 2005; R. A. Z. Schneider et al., 2001). Antennules are one of the most important chemosensory organs of crayfish. Antennules are involved in sending and receiving chemical signals during interactions, sex recognition, and dominance status (Bruski & Dunham, 1987; Gherardi & Daniels, 2003; Pavey & Fielder, 1996; R. A. Z. Schneider et al., 2001; R. A. Schneider et al., 1999).

Recognition of social status in crayfish is perceived through their antennae and antennules via chemical signals (Ann Jane Tierney, Thompson, & Dunham, 1984). Information perceived through the antennules may alter the crayfish's behavior during an interaction. If chemical information is blocked, agonistic interactions are longer in duration and take longer to escalate to higher levels of intensities (R. A. Z. Schneider et al., 2001). When crayfish with a winning experience fought against chemoreceptor blocked individuals, the winner effect was eliminated, indicating that chemicals signals are necessary in the detection of previous social interactions (possibly through recognition of individuals or status) (Bergman et al., 2003). The chemical signals involved in recognition are released in the urine of crayfish (Bergman et al., 2003, 2005; R. A. Z. Schneider et al., 2001; R. A. Schneider et al., 1999). Crayfish will create currents, called information currents, using maxillipeds, pleopods, and gills, along with nephropore propulsion to communicate past social experience. They will use these currents to project or draw an opponent's urine toward their antennules (Bergman et al., 2005; BREITHAUPT, 2001). Crayfish primarily release urine during social interactions, suggesting that urine is used as a social signal (Bergman et al., 2005; BREITHAUPT, 2001). Urine released during these interactions shows differences in the number of times urine was released and duration of release between dominant and subordinate crayfish (Bergman et al., 2005).

The presentation of chemical signals alone is able to bring about a threat display (R. A. Schneider et al., 1999). Hence, chemical signals appear to play a role in the outcomes of social interactions as well as fighting dynamics. Crayfish exposed to dominant or subordinate odors adapted a social status that is contrary to the odors to which they were exposed (Bergman & Moore, 2005). Crayfish exposed to odors from naïve crayfish did not alter behavior. It appears previous odor exposure through urinary signals alter subsequent interactions. Communication using urine demonstrates that chemical signaling plays a large role in agonistic interactions between crayfish.

Visual communication

Visual signals also contribute to crayfish aggression, particularly during the initial stages of fighting (Bruski & Dunham, 1987). During encounters crayfish will exhibit signals such as meral spread, heightened and lowered body posture, and approach and retreat behaviors. These signals communicate information about an individual to influence another conspecific they have encountered. This relayed information will allow individuals to adjust their behaviors for further interaction and can provide benefits to both crayfish. It appears that visual signals are important in agonistic interactions as crayfish exhibited changes in their fight dynamics under differ light conditions (Bruski & Dunham, 1987). Behaviors such tailflipping and retreat were performed by subordinate crayfish when dominant crayfish approached in well-lit conditions. In darker conditions, these behaviors were observed less frequently, suggesting visualization of the dominant crayfish is an important factor for subordinate crayfish (Bruski & Dunham, 1987).

Mechanical Communication

Mechanical signals such as antennal whipping and chelae contact are observed during agonistic interact and are thought to convey tactile information between opponents (Bergman et al., 2005; Bruski & Dunham, 1987). The use of information currents during agonistic interactions can also be considered mechanical communication. Although these mechanical signals have been observed, it is unclear what information is exchanged during antennal whips and chelae grasps.

Resources

Resources also have a large role influencing aggression and social behaviors. The ability to acquire and protect resources (resource holding potential, RHP) can be fined by an individual's likelihood to win a fight (Parker, 1974). The ultimate consequence of attaining dominance is access to resources such as mates, shelter, and food (Fero et al., 2007, Wilson 1975). In agonistic interactions, resources may be acquired through dominance establishment or through allocation with respect to relative dominance rank within a hierarchy.

The presence of shelter and food has been shown to increase aggression in crayfish (Capelli & Hamilton, 1984). Ownership of a resource is more likely to increase aggression to defend the resource against other conspecifics (Peeke et al., 1995). Crayfish have been observed to occupy and defend shelters (Capelli & Hamilton, 1984; Martin & Moore, 2007; Peeke et al., 1995). Crayfish spend a significant amount of time away from shelters in search of food (Davis & Huber, 2007). Agonistic encounters are more intense and last longer on resources that are considered more valuable. Starvation of crayfish has also been shown to increase aggressive interaction and change their behaviors such as foraging (Hazlett et al., 1975; Pecor & Hazlett, 2008). A field study showed the presence of shelters resulted in longer and more intense interactions than those involving available food resources (Bergman & Moore, 2003). Fights on detritus patches exhibited higher overall intensities and ended with more tailflips from an opponent than when on macrophyte beds. It was concluded that fight intensity and duration correlated with resource availability. In summary, fighting intensity and levels of aggression are increased when fights occur over valuable resources.