

Consequences of social dominance on crayfish resource use

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Summary

Our study examined the effect of dominance on feeding, mating behaviour, and shelter use in the crayfish, *Orconectes rusticus*. In three different experiments, dominance and resource use were recorded in male populations, mixed-sex populations, and when crayfish were alone. Crayfish established dominance status in populations or through status conditioning and had access to variable resources (food, mates, and/or shelters) in each experiment. Subsequent resource use was quantified and compared to dominance rank. Our results did not match conventional predictions that dominance would confer increased access to resources. Top ranked dominant crayfish occupied shelter significantly less than lower ranks. This differential shelter use may be due to dominant motivation to reinforce status, as dominants also participated in the most agonistic interactions. When dominant crayfish had access to resources in the absence of conspecifics, dominant crayfish occupied shelter significantly more than subordinate and naïve crayfish. This result illustrates that present social context has a significant impact on behavioural decisions in crayfish. Social history and social context interact to determine shelter occupancy in this case. Feeding and mating was unaffected by social status in our populations. This is a surprising result given current views on the role of dominance and aggression in many animal systems. The consequences of dominance for resource use in crayfish do not follow our current understanding of resource holding potential. We hypothesize that these consequences vary due to changing behavioural motivations in different social contexts. Future studies should examine under which conditions dominance may impact feeding and mating and whether differential resource use results in differential reproductive success.

Keywords: *Orconectes rusticus*, dominance, resource use, shelter, mating, foraging.

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Introduction

Social dominance, defined by Drews (1993), is characterized by the consistent victory of one individual over another in repeated agonistic interactions. Agonistic interactions are aggressive contests between conspecifics and are associated with resource acquisition and defence (King, 1973). Thus, an expected consequence of winning is to possess or control limited resources and thereby increase fitness. Increased resource control due to dominance has been documented in many taxa (Wilson, 1975); however, dominance does not always confer higher fitness. Dominant female lizards, *Eulampris heatwolei*, achieve no increase in fitness as a result of their higher social status (Langkilde et al., 2005). Dominant male jackdaws, *Corvus monedula*, have decreased reproductive success relative to subordinate males (Verhulst & Salomons, 2004). Studies such as these suggest that the relationships among dominance, resources, and fitness are not as straightforward as previously thought (Wilson, 1975).

Resources may be acquired by dominance status established in agonistic contests, or resources may be allocated with respect to relative dominance rank within a hierarchy (Drews, 1993). Individuals may acquire rank based on predetermined qualities associated with dominance, such as physical attributes that contribute to fighting ability (resource holding potential (RHP), Parker, 1974), or ranking may result from 'social dynamics', such as winner-loser-effects or bystander effects (Dugatkin, 1997; Chase et al., 2002). Asymmetries in RHP and resource value have conventionally been examined with respect to their effects on agonistic behaviour (Enquist & Leimar, 1990; Stocker & Huber, 2001). In addition, social dynamics are dependent upon the context in which they take place. Factors such as group composition, sex ratio, and density can alter both the structure of agonism and the fitness benefits of status (Emlen & Oring, 1977; Clutton-Brock et al., 1979; Usio et al., 2001). Yet, the impact of social context on the ecological benefits associated with dominance is rarely tested (Eggleston & Lipcius, 1992). This is particularly true for the well-studied aggressive systems of crayfish.

Decapod crustaceans, such as crayfish, serve as an excellent model for examining agonistic interactions (Dingle, 1983). Crayfish readily establish dominance during dyadic interactions and in laboratory settings form linear hierarchies that exhibit reduced aggression (Guiasu & Dunham, 1997). Crayfish exhibit stereotyped aggression with distinct phases of intensity where

opponents engage each other, even in the absence of resources (Bovbjerg, 1956; Bruski & Dunham, 1987). Because of these characteristics, crayfish aggression lends itself to experimental manipulation and as a result, the neural substrates of aggression (Panksepp et al., 2003), the communication of aggressive state (Schneider et al., 2001), and the factors influencing dominance establishment have all been thoroughly described (Rutherford et al., 1995; Pavey & Fielder, 1996; Daws et al., 2002; Bergman et al., 2003). The outcome and structure of crayfish agonistic interactions are also shaped by the presence of resources, such as shelters, food, and mates (Peeke et al., 1995; Stocker & Huber, 2001; Figler et al., 2005). These resources greatly influence crayfish survival. Although studies have explored proximate mechanisms of dominance in crayfish, the behavioural and fitness consequences of agonism and the function of aggression and dominance remain elusive topics. One measure of fitness consequences is resource acquisition and use. By examining how dominance affects individual resource use, we can gain a firmer grasp on answers to the ultimate mechanisms that give rise to social hierarchies in crayfish.

Many species that exhibit dominance systems show priority of access to a limited food supply (Wilson, 1975). Crayfish are omnivorous detritivores thus food is not likely to be a limited resource. However, foraging behaviour may be affected by such factors as the presence of predators and alarm cues (Pecor & Hazlett, 2003). Motivation to forage may also shift over the course of the year, such as during spring breeding seasons when male crayfish allocate more time toward agonism and copulation with females. When females extrude their eggs later in the spring and subsequently retreat to shelters, males spend more time foraging (Berrill & Arsenault, 1982). Food may be limiting in habitats where food is clumped or patchily distributed. Bergman & Moore (2003) found that agonistic encounters occurred more frequently on detrital patches, indicating these patches were valued resources.

Mates are also a valuable resource for crayfish. Studies examining crayfish mating behaviour have not found conclusive evidence of male or female mate choice, possibly due to male-biased sex ratios (Berrill & Arsenault, 1982). Microsatellite data have shown that *Orconectes placidus* have multi-male broods with skewed genetic contributions from brood fathers (Walker et al., 2002). As a resource, females may not be economically defensible. Male crayfish attempt to interrupt copulating pairs (Berrill & Arsenault, 1982) but

the success rates of such behaviour are undocumented. The extent to which dominant crayfish may monopolize mating opportunities remains unknown.

Considerably more literature has been devoted to examining shelter use in association with agonism. Studies tend to focus on mechanisms of competitive exclusion and species displacement. Several crayfish species commonly evict heterospecifics from shelters in agonistic interactions (Bovbjerg, 1970; Gherardi & Daniels, 2004; Klocker & Strayer, 2004). Crayfish that successfully acquire or defend shelters do not necessarily use these shelters (Gherardi & Daniels, 2004). This behaviour is indicative of 'spiteful behaviour' in which individuals may improve their fitness by excluding others from resources (Davies, 1978). Species displacements across habitats have also been attributed to interspecific differences in chelae size (Garvey & Stein, 1993). Additionally, species distributions with respect to habitat type may change depending on risk of predation where more aggressive species monopolize shelter-rich habitats (Bovbjerg, 1970; Hill & Lodge, 1994). Intraspecific studies have yielded similar findings where dominance is correlated with access to preferred shelter-rich habitat (Levenbach & Hazlett, 1996; Statzner et al., 2000). The mechanisms by which these distributions occur are attributed to exclusion by dominant ranking crayfish; however, there is evidence to suggest that behaviours associated with shelter use may change depending on dominance status (Herberholz et al., 2003). Thus, persisting behavioral effects following agonism may be another factor determining shelter use and crayfish distributions. Differential shelter use with respect to dominance status/rank in crayfish has not been fully explored.

The purpose of this study is to elucidate how resource use is impacted by social status and how this influence changes with varying social context. We examined dominance affects on resource use with three experiments. Experiment 1 tests the effects of dominance rank on shelter occupancy. Since shelter eviction is a commonly documented phenomenon in crayfish (Bovbjerg, 1956; Gherardi & Daniels, 2004; Figler et al., 2005), we predict that higher ranking individuals will exhibit increased shelter use and exclude lower ranking individuals. Experiment 2 tests the effects of social history on shelter occupancy and feeding. If crayfish of differing social status are presented with resources (food and shelter) in the absence of conspecifics, any differences in resource use must be dependent upon social history rather than direct resource competition. Finally, experiment 3 tests the effects of dominance rank of both males and females on shelter occupancy and mating

behaviour. We predict that high dominance rank will correlate with increased mating opportunities.

Material and methods

Animals

Crayfish, *Orconectes rusticus*, were collected from the Portage River, Wood County, Ohio, in the fall of 2001 and 2004. Individual form I (reproductive) males and reproductive females were placed in 10.0 × 10.0 cm ventilated plastic containers in a flow-through holding tank (154.0 × 48.0 × 31.0 cm). Crayfish were fed commercial rabbit food pellets three times a week and maintained on a 12 h:12 h light-dark cycle. All crayfish were isolated for a minimum of seven days to remove any effects of prior social interaction (Schneider et al., 2001). Crayfish were used only once during these experiments.

Experiment 1: Shelter use in the presence of male conspecifics

Test arena

All trials were run in opaque fiberglass tanks (78.0 × 78.0 × 35.0 cm) filled with gravel to simulate the natural substrate in crayfish habitats. The tank was filled with de-chlorinated water to a depth of 25.0 cm and was oxygenated with four air stones placed in the corners of the tank. The tank was placed under a wooden frame (180.0 × 123.0 × 82.0 cm) from which a Remington® security camera (model No. 00807) was mounted to record behavioural interactions. Video was recorded on a time-lapse VCR (Samsung SSC-960) at a rate of 1 image per 3 s. Four lamps were clipped to the frame to illuminate the tanks: white lights were used during diurnal periods and red lights were used during nocturnal periods. Five shelters consisting of a variety of PVC pipe, Plexiglas, and clay flower pots were placed in the tank to simulate natural shelter variability.

Experimental protocol

To test the effects of dominance rank on resource use, agonistic interactions and shelter occupancy were monitored in populations of male crayfish (mean ± SE; 3.5 ± 0.3 cm carapace length). Previous studies have shown

that fight outcomes are predictable by relative size of opponents (Pavey & Fielder, 1996). Therefore, crayfish within a given population were size-matched with no greater than a 10% difference in carapace and chelae length. Reflective tape was placed in different locations on the body in order to distinguish individual crayfish from one another for subsequent analysis. Five male crayfish were placed in the arena at 1900 (the beginning of the nocturnal period) and video taped continuously for 96 h. Ten replicates were performed (50 male crayfish).

Data analysis

Video tapes were analyzed for frequency and intensity of crayfish agonistic interactions and for time spent occupying shelter. An interaction begins when the distance between two crayfish is equal to or less than one body length. Conversely, an interaction ends when the distance between two crayfish exceeds one body length and no interaction occurs for 10 s. Intensity of interactions and winner/loser identification was determined using an ethogram adapted from Bruski & Dunham (1987). Comparisons between days for number and intensity of interactions were made using a one-way MANOVA with a Fisher-LSD post hoc test (Statsoft[®] Statistica, ver. 6).

Dominance activity index (DAI) is a measure of dominance status that equals the proportion of fights an individual wins (Bartos, 1986). DAI was calculated per hour for each crayfish within a population for the first 10 h of a trial. Subsequent calculations were made at 24-h intervals. DAI values were then used to assign hierarchy ranks with '1' indicating the most dominant crayfish.

Finally, the amount of time spent occupying shelter was recorded for each crayfish. Crayfish were considered to be in a shelter if the end of the cephalothorax was not visible past the shelter entrance. Time spent occupying shelter and hierarchy status were compared using a one-way ANOVA.

Experiment 2: Shelter use and feeding in the absence of conspecifics

Test arenas

Test arenas consisted of 37 litre (31.1 × 51.1 × 25.7 cm) aquaria, each containing gravel substrate, one shelter, and a marked feeding area where food was placed (hereafter referred to as 'home tanks'). Black felt was taped around the sides of each home tank in order to visually isolate crayfish

that were inside. PVC pipe, cut in half longitudinally (diameter = 8.7 cm, height = 3.9 cm, length = 12.7 cm), was used as shelter with one end affixed to the tank glass, forming a single opening for crayfish to enter or exit. The feeding area consisted of a 6.4 × 6.4 cm piece of Plexiglas with a darkened perimeter and was placed at the opposite end of the tank from the shelter, approximately 33.0 cm away. Crayfish activity was continuously recorded via a mounted security camera (Model No. SG2281UQ-A), and a time-lapse video recorder as previously described. Tank illumination and light-dark cycle were the same as previously described.

Experimental protocol

To test the effect of social status on shelter use and feeding behaviour, socially conditioned male crayfish (mean ± SE; 3.8 ± 0.1 cm mean carapace length) were monitored for feeding behaviour and shelter occupancy in the absence of other individuals. For each status treatment (dominant, subordinate, and control), social conditioning was applied during each day and resource use behaviour was recorded during each night over the course of a three day period.

Social conditioning

Crayfish to be used in behavioural trials were repeatedly paired with other crayfish in predictable agonistic interactions. This procedure has been demonstrated to sustain social status in crayfish (Daws et al., 2002).

‘Dominant’ treatment crayfish were repeatedly paired with a smaller (between 10% and 30% difference in size) crayfish while ‘subordinate’ treatment crayfish were paired with a larger (between 10% and 30% difference in size) crayfish. ‘Control’ crayfish never interacted with another one. Crayfish were always paired with the same individual to decrease the likelihood of dominance reversals.

Each pair was placed in a fight tank (37 litre aquaria) on opposite sides of an opaque divider and allowed to acclimate to the fight arena for 15 min. Fight tanks are separate from the home tanks described above. After the divider was removed, crayfish were allowed to interact for 15 min. and were visually monitored to confirm predicted dominance establishment and/or reinforcement. All crayfish interactions were also video taped (Canon XL1) for further confirmation. ‘Control’ treatment crayfish were placed in an empty

fight tank for 15 min. to control for possible effects from handling. After the 15 min. interaction, all treatment crayfish were placed in their respective home tanks and the other crayfish were re-isolated. Treatment crayfish were removed from the experiment when pairings did not result in predicted outcomes. As a result, six crayfish (two replicates of each treatment) were removed from the study. Social conditioning was performed three times per day (for three consecutive days), between 1000 and 1800 h with no less than one hour between consecutive sessions.

Behavioural trials

Raw halibut fillet (2.0 g) was tied with twine onto the feeding area of each home tank. Three size-matched crayfish, one of each status treatment (dominant, subordinate, and control) were then placed in the home tanks after one day of social conditioning. Crayfish were then video taped for an average of 16.3 ± 0.1 h during the night to record feeding behaviour and shelter use. Start times for recording periods were variable between 15.30 and 18.30 h and all were ended at 09.00 h. At the end of the recording period, any remaining fish was removed from the tank. This procedure was repeated for two more nights (total three nights of recording). 20 replicates of each status treatment were performed.

Data analysis

Video tapes of shelter/feeding trials were analyzed for proportion of time crayfish spent performing specific behaviours each night. Video tape underwent blind analysis by research assistants that were unaware of status treatments. Video was analyzed for proportion of time each crayfish spent in shelter, out of shelter, and feeding for each night. A crayfish was considered 'in shelter' as previously described. If the tip of the rostrum was within the marked feeding area, the crayfish was considered to be 'feeding'. Otherwise, crayfish were considered 'out of shelter'. Mean proportion of time spent exhibiting these behaviours over three nights was calculated for each crayfish and then square-root arcsine transformed (Zar, 1999) from proportions to degrees for statistical analysis. Comparison of time spent performing specific behaviours across social status was analyzed using a two-way ANOVA with a Fisher-LSD post-hoc test with social status and trial day as factors (Statsoft[®] Statistica ver 6). Size varied between treatment replicates (range = 2.8-4.8

cm) therefore linear regressions were performed to test for effects of size on observed behavioural differences (Microcal™ Origin ver. 6.0).

Experiment 3: Shelter use and reproductive opportunity

Test arena

Test arenas, video recording equipment, and lighting were identical to those described in experiment 1. Trials were run in an environmental chamber with an ambient temperature of 10°C and a 14 h:10 h light-dark to simulate natural conditions during crayfish breeding season.

Experimental protocol

To test the effect of dominance on mating and mate choice, mixed-sex populations of crayfish (mean ± SE; males: 3.9 ± 0.1 cm carapace length; females: 3.4 ± 0.1 cm carapace length) were monitored with respect to agonistic interactions, shelter use, and mating behaviour. Three size-matched males and eight randomly chosen females were placed in a tank with 12 PVC shelters and video taped continuously for 96 h. Crayfish were marked with correction fluid to distinguish between individuals. Ten replications were performed (total 30 males and 80 females).

Data analysis

Videos were analyzed for three classes of behaviours including male-male agonistic interactions, shelter occupancy, and mating behaviour. Analysis of agonistic interactions was performed as previously described. Shelter occupancy was only examined for males. Crayfish were considered 'in shelter' when chelae markings were not visible. Mating behaviour between males and females, as described in Mason (1970), was recorded and timed for duration. Mating events began upon seizure of the female by the male and ended upon release of the female (Mason, 1970). Although mating was quantified, sperm transfer could not be determined and therefore individual reproductive success cannot be inferred. Because crayfish were not visible when they were occupying shelters, only mating events that occurred outside of shelters were recorded.

Final DAI values and rank assignments were calculated for each male crayfish in a population (refer to experiment 1). Linear regressions were used

to compare male DAI, male size (carapace and chelae length), and female-male size ratio to number of mating events, mean time per mating event, total time spent mating, percent time spent mating, time spent in shelter, and number of mates per hour. All regression analyses were performed using Statsoft[®] Statistica ver. 6.

Results

Experiment 1: Shelter use in the presence of male conspecifics

Hierarchy formation

As trial days progressed, overall aggressive behaviour in populations decreased. Nightly agonistic interactions decreased significantly each day until day 3 of the trial period (ANOVA, Fisher LSD, $F = (2, 10) = 29.51$, $p < 0.01$; $N = 10$). Average hourly interactions per day were as follows: (mean \pm SE) 23.0 ± 0.7 (day 1), 11.3 ± 0.4 (day 2), and 7.4 ± 0.4 (day 3). The intensity of interactions also decreased significantly each day until day 3 ($p < 0.05$) (Figure 1). Agonistic interactions were both higher in frequency and in intensity during nocturnal periods (ANOVA, Fisher LSD, $F_{(2,18)} = 83.50$, $p < 0.01$) (Figure 1).

DAI values indicate the rapid establishment of rank 1 dominant crayfish within the first two hours of being in population (Figure 2). Dominant crayfish maintained rank throughout the trial period with little fluctuation. In

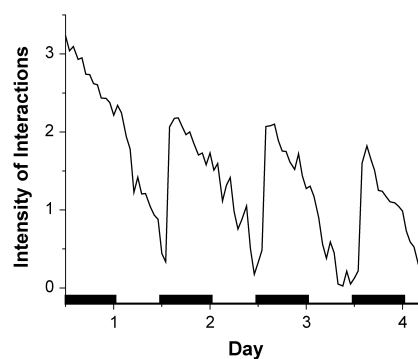


Figure 1. Mean (\pm SE) intensity of interactions for all male groups ($N = 10$) over 96 h. Intensity of interactions is measured on an hourly basis. Nighttime periods are represented by the black boxes.

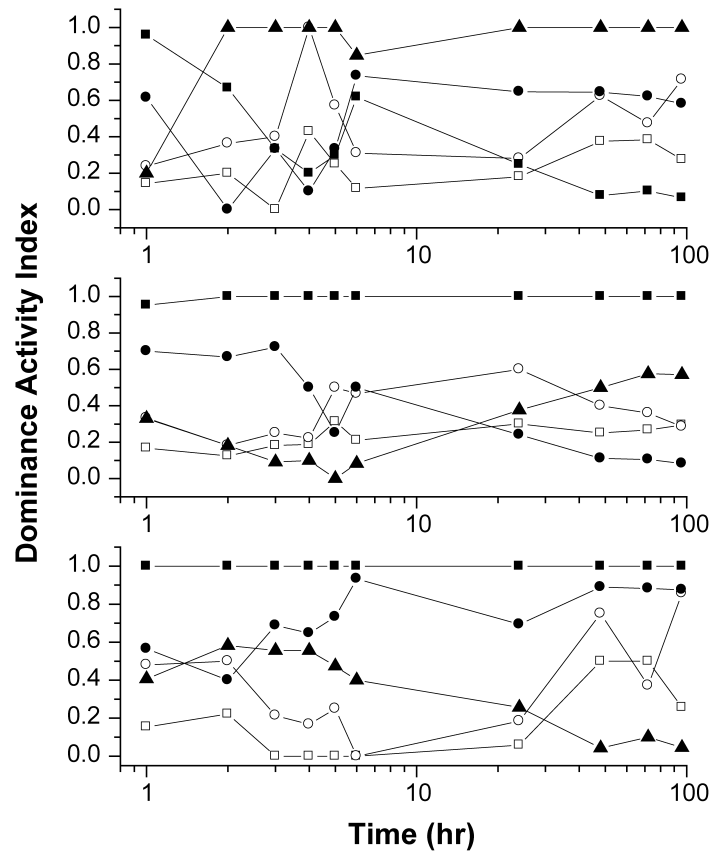


Figure 2. Dominance activity indices for individual male crayfish calculated at different time intervals over a 96-h period. Each graph represents one group of five male crayfish. DAI values indicate hierarchy rank with the most dominant crayfish possessing the highest value. Symbols correspond to initial ranks after the first hour.

contrast, lower ranking crayfish displayed relatively high fluctuations in individual rank until day 3, at which point resulting hierarchies tended to stabilize (Figure 2). Rank 1 dominant crayfish also participated in significantly more agonistic interactions than all lower ranking crayfish (ANOVA, Fisher LSD, $F_{(9,36)} = 35.08$, $p < 0.001$; Figure 3).

Shelter use

Only top and bottom ranked crayfish differed significantly in shelter use in comparison with other crayfish. Rank 1 dominant crayfish spent significantly

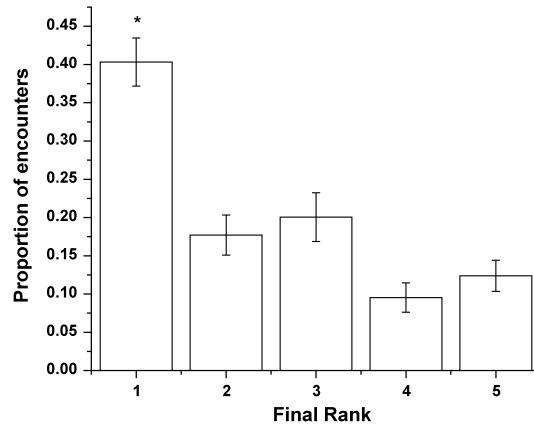


Figure 3. Proportion of agonistic interactions that males within a dominance hierarchy ($N = 10$) participated in. Significant differences between bars are indicated by an asterisk.

less time in shelter, 11.0 ± 1.8 h, than lower ranking crayfish (ANOVA, Fisher LSD, $F_{(9,36)} = 21.91$, $p < 0.05$; Figure 4). Intermediate ranked crayfish spent a mean 14.3 ± 1.1 h to 15.2 ± 0.8 h in shelter and did not differ significantly from each other (ANOVA, Fisher LSD, $F_{(9,36)} = 2.35$, $p = 0.83$). Rank 5 subordinate crayfish spent significantly more time in shelter, 18.0 ± 0.4 h, than all higher ranking crayfish (ANOVA, Fisher LSD, $F_{(9,36)} = 18.56$, $p < 0.05$; Figure 4).

Experiment 2: Shelter use and feeding in the absence of conspecifics

Crayfish across treatments exhibited significant differences in the amount of time spent in shelter, out of shelter, and feeding within home tanks (ANOVA, $F_{(2,38)} = 225.0$, $p < 0.005$; $N = 20$). Crayfish generally spent more than 50% of the time out of shelter and under 5% at the feeding area (Figure 5). Behavioural differences were observed between status treatments over three nights of observation; however, dominant shelter use appears to contradict behaviour observed in experiment 1. Dominant crayfish spent more time in shelter (47.7%) than either control (28.5%) or subordinate crayfish (25.8%) (ANOVA, Fisher LSD; $p < 0.005$) (Figure 5). Control and subordinate crayfish did not differ. Comparing treatments for proportion of time spent out of shelter showed dominant crayfish spent less time out (57.4%) than subordinate crayfish (72.9%) ($p < 0.05$), while control crayfish did not differ significantly compared with either treatment (70.0%) ($p = 0.13$ compared

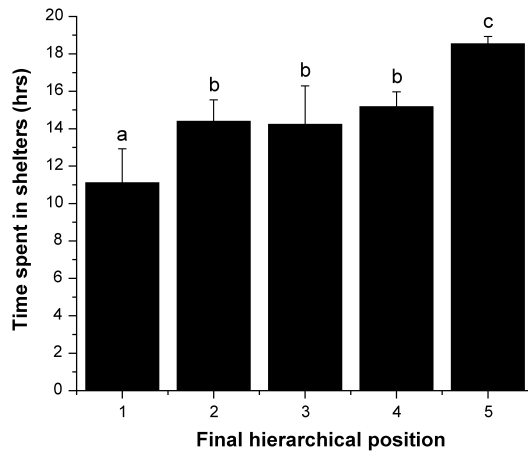


Figure 4. Mean (\pm SE) number of hours that crayfish of differing social ranks spent in shelter over a 96-h period. Represented ranks were calculated at the end of 96 h. Rank is in descending order with '1' indicating most dominant. Bars with the same letter are not significantly different ($N = 10$, ANOVA; $p < 0.05$).

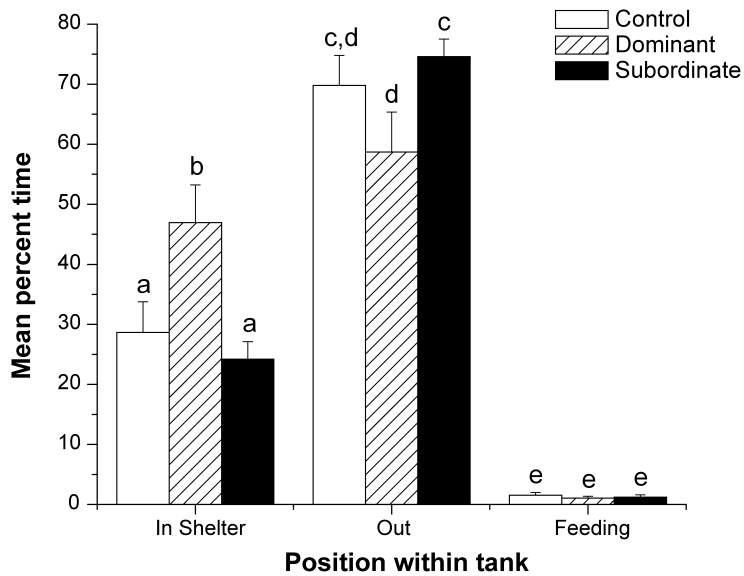


Figure 5. Mean (\pm SE) percentage of time crayfish spent either in or out of the shelter, or feeding. White bars represent naïve control, hatched bars represent conditioned dominant, and black bars represent conditioned subordinate treatments. Arcsine transformation of percentages were performed for ANOVA and LSD post-hoc test ($N = 20$). Bars with the same letter are not significantly different ($p < 0.05$).

with dominant; $p = 0.64$ compared with subordinate). Proportion of time at the feeding area did not differ across status treatments ($p > 0.05$). Neither trial day (ANOVA, Fisher LSD, $F_{(8,92)} = 1.251$, $p = 0.22$) or crayfish size (out of shelter: $p = 0.38$, $r_2 = 0.0121$; in shelter: $p = 0.77$, $r_2 = 0.0013$; no regression was run for food) was correlated with the behaviour of status treatments.

Experiment 3: Shelter use and reproductive opportunity

Male shelter use

Males across trials spent an average of 23.19 ± 3.66 hr occupying shelter over the 96-h period ($N = 30$). Overall, time in shelter was not correlated with male DAI ($p = 0.7547$, $r_2 = 0.0035$; Table 1) but was positively correlated with male size (carapace: $p < 0.005$, $r_2 = 0.2924$; chelae: $p < 0.005$, $r_2 = 0.2790$; Table 1). DAI was not correlated with the small variations in size between males within the same trial (carapace: $p = 0.3405$, chelae: $p = 0.2619$) demonstrating the efficiency of the size-matching.

Table 1. Comparisons between observed behaviors, crayfish dominance activity index (DAI), and size (males: $N = 30$; females: $N = 80$).

	Male DAI	Male carapace length across trials	Male chelae length across trials	Female-male size difference
# of mating events	$p = 0.2738$ $r^2 = 0.0426$	$p = 0.2091$ $r^2 = 0.0557$	$p = 0.4594$ $r^2 = 0.0197$	$p < 0.01$ $r^2 = 0.0885$
Total t spent mating	$p = 0.4417$ $r^2 = 0.0213$	$p = 0.1970$ $r^2 = 0.0587$	$p = 0.1640$ $r^2 = 0.0680$	$p < 0.01$ $r^2 = 0.0837$
# of mates/hr	$p = 0.6470$ $r^2 = 0.0076$	$p = 0.9557$ $r^2 = 0.0001$	$p = 0.5757$ $r^2 = 0.0113$	—
% t spent mating	$p = 0.7555$ $r^2 = 0.0035$	$p < 0.05$ $r^2 = 0.1704$	$p < 0.05$ $r^2 = 0.1645$	—
Mean t per mating event	$p = 0.5346$ $r^2 = 0.0139$	—	—	—
t in shelter	$p = 0.7547$ $r^2 = 0.0035$	$p < 0.005$ $r^2 = 0.2924$	$p < 0.005$ $r^2 = 0.2790$	—

Male reproductive opportunities

Male DAI was not correlated with the number of mating events that a male participated in (4.57 ± 0.44), the total amount of time a male spent mating (5.35 ± 0.66 h), the percent time spent mating ($0.08 \pm 0.01\%$), the mean time spent per mating event (1.22 ± 0.21 h), and mating frequency (matings per hour) (0.07 ± 0.01) ($N = 30$). Results are summarized in Table 1. Male size, across trials, was negatively correlated with the percent time that males spent mating (carapace: $p < 0.05$, $r_2 = 0.1704$; chelae: $p < 0.05$, $r_2 = 0.1645$; Table 1). Male size was not correlated with other observed mating behaviours (results summarized in Table 1).

Female reproductive opportunities

Females across trials participated in an average 1.71 ± 0.19 mating events, each lasting 1.22 ± 0.21 h, and spent a total 2.00 ± 0.31 h mating ($N = 80$). Female size (carapace length) was not correlated with time spent mating ($p = 0.0547$, $r_2 = 0.0465$), number of mating events ($p = 0.2765$, $r_2 = 0.0152$), or mean time spent per mating event ($p = 0.1943$, $r_2 = 0.0215$). However, female-male size ratio turned out to be the most predictive of whether mating would occur. The closer in size a female was to the size-matched males in her trial, the more mating events she participated in ($p < 0.01$, $r_2 = 0.0885$; Table 1) and the more total time she spent mating ($p < 0.01$, $r_2 = 0.0837$; Table 1).

Discussion

Overall, our study demonstrates that dominance in crayfish correlates with shelter use but not with feeding or mating. This is a surprising result given current views on the role of dominance and aggression in many animal systems (Wilson, 1975). Both feeding and mating are behaviours that are heavily associated with the health and fitness of individuals, yet we find no indication that dominance confers an advantage with respect to these behaviours. Likelihood of mating in crayfish may instead be more dependent upon biomechanical factors involved in mating. Shelter use, however, is affected by dominance and in addition, we find variable behavioural responses of dominants and subordinates depending on the social context. Such responses may represent particular behavioural strategies or motivations that arise in different situations.

Feeding

When conspecifics are not present, crayfish spend the same amount of time feeding independent of dominance status (Figure 5). Thus, we find no indication that hunger state or some other motivating factor involved in feeding is altered by previous social interactions. Differential feeding success in crayfish would therefore be more attributable to direct competition for food resources. Bergman & Moore (2003) found that under natural conditions, when resources are patchily distributed, agonistic interactions occur more frequently on food patches. Whether dominant crayfish obtained increased access to food patches was undetermined. In our experiment, food was abundant and there was no competition; dominance may only impact feeding behaviour when food is limited and defensible.

Mating opportunities

Dominance in many animal systems confers increased reproductive opportunity (Clutton-Brock et al., 1979) yet we found no correlation between mating and dominance in mixed sex populations of *O. rusticus* (Table 1). Much like food resources, dominance may only confer a mating advantage when females are limiting. In our experiment, females were abundant and were all in reproductive state. Although dominant males did not acquire increased access to females, we cannot conclude that dominance does not correlate with differential reproductive success as sperm deposition and fertilization were unobservable.

We did observe a correlation between mating and crayfish size (both carapace and chelae length), independent of dominance. Overall, larger males spent a smaller proportion of time mating and the most mating occurred between males and females of similar size (Table 1). A possible interpretation is that considerable size differences between males and females impose constraints on successful handling of females. Larger chelae are thought to confer an advantage to males in controlling females during mounting (Stein, 1976) and larger females are often more fecund (Rahman et al., 2004). Relative fecundity may then produce a preference in males to approach females that are as large as possible that the male can successfully handle. The trend we observed, in which smaller males spent a higher percent of the time mating (Table 1), may have resulted from smaller average female size (refer to exp. 3; experimental protocol). It would be necessary to determine if males

had less success seizing or mounting females that differed considerably in size.

Shelter

As an ecological resource for crayfish, shelter plays an important role in providing protection from predators and conspecifics during different phases of their life cycle (Gherardi, 2002). As predicted, shelter occupancy was found to correlate with dominance but only in experiments one and two. No effects of dominance were observed in experiment three. An additional finding is that status specific shelter use appears to vary depending on the social context presented in each experiment. In male populations, dominant crayfish spent less time in shelter (Figure 4), whereas when dominant males were alone, shelter use increased relative to other statuses (Figure 5). When females are present in a population, no differential shelter use exists between ranks (Table 1). By altering group composition and presence of direct versus indirect social interactions, we altered the social context under which shelters were used. Behavioural choices regarding shelter use were subsequently altered. We hypothesize that this variable affect of dominance on shelter use is due to changes in the underlying behavioural motivations that arise in different social contexts.

Motivation to use shelter may be influenced by causal factors such as sensory information concerning shelter quality, perception of a threat (predator), reproductive state, degree of shelter competition, etc. (Eggleston & Lipcius, 1992; Alberstadt et al., 1995). Interactions between these factors determine how shelter use behaviour manifests itself. In these three experiments, reproductive state and resource quality (e.g., shelter type, resource abundance, etc.) were the same for all crayfish, whereas individual social status and the social interactions crayfish were exposed to (e.g., in population versus alone) varied. Underlying causal factors motivating shelter use appeared to change due to the interaction between dominance status and the social context of the experiment. These behavioural differences across status/rank may be attributed to changes in crayfish physiological state that are apparent at the onset of dominance establishment (neurology: Edwards & Kravitz, 1997; excretion: Schneider et al., 2001; metabolism: Schapker et al., 2002), or they may be due to the use of different strategies in different situations.

The males in experiment 1 appear to invest more time towards status reinforcement and may consequently exhibit reduced time in shelter (Figures 3).

Males that are alone have no need to reinforce status thus motivating factors to use shelter may have been altered. Since conspecifics were absent and differential shelter use is still observed, these differences must be due to causal factors that were affected by previous social interactions. Dominant crayfish may have increased relative shelter use when conspecifics were absent as a result of lack of competition for shelter or decreased need to reinforce status. Other evidence of shifting motivation to possess shelter has been found in female crayfish where ovigerous females will defend shelter more intensely than females without young (Peeke et al., 1995). Males of all ranks were similarly motivated to use shelter when females were present. While shelter is necessary for mate acquisition and defence in some decapod crustaceans (Rahman et al., 2004), this is not the case for crayfish species. Females acquire shelters on their own when extruding eggs and have been found to be able to defend shelter from male and female intruders (Peeke et al., 1995). Shelter possession by males does not appear to apply an advantage towards acquiring mating opportunities. Worth noting is a correlation between body size and shelter occupancy when data were examined across trials in experiment three. Larger males may have spent more time in shelter due to different preferences for shelter size. Explanations for the observed size affect on shelter use remain speculative.

Hierarchy formation

The hierarchy formation observed in experiments 1 & 3 was congruent with typical formation in laboratory crayfish populations (Goessman et al., 2000), being characterized by high frequency and high intensity agonistic interactions when individuals were first introduced, followed by declining agonism as ranks were established (Figures 1 & 2). It is worth noting that the process of hierarchy formation itself may certainly lend insight into how differential resource use arises. As agonism changes during rank establishment, individual resource use may also change. Examining differential resource use at different points of time during the course of hierarchy formation should be examined in future studies.

Conclusions

Our results characterize an animal system that does not adhere to conventional predictions concerning the consequences of social dominance. We find

no apparent consequences of social interactions on feeding or mating, two primary behaviours impacting fitness. In contrast, social interactions do affect shelter use, thus shelter may be closely associated with aggression and individual fitness. These findings highlight the importance of social history and social context as factors in behavioural strategies and motivation in crayfish. This should be taken into account in future studies that attempt to extrapolate fitness consequences in nature. Crayfish live in a variety of habitats, are highly mobile, and experience seasonal changes in food and mate availability (Berrill & Arsenault, 1982; Gherardi, 2002; Light, 2003). We expect to see resource use manifest itself in nature as in our experiments given similar conditions. We predict that the addition of predation pressures and low resource availability or patchiness would alter crayfish resource use but our experiments indicate that crayfish with differing social histories will react to these changes in different ways. Future studies should examine under which conditions dominance may impact feeding and mating and whether differential resource use results in differential reproductive success.

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