The Smell of Success and Failure: the Role of Intrinsic and Extrinsic Chemical Signals on the Social Behavior of Crayfish[1]

Paul A. Moore[2],* and Daniel A. Bergman[3],*

Laboratory for Sensory Ecology, J. P. Scott Center for Neuroscience, Mind & Behavior, Department of Biological Sciences, Bowling Green State University, Bowling Green, Ohio 43403

Synopsis. Animals commonly modify their behavior in the presence of a conspecific or in response to signals. This is particularly true in the context of aggressive exchanges, which animals use to form networks of social relationships and to communicate social status associated with those relationships. Although hierarchical structures are a widespread phenomenon that has been studied extensively, the dynamic communication processes, specifically chemical communication in this review, is relatively overlooked. In particular, it is the exchange of information during agonistic interactions that mediates hierarchies and/or alters the outcomes of agonistic interactions. Given the theoretical appeal of these interactions, and the evolutionary importance and taxonomic diversity associated with social hierarchies, it is not surprising that the sensory mechanisms involved in the formation and maintenance of hierarchical structures have received recent attention. In crayfish, dominance is thought to be largely determined by physical superiority, where encounters are largely dyadic and fighting behavior is highly stereotyped. However, recent evidence has shown that the outcome of dyadic encounters are dependent upon a number of factors other than physical size, that include the exchange of chemical information during encounters, previous social history, and the intrinsic neurochemical state of opponents. We have attempted to provide a comprehensive analysis of the extrinsic chemical processes (previous history, sensory communication, etc.) and intrinsic chemical processes (neurochemical state) that produce and maintain dominance relations and social hierarchies in crayfish. We hope that this review will bring together a global picture of the processes that determine a crayfish's social standing and how intrinsic and extrinsic chemicals have substantial effects on aggressive states and agonistic bouts.

Introduction

Social behavior

Aggressive acts between conspecifics are termed agonistic interactions. It is through these types of interactions that dominance hierarchies are established (Bell and Gorton, 1978; Copp, 1986; Mesterton-Gibbons and Dugatkin, 1995). A higher social status within a social hierarchy can allow for increased access to food, mates, and shelters (Maynard Smith and Price, 1973). The use of a dominant status to achieve a higher fitness is found in many invertebrates and vertebrates (Tilson and Hamilton, 1984; Beacham and Newman, 1987; Moore *et al.*, 1997; Schuett, 1997; Lopez and Martin, 2002; Correa *et al.*, 2003). More specifically, decapods can acquire shelters by defeating residents in agonistic bouts and thereby increase access to available food and mates, and to reduce predator pressure (Capelli and Hamilton, 1984; Karnofsky *et al.*, 1989; Cromarty *et al.*, 1999; Vorburger and Ribi, 1999; Usio *et al.*, 2001). Consequently, dominant individuals experience increased fitness over subordinate individuals due to the utilization of these benefits (Wilson, 1975).

When using agonistic interactions to establish and reinforce social hierarchies, the energetic cost can be great and possibly even result in injury. However this energetic cost in acquiring resources can be offset by the benefits afforded by these resources that can lead to increased growth and mating opportunities, and decreased predation risk involved (Wilson, 1975). By detecting or communicating with conspecifics within a social hierarchy, dominant or subordinate animals can avoid injury by reducing the number of competitive interactions or intensity of conflicts over resources. Communication of social position when resources are in conflict involves the exchange of information between a sender and a receiver, and then the subsequent use of this information by the receiver to make decisions on the appropriate response (Dawkins and Krebs, 1978; Bradbury and Vehrencamp, 1998). Consequently, the signaling of status level can be important because it functions in reducing fight intensity and duration, thus resulting in a reduced risk of injury (Enquist, 1985; Beecher, 1989; Adamo and Hanlon, 1996). Within this framework, agonistic behavior may be regarded as a behavioral tool, *i.e.,* a means of interacting with other conspecifics, to enhance the survival and/or reproductive effort of the individuals involved in the interaction (Wilson, 1975). Communication of one's status may be used to influence the outcome of an encounter with or without direct physical interaction (Wilson, 1975). During agonistic encounters, a contestant may signal whether the encounter should escalate or decrease its fighting intensity.

Social behavior from largely asocial animals

Fighting behavior of clawed decapod crustaceans has attracted considerable interest in the broad behav-

ioral literature on aggression due to the presence of conspicuous visual displays and potentially lethal weaponry (Thorp and Ammerman, 1978; Smith and Dunham, 1990; Caldwell, 1992; Rutherford *et al.*, 1995). The ultimate goal of any aggressive encounter is to obtain an elevated social status that confers an advantage to an individual in obtaining a resource (Wilson, 1975). Conversely, a subordinate individual may lose access to resources through unsuccessful bouts, but may obtain a net benefit by avoiding such costs as increased energy expenditure, injury from a conspecific or increased predation risk (Wilson, 1975). If a subordinate does not gain a benefit, then the lower status will have a negative effect on fitness by reducing the number of resources available.

Decapods have been used as a model system to study social behavior and the use of aggression (Dingle, 1983), specifically because of the ritualized nature of their agonistic bouts (Huber and Kravitz, 1995), the presence of chelipeds used as weapons (Garvey and Stein, 1993), and the use of sensory information during such encounters (Bruski and Dunham, 1987; Zulandt Schneider *et al.*, 1999; Bergman *et al.*, 2003). From this work, it appears that most crustaceans are short on negotiation skills, with the exception of may be spiny lobsters that are quite social. In most instances, a meeting between two decapods of similar size leads to agonistic interactions, which progressively escalate until one of the opponents withdraws (Huber and Kravitz, 1995). A typical escalation advances through several stages of intensity starting with threat displays, then ritualized aggression with restrained use of the claws and finally brief periods of unrestrained combat (Bruski and Dunham, 1987; Glass and Huntingford, 1988; Huber and Kravitz, 1995). Fighting success depends upon a variety of factors, including physical superiority (Hyatt, 1983; Ranta and Lindström, 1992; Smith *et al.*, 1994), larger weapons (Garvey and Stein, 1993; Rutherford *et al.*, 1995; Barki *et al.*, 1997), visual agonistic displays (Levenbach and Hazlett, 1996), behavioral strategies (Guiasu and Dunham, 1997), knowledge of resource value (Smith *et al.*, 1994, Bergman and Moore, 2003), prior residence (Peeke *et al.*, 1995), past social history (Daws *et al.*, 2002; Bergman *et al.*, 2003), and chemical communication (Zulandt Schneider *et al.*, 1999, 2001).

An ability to form complex social relationships is widespread in most animal species where individuals will modify their behavior during interactions with conspecifics (Francis, 1988; Dugatkin *et al.*, 1994). Crayfish, even though having less complex relationships, are no exception to modifying their behavior when confronting conspecifics. Decapods alter their behavior when confronting members of the opposite sex than when interacting with the same sex (Villanelli and Gherardi, 1998). The presence of highly structured, quantifiable behavioral systems, combined with the potential to bring future analysis to the level of individual neurons (Kravitz *et al.*, 1985), offers unique opportunities to explore a variety of issues. These issues include individual differences in aggressive behavior, neural changes as a result of dominance, the importance of such changes to the functioning of chemical signals, and the possible interactions of neuromodulators with the chemical communication system. All of these factors can be very important in the organization of social behavior.

Communication modalities used during social interactions

Environmental stimuli can be used for a variety of purposes. Animals use environmental information to locate both food and mates, avoid predators, and navigate through their surroundings (Bell, 1985; Mathis and Smith, 1993; Lohmann and Lohmann, 1996; Tomba *et al.*, 2001). Animals can also use stimuli to communicate during social interactions. Social communication can provide information to conspecifics on genetic relationships, mate choices, territoriality, and social hierarchies. (Atema and Engstrom, 1971; Beacham and Newman, 1987; Rendall *et al.*, 1996). In many of these instances, information in social signals can be used to make a decision on how to interact with or respond to the signaler (Hazlett and Bossert, 1965). Therefore, social signals can be important to the survival and reproductive success of signal senders and receivers.

A variety of sensory modalities (visual, acoustical, chemical, and electrical) can be used for species-specific social communication. Some organisms use visual signals in the form of elaborate body designs, coloration, ornaments, or display movements to communicate (Vannini and Gherardi, 1981; Adamo and Hanlon, 1996; Grasso *et al.*, 1996). These types of signals are specifically useful in most terrestrial habitats because visibility is not limited, except during nocturnal periods. Visual signals are also used in aquatic environments, however turbid water reduces visibility very rapidly and may adversely effect visual communication (Abrahams and Kattenfeld, 1997). Acoustic signals can also be transmited over long distances in both terrestrial and aquatic environments to communicate (Cheney and Seyfarth, 1988; Travassos and Pierce, 2000; Madsen *et al.*, 2002). Decapod crustaceans have been shown to be very good at acoustic detection and communication (Popper *et al.*, 2001). Electrical signals are also used for social communication, but are usually limited to short range use in relatively calm water by fish (Dulka, 1997; Scheffel and Kramer, 2000). Finally, chemical communication is commonly used for social signaling, largely because these signals can flow around obstructions and are easily broadcast in terrestrial and aquatic environments over both small and large distances (Vickers *et al.*, 1991; Pearce *et al.*, 2001).

Influences on agonistic behavior

A number intrinsic and extrinsic variables can affect crayfish aggression. For example, size (Bovbjerg, 1953, 1970; Rubenstein and Hazlett, 1974; Berrill and

Arsenault, 1984; Garvey and Stein, 1993; Rutherford *et al.*, 1995), sex (Peeke *et al.*, 1995, 1998), reproductive state (Stein, 1976), hunger state (Hazlett *et al.*, 1975), and social experience (Rubenstein and Hazlett, 1974; Daws *et al.*, 2002) are intrinsic factors that have been shown to affect aggression. While status and/or individual recognition (Karavanich and Atema, 1998; Zulandt Schneider *et al.*, 2001), resource availability and variability (Hazlett *et al.*, 1975; Bergman and Moore, 2003), prior residence (Peeke *et al.*, 1995, 1998), and shelter presence (Capelli and Hamilton, 1984; Bushmann and Atema, 1997) are extrinsic factors that affect crustacean aggression. Asymmetries in fighting ability may exist through some of these intrinsic features or extrinsic circumstances and consequently favor one contestant over the other (Parker, 1974; Maynard Smith and Parker, 1976). All of these factors appear to affect crayfish aggression, but the detection of chemical signals from conspecifics seems to be a critical factor in determining the outcome of fights (Zulandt Schneider *et al.*, 2001; Bergman *et al.*, 2003).

Chemical communication

Vision plays an important role in crustacean social interactions, particularly when the environment relatively transparent (Vannini and Gherardi, 1981; Bruski and Dunham, 1987). However when water clarity is reduced, many animals will rely on acoustic and/or olfactory signals for communication. Olfaction is equally as important, if not more important, for determining aggressive behavior than visual cues (Caldwell, 1992; Zulandt Schneider *et al.*, 2001; Bergman *et al.*, 2003). Antennules, arguably the most important chemosensory organ of crustaceans, are involved in detecting tactile and chemical signals associated with sex (Ameyaw-Akumfi and Hazlett, 1975; Dunham and Oh, 1992; Bushmann and Atema, 1997), molt state (Atema and Cowan, 1986), and dominance status (Karavanich and Atema, 1991; Rutherford *et al.*, 1996; Zulandt Schneider *et al.*, 1999, 2001). One possible source of information for these behaviors may be the urine. Urine signals, excreted through nephropores located near the base of the antennae, are a likely source of pheromonal cues in decapods (McLeese, 1973; Atema, 1986; Atema and Cowan, 1986; Bergman *et al.*, 2003). The presence of urine increases olfactory sampling through antennules flicking during fights (Ameyaw-Akumfi and Hazlett, 1975; Rutherford *et al.*, 1996). A gill current, the direction of which can be controlled by the animal, projects the urine and its component substances several body lengths into the surrounding habitat (Atema, 1995, 1996; Bergman *et al.*, 2005). Thus, crustaceans have an efficient system for broadcasting and detecting social pheromones.

Crustaceans are well-suited for chemical communication because they have a highly-developed sense of olfaction used to detect courtship pheromones (Atema and Engstrom, 1971; Ameyaw-Akumfi and Hazlett, 1975; Tierney and Dunham, 1982; Snyder *et al.*, 1992; Bushmann and Atema, 1997), maternal pheromones (Little, 1975), food sources (Moore and Grills, 1999), molt stage (Adams and Moore, 2003), predators (Hazlett and Schoolmaster, 1998), and agonistic chemical signals (Caldwell, 1992; Karavanich and Atema, 1998). In addition, crayfish are ideally suited for the study of chemical communication because of their largely nocturnal behavior and occupation of turbid environments which both can limit visual communication (Bovbjerg, 1970). Chemical signals (or pheromones) are likely released with the urine (Breithaupt and Atema, 1993; Zulandt Schneider and Moore, 2000), which is corroberated by the fact that urine is released almost exclusively during social interactions (Zulandt Schneider *et al.*, 2001; Breithaupt and Eger, 2002; Bergman *et al.*, 2005).

Chemical communication and agonistic behavior

The release of urine is detected at the periphery by the antennae and, more so, the antennules (Shepheard, 1974; Tierney *et al.*, 1984; Dunham and Oh, 1992; Bergman *et al.*, 2003). Chemical information is then transferred to the higher-level neurons of the crayfish olfactory pathway (Mellon, 2000), which in turn could cause changes in the neurochemistry of the receiving crayfish (Kravitz, 1988). Alteration in the neurochemistry of crustaceans has profound effects on subsequent social behavior (Antonsen and Paul, 1997; Huber *et al.*, 1997; Edwards and Kravitz, 1997; Sneddon *et al.*, 2000). Thus, exposure to social odors that alter neurochemistry in the receiver could function to create a sort of "pre-status" role, where exposure to a particular social odor would bias the outcome of future interactions. For example, when naive crayfish are exposed to dominant odor for extended periods of time (5 days), they respond by behaving similar to subordinates and lose subsequent fights, whereas those crayfish exposed to subordinate odor behave similar to dominant animals and win fights (Bergman and Moore, 2005). Thus, chemical signals may be used for more than simply communicating with a receiver. In addition, they may act to alter the social status of receivers.

Intrinsic neurochemical alterations

Chemical signals are used to communicate social status and can consequently alter aggressive behavior. However, it appears as though communication of status from a sender to a receiver is not the only purpose of chemical signals. These signals may also influence or reinforce the status role of the receiver. The proximate causation of dominance hierarchies may also include changes in serotonin levels, which have been shown to produce heightened aggressive states (Huber *et al.*, 2001). If intrinsic causation is responsible for resulting agonistic interactions, an animal with a prior winning experience may function as a "successful" fighter and thereby fight more readily in future agonistic interactions. In fact, recent wins and loses in a series of fights alters the likelihood of winning sub-

sequent interactions, despite an apparent disparity in size between opponents that would otherwise serve as an accurate predictor of the outcome (Daws *et al.*, 2002). Recognition of this aggressiveness (dominance or subordinance) could be accomplished visually (Thorp and Ammerman, 1978) or through chemical detection of the physiological state of the opponent (Zulandt Schneider *et al.*, 1999). For example, the role that serotonin plays in behavior is different in dominant individuals than in subordinates (Yeh *et al.*, 1996). This biological dichotomy could possibly be detected through postural changes or chemical signals that are released by the individual with previous experience during an agonistic encounter (Zulandt Schneider *et al.*, 2001; Bergman *et al.*, 2005). The presentation of chemosensory cues alone is sufficient to bring about investigative behavior and threat display in crayfish (Zulandt Schneider *et al.*, 1999), suggesting that chemical signals do play a role in agonistic interactions.

The behavioral plasticity associated with dominance seems to influence brain neurochemistry. Biogenic amines, a family of small neuroactive substances, include several behaviorally active compounds. Serotonin (Glanzman and Krasne, 1983; Oliver *et al.*, 1995), octopamine (Kravitz, 1986, 1988; Adamo *et al.*, 1995), norepinephrine (Barrett *et al.*, 1990) and dopamine (Nikulina and Kapralova, 1992; Shively *et al.*, 1997) have all been strongly implicated in the control of various forms of aggression in animals, as well as in human neurological disorders, psychiatric disturbances, alcoholism, and drug abuse (Eichelman, 1990; Goodman *et al.*, 1990; Mauri *et al.*, 1996). Serotonin has received a disproportionate amount of attention in recent years as evidence of its involvement in a broad spectrum of behavioral phenomena has mounted (Weiger, 1997).

The nature of the linkage between olfactory communication and aggression is not simple and its underlying mechanisms are difficult to tie to the precise role of neurochemistry in aggressive behavior. In addition to serotonin, other biogenic amines such as octopamine and dopamine or their precursors and derivatives, have also been shown to play an important role in the social behavior of decapod crustaceans (Kravitz, 1988; Antonsen and Paul, 1997; Edwards and Kravitz, 1997; Huber and Delago, 1998; Sneddon *et al.*, 2000). The previous social experience of a crayfish can modulate the functioning of serotonin in the nervous system of those crayfish (Edwards and Kravitz, 1997; Hörner *et al.*, 1997; Yeh *et al.*, 1997). In lobsters and crayfish, serotonin not only affects aggressive state (Livingstone *et al.*, 1980), but can also modulate an individual's posture such that it mimics those postures associated with dominance status (Livingstone *et al.*, 1980; Edwards and Kravitz, 1997; Hörner *et al.*, 1997) and alters tailflip escape responses (Yeh *et al.*, 1997). If intrinsic changes in biogenic amine neurochemistry occur because of winning or losing experiences, these changes may be reflected in the types of chemicals

released into the urine of dominant and subordinate crayfish. Exposure to social odors may alter the functioning of biogenic amines or some other unrelated compound in the nervous system of the receiving crayfish, resulting in the extrinsic release of urine that contains different chemical information that is dependent upon status.

Urine release and behavioral alterations

Urine-borne chemical cues influence the progression and outcome of agonistic encounters in lobsters and crayfish (Breithaupt *et al.*, 1999; Zulandt Schneider *et al.*, 2001). When crustaceans are deprived of the ability to detect odors, either by the obstruction of chemoreceptors or prevention of urine release, agonistic bouts increase in duration and intensity, and the predictability of the eventual victor is altered (Karavanich and Atema, 1998; Breithaupt *et al.*, 1999; Zulandt Schneider *et al.*, 2001; Bergman *et al.*, 2003). These studies indicate that important agonistic/status information is transmitted through chemicals in the urine and these chemicals play an important role in the determination and progression of agonistic bouts.

At a mechanistic level, an intrinsic chemical change associated with changes in social status can consequently, be extrinsically released with the urine to reduce fight intensity and decrease the chance of injury (Breithaupt *et al.*, 1999; Zulandt Schneider *et al.*, 1999, 2001). Extrinsic chemical detection may feedback onto the physical nervous system of both sender and receiver such that changes in receptor excitability (Krasne *et al.*, 1997) and serotonin receptor subtype populations (Yeh *et al.*, 1996, 1997) have been reported as a consequence of dominance. Moreover, social status has been shown to determine the concentrations of neuromodulators in blood (Knoll and Egberink-Alink, 1989), the efficacy of modulators at identified synapses (Yeh *et al.*, 1996, 1997; Krasne *et al.*, 1997) and the concentration of monoamines in different brain regions (Holladay and Edens, 1987; Winberg *et al.*, 1996).

A variety of factors influence the formation of hierarchical structures, including a crayfish's intrinsic aggressive state, an ability to physically dominate, previous agonistic experience and dominance pheromones. Chemical communication via urine signals plays a significant role in the recognition of aggressive state and carries information on dominance status (Zulandt Schneider *et al.*, 1999, 2001). It also appears that the long-term presence of olfactory cues from conspecifics can alter the subsequent agonistic behavior of crayfish, causing them to behave analogous to dominants or subordinates (Bergman and Moore, 2005). Intrinsic changes in neuro-hormones are likely expressed extrinsically in the urine of the experienced animal. It has been demonstrated that not only the chemical composition of urine, but also the mechanics of urine release are altered by social status (Bushmann and Atema, 1997; Breithaupt *et al.*, 1999; Bushmann and Atema, 2000; Zulandt Schneider *et al.*, 2001; Bergman *et*

al., 2005). These alterations in urine release can be visualized by dye and show that crayfish release urine more often during social activities, and also that the eventual winner of an agonistic bout will release urine more often than the loser (Breithaupt and Eger, 2002; Bergman *et al.*, 2005). This suggests that chemicals in the urine are used to communicate status level and alter decisions made during fights.

DISCUSSION

The most parsimonious explanation for the comprehensive literature presented above is a scenario in which changes occur in the neurochemistry of a sender crayfish and these changes are expressed in the urine or leaked elsewhere from the sender's body and transmitted to a receiver. The receiver either detect these chemicals through sensory mechanism (more likely) or takes up these chemicals (less likely), which then alters its neurochemical function either directly or indirectly through activation of certain neural circuits associated with social behavior. 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 in an artificial habitat such as confined laboratory environment (see Bergman and Moore, 2003). Consequently, these signals can function to reduce or increase both 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 to manipulate an opponent's intrinsic neural state and behavior.

We have reviewed that agonistic experiences alter social-status odors, which in turn modify the subsequent social behavior of receivers. Since social interactions in decapods are correlated with neurochemical alterations, we suggest that short-term exposure to social odors communicate these changes, whereas long-term exposure may alter the functioning of some neuro-hormone in the receiving crayfish's nervous system. Consequently, exposure to status odors appear to be more responsible for dominance-subordinance 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.

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