Behavioral Syndromes in Crayfish: Agonistic Behavior and Mating

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ABSTRACT

Behavioral Syndromes are behavioral patterns displayed consistently by individual organisms within given behavioral contexts or across several different contexts. Such behavioral patterns can lend themselves to the identification of discrete 'personalities' or behavioral types. As an application of the behavioral syndrome model, this study was aimed at finding a correlation between increased aggression in same-sex territorial interactions and the use of agonistic mating strategies in male-female interactions. I observed 24 pairs of crayfish interact within a tank containing an artificial shelter, taking note of all aggressive behaviors displayed. Twelve pairs of male and female crayfish were then observed under similar conditions. Aggression was variable within gender-specific groups and was significantly lower in female-pair interactions, but aggression levels did not significantly affect whether male crayfish employed agonistic mating strategies. This suggests that use of the agonistic mating strategy is not the extension of an aggressive behavioral pattern but derives from alternate factors; it may be a selected response to female aggression or the limited success of non-agonistic mating attempts.

INTRODUCTION

Sih et al. (2004) define behavioral syndromes as "…[suites] of correlated behaviors expressed either within a given behavioral context… or across different contexts." For example, certain individuals within a population may exhibit generally more aggressive behaviors within a variety of situations, exhibiting what might be referred to as a "bold" or "reactive" behavioral syndrome, or personality. One idea regarding behavioral syndromes is that these behavioral correlations generate 'tradeoffs', where they result in differing fitness within different contexts. A highly aggressive female spider, for instance, might prove highly successful at acquiring food, but might also display such foraging-related aggressiveness in the form of cannibalism when confronted with any male spider, thus limiting her reproductive success.

Due to the complexity of behavioral studies, it is often necessary to focus on behavioral systems with known (or suspected) key correlations, such as aggressive behavior, across contexts. In this experiment, I examined agonistic behavior patterns in the rusty crayfish, *Orconectes rusticus*, a highly aggressive, invasive species which has recently begun to displace several native crayfish species in the Otsego County area (Kuhlmann and Hazelton, 2007). Crayfish are territorial animals and will exhibit agonistic behaviors and form dominance hierarchies when confronted with one or more other crayfish (Hyatt, 1983). Previous studies have shown variable levels of aggression among different crayfish species (Tierney et al., 2000), but there have not been any studies concerning intraspecific variability or behavioral syndromes.

Behavioral syndromes have been studied in only a small number of animal species, and by examining the potential presence of such in crayfish, I hoped to contribute to an understanding of the evolution and ecology of behavioral patterns. The behavioral syndrome model might serve as a precursor to the more advanced 'personality' attributed to organisms of higher intelligence and emotional complexity. Crayfish aggression is of particular interest

because of the detrimental effects aggressive non-native species have had on native species in various regions.

Studies of crayfish mating behaviors have delineated both agonistic and non-agonistic mating behaviors in *Orconectes* crayfish (Thomas, 1983). Non-agonistic mating behavior consists of the male mounting the female dorsally and using his pereiopods to rotate her onto her back. Agonistic mating behavior involves precopulatory behavior typically resembling the aggressive interactions observed between crayfish of the same sex, followed by the male seizing the female by the chelae and flipping her onto her back. In these same studies, most non-agonistic mating attempts were observed to have failed, suggesting non-agonistic mating behavior as a possible example of a maladaptive behavior.

I hypothesized that a) competitive agonistic behavior would vary among individuals within a sample population of male and female crayfish; b) female pairs would display less territorial aggressiveness than male pairs; c) highly aggressive males would engage in agonistic mating behaviors more often than less aggressive males, and d) highly aggressive females would display more agonistic behaviors in a courtship context than less aggressive females.

METHODS

Forty-eight individual *O. rusticus* (24 males, 24 females) were captured in several streams of the Upper Susquehanna River watershed (Delaware and Otsego Counties, NY). Crayfish were selected to be of similar size, as size may be a factor in determining whether agonistic behavior occurs (Thomas, 1983). Crayfish were measured from the posterior edge of the carapace to the tip of the rostrum. Male crayfish were also checked for reproductive phase: Male crayfish alternate between reproductive (Form 1) or none-reproductive (Form II) phases throughout the year. All males used in the experiment were ultimately found to have been Stage 1 males at the time. Immature crayfish, as well as crayfish with missing limbs, were excluded.

Twelve males and 12 females were designated at random to be test subjects; the remainder served as competitor males/females. The competitor crayfish were housed together in community tanks separated by sex. Test crayfish were housed individually in small containers. Each tank and container was filled with a layer of gravel and small rocks which served as shelters. All the crayfish were fed regularly on alternating days.

A clear plastic container served as an observation tank for all behavior tests. Half of a small flower pot was used as an artificial shelter meant to provoke territorial behavior. A divider was used to keep each member of a matched pair separated during a ten minute acclimation period wherein each was placed within one part of the tank. The divider was then removed, and the crayfish were observed for a 15 minute period. The observation tank was cleaned and re-filled after each observation period. After the 24 sets of same-sex interactions between test crayfish and competitor crayfish, the 24 test crayfish were then divided into male-female pairs, and mating interactions were observed.

For each set of interactions, I recorded the occurrence and frequency of all behaviors which occurred. Seventeen agonistic behaviors, as described by Tierney et al. (2000), were used as a base list of expected interactions; this list was reduced to 9 behaviors I observed and could regularly differentiate during the experiment (Table 1). No behaviors outside of these 17 were observed during the experiment. Agonistic behaviors include: approaches, lunges, meral spreads, chela strikes and grasps, and aggressive flicking of the antennae. For mating

pairs, mating behavior was recorded according to the descriptions given by Thomas (1983); agonistic mating behavior involves precopulatory behaviors similar to agonistic encounters of the same sex, followed by the male seizing the female by the chelipeds and flipping her onto her back.

Aggression was then quantified via the number of aggression interactions an individual crayfish initiated with a competitor crayfish, and analyzed using SPSS correlation tests.

Table 1. Description of aggressive behaviors

Behavior	Description
approach	crayfish approaches another to initiate an aggressive bout
lunge	crayfish lunges forward in a "hop"; sometimes associated with chelae grips
retreat	crayfish either backs away from an aggressor or turns and flees
Chelae grip	crayfish grips the chelae of opponent; sometimes prelude to wrestling
Chelae rap	crayfish strikes the chelae of opponent with own, closed chelae
Chelae thrust	crayfish extends one chelae towards
Chelae enclosing	crayfish holds chelae of opponent in own, without closing chelae
Chelae spread	crayfish extends both chelae sideways, perpendicular to body
rotate	crayfish moves around opponent to strike from new angle

RESULTS

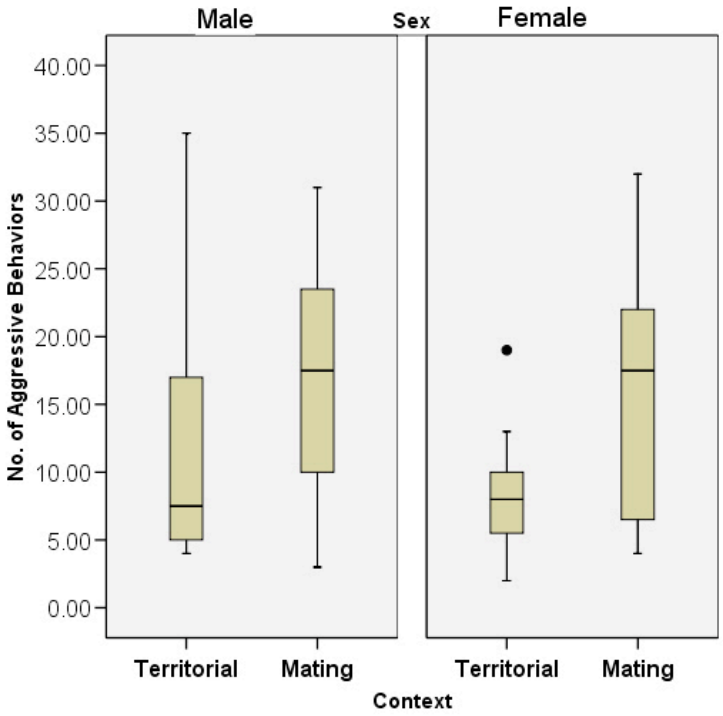

Figure 1. Frequency of aggressive behaviors in male and female test groups in territorial and mating contexts.

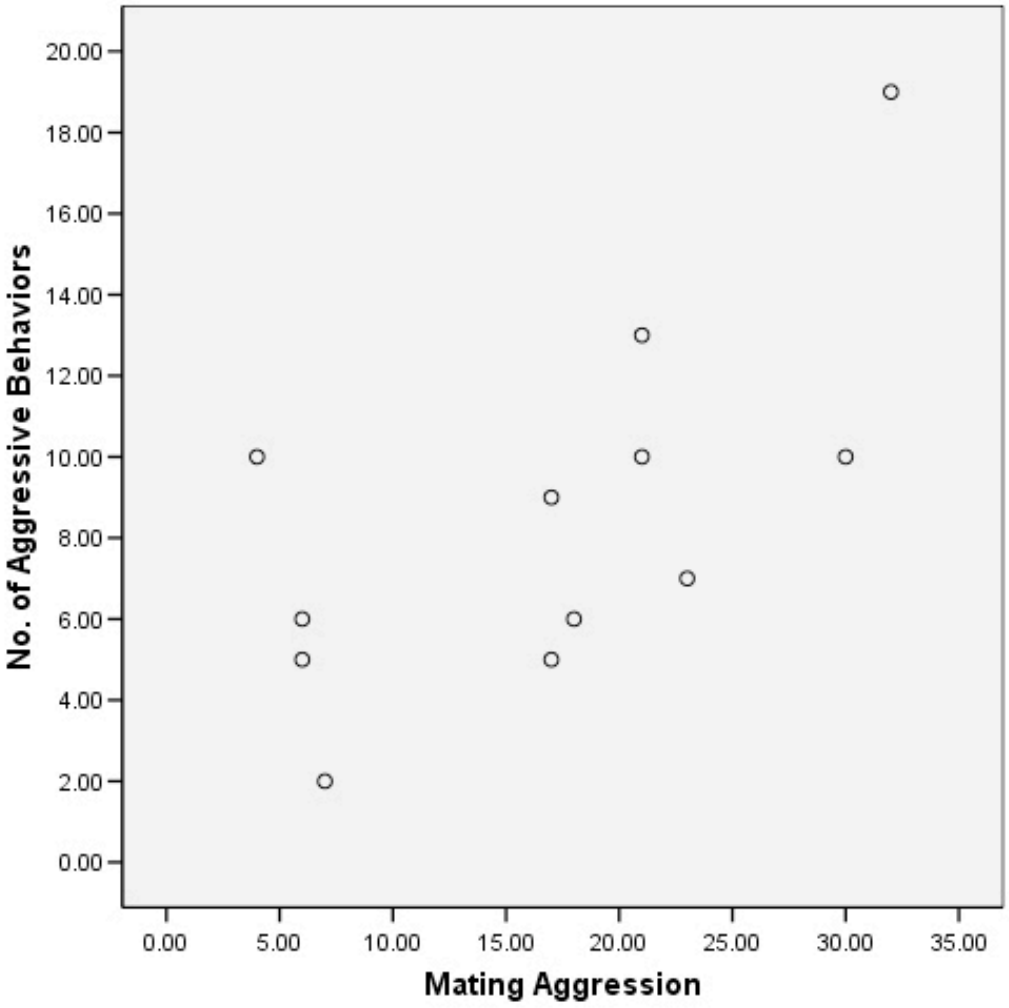

Figure 2. Correlation between levels of aggression in territorial/competitive context (vertical axis)and aggression in a mating context (horizontal axis), in the female crayfish group ($r= 0.652$, $p= 0.022$).

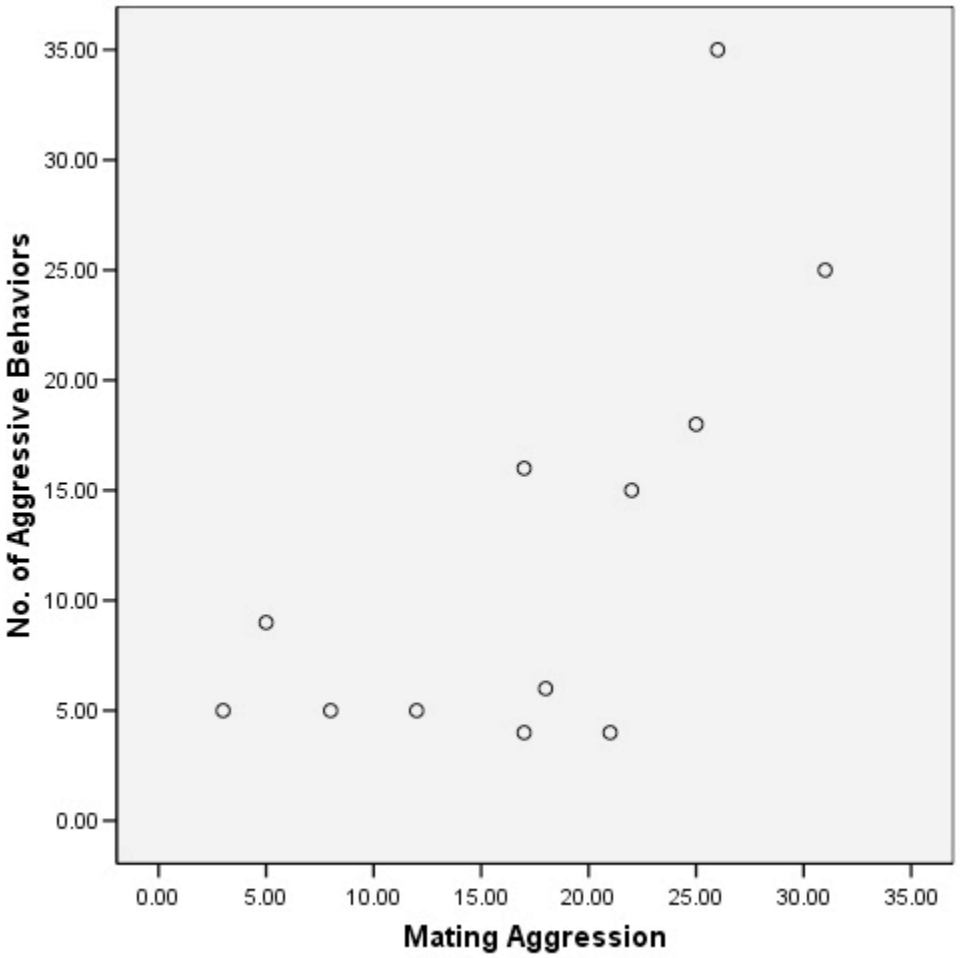

Figure 3. Correlation between levels of aggression in territorial/competitive context (vertical axis) and aggression in a mating context (horizontal axis), in the male crayfish group. ($r = 0.683$, $p=0.014$).

Figure 4. Aggression scores for male crayfish across both contexts.

All but one of the male crayfish exhibited agonistic mating behavior in the mating scenario (Fig. 4), indicating that there is no correlation between a higher or lower frequency of aggressive acts observed in test group males and use of the agonistic mating strategy.

In both sexes, individuals who performed high numbers of aggressive behaviors in same-sex encounters tended to behave similarly in male-female pair encounters (Figures 2 and 3).

Two males (Test Males #9 and #11) exhibited mating behavior during the same-sex tests; this behavior typically halted most aggressive behaviors in favor of copulatory behavior, and so may have skewed aggression counts. Similarly, three males were successful in their

agonistic mating behavior during male-female tests; as copulation halted typical aggressive behaviors, aggression counts may be lower than they might have been.

Females generally exhibited lower frequencies of aggression in same-sex encounters than males (Fig.1); both sexes exhibited higher aggression in mating contexts than in territorial contexts.

DISCUSSION

The significant correlation between high aggression in territorial scenarios and high aggression in mating scenarios suggests that individuals may exhibit patterns of behavior as described by the Behavioral Syndrome model; in this case, the most aggressive individuals might be described as fitting the Aggressive Type.

The widespread use of the agonistic mating strategy by all but one of the test males suggests that it is not the extension of an aggressive behavioral pattern, but derives from alternate factors; it may be a selected response to female aggression or the limited success of non-agonistic mating attempts. Agonistic mating behavior may, in fact, be size-specific. Future studies might be done with a larger number of individuals of varying size, with mating pairs set up in three groups: small male/large female, same size male/female, large male/small female. If particular size differences gave rise to an increased frequency of agonistic mating behavior, this might indicate that it is only used under specific circumstances.

Another possibility is that agonistic mating behavior, even if used only when males are faced with smaller females, has been sexually selected for, as large, aggressive females can and will often fend off male copulatory attempts. The nonagonistic mating attempt by the single male was unsuccessful, similarly to mating behaviors observed by Thomas (1983), wherein most non-agonistic males weren't successful. All but three of the agonistic mating attempts, however, were equally unsuccessful. Further examination of the non-agonistic mating strategy – that is to say, when it occurs, and under what circumstances it is successful – is required to determine whether a less aggressive personality type represents a disadvantage, or what Sih et al. (2004) refer to as "suboptimal" behavior.

Alternatively or concordantly, the agonistic mating strategy may be a selected response to the aggressive behavior of females, in turn selected for due to the benefits associated with interspecies competition. Highly aggressive crayfish would presumably fare better against intra- and inter-specific competitors, as suggested by studies of the effects of invasive rusty crayfish populations on native crayfish species (Hill and Lodge, 1999; Kuhlmann and Hazelton, 2007). If high agression in males is linked to increased competitive success and agonistic mating strategies are linked to increased reproductive success, selection would favor populations wherein the majority of males are highly aggressive and display agonistic mating behaviors. The degree to which the non-agonistic mating strategy persists in the population might present an interesting subject for future studies.

Generally, females were less aggressive than males in same-sex trials. This may be a reflection of gender-differentiated reproductive concerns: male aggression against other males would serve the purpose of acquiring or maintaining access to territory and/or females, and highly aggressive males would presumably be the most successful. Female aggression might be a crucial factor in determining the acquisition of the best shelters, but would not, presumably, affect parentage. Accordingly, continuous aggression between females seems

less common; aggressive behavior usually terminated after a brief initial period, after which several female pairs proceeded to share the shelter in the observation tank without incident.

Female aggression was far higher in male-female trials, perhaps simply as a reaction to male aggression. It may, however, reflect a means of sexual selection. Ritualized aggressive bouts may serve as a means of determining male fitness, both in terms of aggression and general physical health. The formation of dominance hierarchies suggests a capacity for differentiating specific physical features such as size (Bruski and Dunham, 1987), which might easily be extended to constitute a motivating factor for females to participate in highly aggressive bouts with potential male partners.

If one considers aggression as a heritable trait that may be continuously selected for, this may explain the success of *O. rusticus* in novel environments. Similar correlations between reproductive success and specific personality traits were observed in a study involving an avian population (Dingemanse et al., 2005). Further examination of the non-agonistic mating strategy – that is to say, when it occurs, and under what circumstances, if any, it is successful – is required to determine whether a less aggressive personality type represents a disadvantage, or what Sih et al. (2004) refer to as "suboptimal" behavior.

Further examination of the Behavioral Syndrome theory might involve continued study of aggression patterns over the crayfish life cycle, in order to determine whether "personality shifts" occur over time. Studies combining aggression scenarios and foraging behavior could explore whether broader suites of behavior (e.g., aggression and 'boldness') can be encompassed by a given 'personality'. The behavioral syndrome model in and of itself might serve as a means of evaluating precursors to what is referred to as a "personality" in human beings. These might comprise 'simpler' forms of personality without, necessarily, any associations with sets of emotional responses or "emotion-prompted" behaviors. At the same time, we can trace the development of early behavioral 'sets' and see where in evolutionary history behavioral complexity, and even intelligence, begins to arise.

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