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The Role of Chemical Signals in the Social Behavior of Crayfish

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Agonistic behavior is a fundamental aspect of ecological theories on resource acquisition and sexual selection and is thus an important aspect of crustacean behavior and ecology. When examining agonistic behavior in crustaceans, one must keep in mind that a myriad of extrinsic and intrinsic factors can influence intraspecific aggression and both should always be recognized as significant influences on agonistic behavior (Bovbjerg, 1956). Extrinsic factors such as the presence of shelters, mates, predators and food availability can alter agonistic behavior (Hazlett *et al.*, 1975; Bergman and Moore, 2003). For example, fights in the presence of shelters are longer and more intense than fights in the presence of food resource (either detritus or macrophytes), which suggests that shelters have a higher perceived value than the food resources (Bergman and Moore, 2003). Within food resource habitats, fights in the presence of detritus patches were more intense than macrophytes, suggesting that detritus was a more valuable food resource than macrophytes (Bergman and Moore, 2003). These extrinsic factors are of immense significance for all animal agonistic behavior because these factors are usually the goal of the conflict. However, we contend that agonistic bouts are further mediated by chemical signals and that these signals are essential to the formation and maintenance of a social hierarchy (Zulandt-Schneider *et al.*, 2001; Bergman *et al.*, 2003).

A variety of factors influence the formation and maintenance of hierarchical structures. These factors can include an altered aggressive state, an ability to physically dominate and previous agonistic experience (Guiasu and Dunham, 1999). Within these aforementioned factors resides the winner effect, which was found to be influenced by varying the time between two fights and by blocking the chemoreceptors on the antennae and antennules (Bergman *et al.*, 2003). The winner effect was observed to have short-term duration when only reinforced by one agonistic interaction. It may be that repeated interactions would strengthen the winner effect. In addition to this short duration of the winner effect, the absence of odor perception during agonistic interactions altered the stability of the winner effect (Zulandt-Schneider *et al.*, 2001). Individuals fighting an opponent with this loss of chemosensory information had a decreased chance of winning an agonistic bout. Chemical cues appear to alter this initial intrinsic stage (winner effect) of social hierarchy development (Bergman *et al.*, 2003).

It has been suggested that winner effects are caused by recognition of a conspecific's heightened aggressive state (Copp, 1986). Results from our laboratory demonstrate that winner effects observed in crayfish are possibly due to chemical recognition by an opponent (Zulandt-Schneider *et al.*, 2001; Bergman and Moore, 2003). When the opponent's antennae and antennules were impaired, they were in all likelihood unable to recognize the dominant state of the previous winner. Consequently, a lack of information transfer decreased the probability that the winner would win the subsequent agonistic encounter. If neurochemical changes in serotonin levels in a crayfish with a previous win were the sole influential variable for this agonistic behavior (Huber *et al.*, 1997; Yeh *et al.*, 1997; Huber and Delago, 1998), then a 'winner' crayfish should win even against a crayfish in the blocked olfactory condition. The fact that the previous winner no longer consistently defeats a blocked opponent suggests that chemical or mechanical signals received by the antennae and/or antennules are a vital component of the winner effect (Bergman *et al.*, 2003).

Thus, chemical signals in aquatic systems are used to communicate social status and consequently alter aggressive behavior. In addition, they may also function to influence the status roles of potential opponents or in part pre-determine the outcome of these interactions. Exposure to social odors for five consecutive days, in the absence of other sensory contact with a 'sender', alters subsequent agonistic behavior. 'Receiver' crayfish exposed to winner (dominant) odors behaved analogous to a subordinate role. These animals exhibited more defensive behaviors and lost the majority of their fights. Conversely, when crayfish were exposed to loser (subordinate) odors, they demonstrated less defensive behaviors and subsequently won more encounters. These results suggest that agonistic experiences modify social odors in 'sender' crayfish through an intrinsic alteration, such as a change in neurochemistry. This intrinsic change is then extrinsically observed through direct neurochemical leakage into the urine or through a dependent chemical addition to the urine that modifies the subsequent agonistic behavior of 'receivers'.

Previous work by our laboratory and the work of others has shown that urine from dominant individuals contains cues that can be perceived by an opponent and communicate status (Zulandt-Schneider *et al.*, 1999, 2001; Bergman *et al.*, 2003). The most parsimonious explanation is that neurochemical differences between dominant and subordinate individuals are expressed extrinsically in the urine or leaked elsewhere from the sender's body, and information contained in that chemical signal is transmitted to a receiver crayfish. Status cues may in fact affect the neurochemistry of the receiver and consequently alter the behavior of this individual in future interactions. Receivers either detect these chemicals through sensory mechanisms or absorb them, leading to an alteration of neurological function by either directly or indirectly activating or deactivating neural circuits associated with social behavior. A possible consequence of this type of 'sender–receiver' model is that a chemical feedback may be present. Alterations in the intrinsic neurochemistry of the sender are expressed extrinsically and these cues are then detected by the receiver, which likely alters its neurochemistry. Changes in the intrinsic neurochemistry of the receiver are then expressed extrinsically. These changes likely reinforce the status of the sender and the receiver without any physical contact. In addition to communicating social status, chemical signals have the capability to alter the social status of neighboring crayfish under stable hierarchical conditions, such as in a defined shelter habitat or a confined laboratory environment. Consequently, these signals can function to reduce the incidence of fights, decrease the intensity of fights, and possibility of injury. Urine-borne chemical cues are thus expressed extrinsically as both a signal to communicate social status and as a tool to manipulate an opponent's intrinsic neural state and behavior (Breithaupt and Eger, 2002; Bergman *et al.*, 2004).

This transfer of social information via chemical and mechanical signals can be significantly impinged upon by the extrinsic environment. When examining a dyadic agonistic interaction, we have demonstrated that both dominant and subordinate crayfish generate water currents that facilitate the sending and sampling of signals. However, dominant crayfish generate more of these currents and release urine more frequently during an encounter than subordinates. This result suggests that the transfer of social information occurs differently when a status role is achieved. A correlation of urine releases with water current generation and agonistic behaviors appears to be the eventual predictor for dominant-subordinate relationships. This may indicate that agonistic behaviors may be associated with chemical signaling that likely alters or possibly controls a receiver's behavior during the course of an interaction.

Other extrinsic factors can play a role in how sensory signals are received. For example, the physics of different environments can influence how sensory signals are transmitted within those environments. Consequently, this physical effect on sensory signals can influence how animals send or sample sensory signals. In fact, habitat specific physics may constrain or enhance signal transmission (i.e. light transmission in a shaded forest versus an open field) and may provide a mechanism for the evolution of sensory biases. The transmission of chemical signals is heavily dependent upon environmental flow regimes, thus crayfish found in lotic (flowing water) systems appear to be adapted for more effective communication within a lotic environment. This hypothesis is an extension of the 'matched filter' theory of Wehner (1987) to the behavioral level. When crayfish collected from lotic systems had agonistic bouts under lotic conditions, dominant crayfish spent more time upstream than subordinate crayfish. In contrast, when crayfish were allowed to fight under lentic (no flow) conditions, regardless of status, crayfish were positioned randomly within the flume (Bergman and Moore, unpublished results). By chemically visualizing urine release during these agonistic bouts, it was possible to elucidate that crayfish released urine more often when upstream of an opponent when experiencing lotic conditions. Environments obviously constrain communication systems. The results of the flow versus no flow fighting conditions suggest that crayfish urine is deliberately released to increase the probability of communicating one's status chemically.

We have attempted to expose a few of the essential factors that influence agonistic interactions. Namely how different extrinsic and intrinsic factors alter crayfish agonistic behavior. Since social interactions in decapods are correlated with neurochemical alterations, we suggest that short-term exposure to social odors communicate these changes in some form, whereas long-term exposure may alter the functioning of serotonin or other biogenic amines in the receiving crayfish nervous system. Consequently, exposure to status odors appears to be more responsible for dominant–subordinate relationships than previously given credit. With most levels of organization, from ecology to neurons, readily accessible for detailed introspection, this model system for social behavior offers unique opportunities for exploring the dynamic sensory processes involved in social behavior. The outcome of one or several agonistic bouts creates a lasting behavioral polarity between the opponents that is highly dependent upon the internal (neurochemistry) and external chemistry (chemical signals) of the behavioral system. Thus, chemical signals not only communicate immediate status, but additionally mediate long-term social hierarchies. Many factors obviously feed into and onto agonistic behavior, yet chemical communication may be one of the most important components when it comes to stability in social systems. This point may even be evident in other 'higher' organisms where chemical signals, whether consciously or unconsciously detected, may be instrumental to the reinforcement or generation of social hierarchies through the use of social chemical feedback system.

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