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Social spacing of crayfish in natural habitats: what role does dominance play?

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Abstract We examined the impact of dominance on crayfish social spacing and resource control. Spatial distributions of individual crayfish, *Orconectes propinquus*, were recorded from five sample sites in Douglas Lake, MI, USA. Crayfish populations from each site were collected and then immediately transferred to artificial ponds in order to reproduce potential dominance hierarchies. After 15 h of observation in the artificial ponds, hierarchies were found to stabilize and dominance for each crayfish was scored based on the percentage of total fights an individual won. These dominance scores were then regressed against nearest neighbor distance obtained from field data, crayfish size, and shelter evictions observed during hierarchy formation. Dominant crayfish were found to have greater nearest neighbor distances than lower ranking crayfish. In addition, as the difference in dominance score between nearest neighbors increased, the distance between them also increased. Although claw size was an accurate predictor of dominance, size did not correlate with nearest neighbor distance. Factors such as social dynamics may thus play a larger role in natural crayfish populations than previously thought. Dominant crayfish also performed more shelter evictions during hierarchy formation, which were correlated with nearest neighbor distance, suggesting that eviction by dominant crayfish may enforce spacing. Social status appears to significantly impact crayfish spatial distribution and shelter acquisition such that more dominant crayfish exhibit increased control over space and shelter. Finally, this study suggests the possibility that stable crayfish dominance hierarchies exist in nature.

Keywords Crayfish · Nearest neighbor · Dominance · Hierarchy · Shelter

Introduction

The manner in which animals are distributed relative to conspecifics often represents a trade-off between the costs and benefits of proximity. The benefits of closer spacing may include increased protection from predators ("selfish herd": Hamilton 1971; Treisman 1975) and increased foraging efficiency (Beauchamp 1998). Conversely, these benefits may be offset by the costs incurred through increased competition for resources (Amano et al. 2006) and the risks of conspecific aggression (Alexander 1974). These costs and benefits arise from and are modulated by various environmental and behavioral factors. Specifically, environmental factors such as resource availability, dictate habitat choice and where animals will aggregate. Resource availability can vary temporally (Weir and Grant 2004), spatially (Grant 1993), with competitor-to-resource ratio (Noel et al. 2005), or change in response to population density (Mares et al. 1982). Behavioral factors, such as species specific individual distances (Hediger 1955), social cues (Webster and Hart 2006), conspecific aggression including distances imposed by territorial behavior (Maher and Lott 1995), and social dominance (Hemelrijk 2000), may further impose constraints on how animals are spaced relative to one another. The interaction of all of these factors ultimately defines the consequences that spacing has

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for individual fitness. Identifying the factors and interactions that have the most influence in determining social spacing in a given animal system may lend insight into the selection pressures on different suites of behavior.

When resources are limited or economically defensible, competitive interactions play a significant role in spacing (Grant 1993). Habitat complexity and the degree to which food resources are clumped have a significant impact on the frequency and intensity of aggressive interactions (Jensen et al. 2005). Aggressive animals that group with regard to resource distribution consequently experience higher encounter rates and thus increased levels of aggression. At intermediate levels of competitor-to-resource ratio, aggression is highest at that point when resource patches are the most economically defensible (Noel et al. 2005). The presence of territories may modulate aggression within these groups. Maher and Lott (1995) define a territory as “a fixed space from which an individual or group of mutually tolerant individuals, actively excludes competitors from a specific resource or resources.” Actively defended territory boundaries and the factors that affect territory size and shape, such as resource availability and population density, may create observed spatial distributions of conspecifics (Adams 2001).

In animal systems that are characterized by social dominance, dominant individuals (i.e., those that are consistently successful in agonistic contests) are predicted to control preferred territories and/or spatial positions. Dominants have been shown to inhabit preferred spatial positions within a group (Hall and Fedigan 1997; Herrera and Macdonald 1993); however, this spatial pattern may result from avoidance by other group members rather than interference competition (Hall and Fedigan 1997). When food resources are abundant, subordinate animals may need to travel further from dominant ones as a result of socially mediated foraging (Rands et al. 2006). In convict cichlids, dominance impacts territory size and the use of defended refuges (Hamilton 2004). Additionally, different factors affecting the decision to engage in or retreat from agonistic interactions may produce unique spatial patterns with regard to social status (Hemelrijk 2000). Examining spatial distributions that result from dominance interactions may reveal whether dominance functions to confer control over resources or to decrease aggression within a population (Drews 1993; Hemelrijk 2000).

Crayfish are aggressive animals that exhibit ritualized agonistic behavior and form sustained dominance relationships (Dingle 1983). Extensive research has elucidated many aspects of the neural basis of aggression, as well as the behavioral ecology of aggression in crayfish (Bergman and Moore 2003; Bovbjerg 1970; Edwards and Kravitz 1997; Edwards et al. 2003; Hazlett et al. 1992). However, the degree to which crayfish aggression and social dominance function in the acquisition and control over resources and ultimately impact individual fitness in natural contexts remains unclear. In crayfish, dominance has been shown to increase access to shelter resources in the laboratory (Gherardi and Daniels 2004; Klocker and Strayer 2004) and resource holding potential (RHP; Parker 1974) has been correlated with preferred habitat (Garvey and Stein 1993; Statzner et al. 2000). Bergman and Moore (2003) demonstrated that the intensity of crayfish agonistic interactions was influenced by perceived resource quality. Resource quality and the context in which resources are presented may also impact whether dominant crayfish monopolize resources (Fero et al. 2007; Hill and Lodge 1994). Exclusion of subordinates from shelter resources may create patterns of distribution based on status or hierarchy rank. Shelter or burrow use has been found to increase during agonistic competition (Gherardi and Cioni 2004; Edwards et al. 2003), but it remains unclear how individual resource use affects group dynamics and what specific factors motivate the increased use. In addition to shelter, space may be a valuable resource for crayfish as ready access to multiple shelters may facilitate foraging in the presence of predators, may grant exclusive access to valuable food resources, and may attract potential mates.

We investigated social dominance as an underlying mechanism of social spacing of crayfish in natural habitats. We also assessed the likelihood of territoriality as a mechanism for social spacing. The spatial location of individual crayfish in situ was recorded and then dominance was quantified by reconstructing social hierarchies in the lab. Dominant crayfish were predicted to exhibit increased control over space, evidenced by larger nearest neighbor distances (NND). Dominant crayfish, in particular, were predicted to enforce increased individual distance by territorial shelter defense, based on shelter eviction data from the literature (Gherardi and Daniels 2004; Klocker and Strayer 2004). If crayfish distributions within sample sites are correlated with reconstructed hierarchy rank, then social history can affect individual spacing within habitats.

Materials and methods

Study site

Site observations and population sampling were conducted in an area approximately 40 m offshore of Grapevine Point, Douglas Lake at the University of Michigan Biological Station (UMBS), Pellston, MI, USA (45° 33′ N, 84° 40′ W) from July to August 2005 (site number: sample date; 1: 7/14; 2: 7/24; 3: 7/28; 4: 7/30; 5: 8/02). Douglas Lake contains three known species of crayfish: native *Orconectes propinquus*, native *Orconectes virilis*, and invasive *Orconectes rusticus*;

only *O. propinquus* was observed in this section of the lake. Water depth never exceeded 1.5 m. The lake substrate in this area was characterized by sand covered with a mat of blue-green algae and diatoms (approximately 1 cm thick), which was also interspersed with outcroppings of cobble and small boulders and patches of small macrophytes. Crayfish were observed using cobble and eroded substrate for shelter. Five sample sites were then selected based on the presence of available shelter and visual confirmation of crayfish in the area. Due to the nature of the shelter resources at the sampling area, quantifying resource distribution was infeasible as discrete shelters could not be identified. Thus, only sites that possessed abundant potential shelter were selected for sampling. This was also done in order to minimize the effect of resource distribution on crayfish spacing.

Crayfish sampling

Sampling took place during daylight hours, between 1300 and 1900 h, when crayfish activity is relatively low (personal observations; Martin and Moore 2007). Mean daily movements of crayfish (*Austropotamobius pallipes*) have been shown to be less than 5 m per day (Robinson et al. 2000) and movements of *O. virilis* have been shown to be highly variable but most frequently range from 0 to 5 m between capture events (Hazlett et al. 1974). Taken together with observations of abundant shelter and crayfish (crayfish density noted further in this section) at the sample site, we predicted that a 4×4 m area would be of sufficient size to contain individuals that repeatedly interact. Thus, crayfish were collected from 4×4 m square plots in order to sample individuals that likely had preexisting dominance relationships. After a site was selected, a fenced enclosure was used to delineate the site boundaries and avoid the loss of any individuals while collecting. Researchers, in positively buoyant dive suits and snorkels, floated above the site and placed numbered flags by shelters where crayfish were visible. All crayfish were found inhabiting shelters and were collected either by hand or by suction pump, and then immediately placed into individually labeled containers that corresponded with flag numbers. Crayfish spatial distributions within the site were quantified by measuring marked flag locations on an X,Y coordinate system using the NW corner of the site as the origin (0,0). The NW corner was also designated as a global positioning system reference point for each site. Following collection and spatial measurements, researchers then dug into the substrate, turned over cobble, and pumped deep holes ensuring that sites were exhaustively sampled. No crayfish were missed at the five sample sites. All crayfish were immediately transported to the UMBS research facility.

Animals

Upon transport to UMBS, crayfish species (*O. propinquus*) was confirmed and sex, reproductive form, and bodily injuries were recorded. All crayfish possessed intact chelae, walking legs, and sensory appendages. Carapace (from the tip of the rostrum to the end of the cephalothorax) and chelae length were also measured (mean±SE; 2.36±0.04 cm carapace; 1.76±0.07 cm chelae). A total of 53 *O. propinquus* individuals were collected (10.6±1.0 crayfish per site) with a mean density of 0.7 crayfish/m^2 per site. Overall sex ratio was 2:1 (males to females) but varied within the five sites: 1:6, 8:1, 3:1, 1:0, and 1:1, respectively. All males were in reproductive form I and females were in nonreproductive (non-glair) form. Of the 53 collected crayfish, five were juveniles (carapace <1.0 cm) and were subsequently excluded from this study, leaving 48 total crayfish.

Hierarchy reconstruction

Preexisting in situ dominance relationships were reproduced by transferring each sampled population to an artificial pond, housed at UMBS, to allow for hierarchy formation. Each pond consisted of a 2-m diameter plastic-lined wading pool containing lake water, sand, detritus, and 11 halved terra cotta pots, 9 cm in diameter, were used for shelter. The number and distribution of shelters was kept constant across populations in order to control for potential effects of resource availability and distribution on aggressive interactions. Shelter resources were not limited in either the lab or field conditions. Because of the limitations of available space and resolving power of the video equipment used to record crayfish behavior, artificial ponds were decreased in area as compared to the 4×4 m sites from which crayfish were sampled. Crayfish were marked with correction fluid on the back of the carapace or chelae in order to differentiate individuals and were left in the pond for 3 days to allow for hierarchy formation (Fero et al. 2007; Goessmann et al. 2000). All agonistic interactions were video recorded using a mounted security camera (Model# SG2281UQ-A) and a time-lapse video recorder (Samsung SSC-960) set at one frame per 3 s. Red lights (25-W bulbs) were mounted around the perimeter and lit continuously in order to illuminate the pond at night. Ponds were exposed to natural light and temperature regimes. The light–dark cycle for housed populations did not deviate from that of sample sites being approximately 15:9 h light–dark. At the end of the recording period, crayfish were returned to Grapevine Point approximately 500 m away from the sample area to prohibit recollection of any individuals as populations were sampled sequentially over the month of July.

Data analysis

Crayfish dominance and hierarchy stability were determined through analysis of video recordings. Agonistic bouts were analyzed using a standard ethogram adapted for our lab (see Bergman and Moore 2003). Bouts began when crayfish were within one body length of each other and concluded when a retreat was followed by no interaction for 10 s and with more than one body length between opponents (Bergman and Moore 2003). Dominance scores (DS), ranging from 0 (low dominance) to 1 (high dominance), were calculated based on the percentage of agonistic bouts an individual won, both per 5-h intervals and over the total course of analysis. Five-hour interval dominance scores were used to plot hierarchy stability (Fero et al. 2007) and total dominance score was used for all other analyses (Poisbleau et al. 2006). Dominance hierarchies may be considered stable at the point where the change in individual dominance scores decreases appreciably throughout continued interactions (Fero et al. 2007). For this study, we defined stability as the point when mean shifts in dominance score over time decreased to below ±0.015 Δ dominance score/5 h (Fig. 1) and mean DS shifts at each time interval were compared using one-way analysis of variance (ANOVA) with a Tukey honestly significant difference (HSD) post hoc. Additionally, ordinal rank (only alpha, intermediate, and omega ranks) and average total shifts in dominance score over 15 h for each population were compared using a one-way ANOVA with a Tukey HSD post hoc. Intermediate rank was determined by either taking the median DS of a population or by taking the average when two median ranks were present (e.g., populations with an even number of individuals). These three ranks were examined in order to analyze the timing of hierarchy formation in the present study with previous work. Once we had established a criterion for hierarchy stability, all crayfish within a population were used in the subsequent analysis involving nearest neighbor distance. When hierarchies reached stability, video analysis of agonistic interactions was concluded. To determine whether dominant crayfish actively defend shelters and surrounding areas, the number of shelter evictions that crayfish performed was also quantified during hierarchy formation. Shelter evictions occurred when the approach of a crayfish into a shelter was immediately followed by the retreat of the shelter resident.

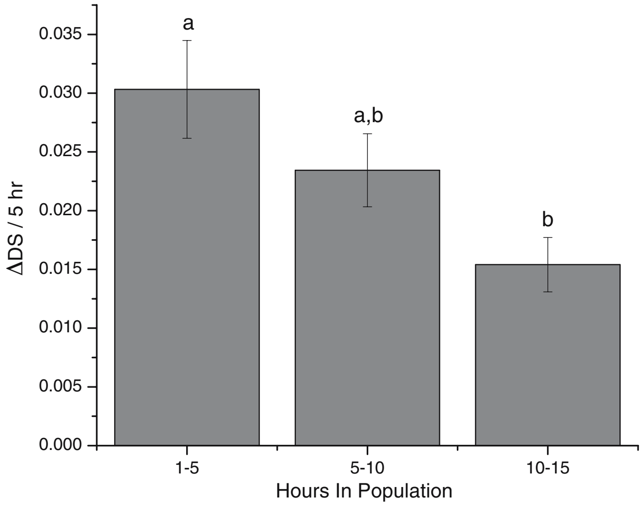

Fig. 1 Mean shifts (±SE) in dominance score over 5-h intervals while in population (n=48). The shift in dominance is calculated as (dominance score at t−dominance score at $t-1$)/time. Hierarchies were considered stable when mean shifts in dominance score over time decreased to ±0.015 Δ DS/5 h, which occurred by the 15th hour. Differing *letters* above *bars* indicate statistical significance (ANOVA; P=0.004)

From the spatial data obtained at collection sites, nearest neighbor distances were calculated for each individual and subsequently used as our measure of social spacing. Nearest neighbors were identified for each individual by the shortest distance between one crayfish and the next (hence forth referred to as “nearest neighbor distance”). The difference in dominance scores between nearest neighbors was also calculated ($|DS_{Individual}-DS_{Neighbor}|$). Linear regression was used to examine the relationships between dominance score, chelae length, shelter eviction, and nearest neighbor distance. Neither sample site nor crayfish sex were significant predicting factors in the spatial analysis (NND×site×DS: $F_{2,\ 45}$=5.51, P=0.007; site beta=0.01, P=0.94; DS beta=0.44, P=0.002), (NND × sex × DS: $F_{2,\ 45}$=5.96, P=0.005; sex beta=0.13, P=0.39; DS beta=0.49, P=0.002); therefore, data from all five populations were pooled for statistical analysis (n=48). All statistical tests were performed using Statistica ver. 6.0.

Results

Hierarchy stabilization

Hierarchies of sampled populations stabilized when mean shifts in dominance score decreased to below ±0.015 Δ DS/5 h (Fig. 1). Dominance shifts at 5 h were significantly higher than shifts at 15 h (ANOVA; n=48, $F_{2,\ 137}$=5.27, P=0.004), at which point behavioral analysis was concluded. Ordinally ranked alpha (mean DS±SE=0.99±0.002), intermediate (0.37±0.05), and omega individuals (0.09±0.03) from each of the five populations significantly differed in the sum of dominance shifts each individual experienced (ANOVA; n=5, $F_{2,\ 12}$=0.69, P=0.01; Fig. 2). Alpha individuals experienced significantly smaller magnitudes of dominance shifts, 0.09±0.05, than did intermediately ranked individuals, 0.80±0.21 (P=0.008). Omega dominance shifts (0.37±0.10) did not differ from alpha or intermediate ranks

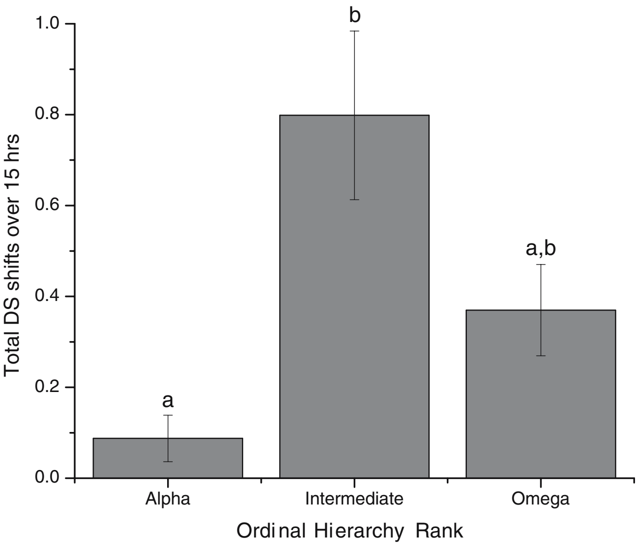

Fig. 2 Mean of total shifts (±SE) in dominance score over 15 h for three different hierarchy ranks in each population (n=5). 'Alpha' refers to the most dominant crayfish in a hierarchy. 'Intermediate' refers to the crayfish with the median dominance score. 'Omega' refers to the least dominant (i.e., most subordinate) crayfish. Differing *letters* above the *bars* indicate statistical significance (ANOVA; P=0.01)

(P=0.34 and P=0.11, respectively). Dominance hierarchies in this study stabilized rapidly relative to previous crayfish studies (Fero et al. 2007; Goessmann et al. 2000); therefore, video was not analyzed for the entire 3-day recording period.

Spatial distribution and dominance

Nearest neighbor distances in field sites (mean±SE; 68.7± 2.0 cm) were significantly greater for crayfish that acquired higher DS in reconstructed hierarchies (R^2=0.19, $F_{1,\ 4}$= 11.25, P=0.002). Thus, we found that dominance is correlated with increased space between individuals. Additionally, the difference between dominance scores of nearest neighbor pairs was positively correlated with the distance between them (R^2=0.08, P=0.05). Not only is dominance correlated with increased space, but the relative dominance between two individuals is also correlated with space; the larger the difference in dominance, the greater the distance between individuals. Chelae size accurately predicted dominance (R^2=0.50, P<0.0001) but size did not predict nearest neighbor distance (R^2=0.01, P=0.59). Thus, the effect of dominance on nearest neighbor distance is not attributable to size alone. These results are summarized in Table 1.

Shelter eviction

Shelter eviction behavior varied considerably across individual crayfish. The total number of evictions an individual performed ranged from 0 to 17 (2.6±0.5) during the 15-h observation period. Fifteen crayfish did not perform any evictions, while only three crayfish performed ten or higher. Overall, we found that the number of evictions that crayfish performed increased with higher dominance scores (R^2=0.48, P<0.0001) as well as with nearest neighbor distance (R^2=0.19, P=0.002; Table 1). As dominance increases, crayfish perform more evictions and evictions are also independently correlated with the amount of space between nearest neighbor pairs.

Discussion

This study demonstrates that crayfish social status significantly impacts the spatial distribution of individuals in nature. Crayfish that were dominant had greater nearest neighbor distances within the field sites (Table 1). In addition, as the difference in dominance score between nearest neighbors increased, the distance between neighbors also increased, further indicating a correlation between dominance and social spacing. Dominant crayfish also performed significantly more shelter evictions during hierarchy formation and eviction rate predicted nearest neighbor distance (Table 1). Crayfish size did not significantly impact spatial distribution, even though size significantly predicted individual dominance score (Table 1). Social status appears to have a significant impact on crayfish spatial distribution and shelter acquisition such that dominant crayfish may possess increased control over space and shelter. Finally, the observed correlations

Table 1 Results of linear regressions between dominance score (DS), difference in DS between an individual and its nearest neighbor ($|\mathrm{DS}_{\mathbf{Individual}}-\mathrm{DS}_{\mathbf{Neighbor}}|$ =absolute difference in DS), number of shelter evictions performed, chelae length (cm), and nearest neighbor distance (cm; n=48)

	Factors	$F_{1,\ 46}$	R^2	P
Nearest neighbor distance (cm)	DS	11.2518	0.1965	0.0016
	$\lvert \mathrm{DS}_{\mathrm{Individual}}-\mathrm{DS}_{\mathrm{Neighbor}} \rvert$	4.2517	0.0846	0.0448
	Evictions performed	10.7730	0.1898	0.0019
	Chelae length (cm)	0.2948	0.0064	0.5897
Dominance score	Evictions performed	40.6654	0.4692	<0.0001
	Chelae length (cm)	45.8722	0.4993	<0.0001

between data from reconstructed hierarchies and field spatial data suggest the possibility that stable crayfish dominance hierarchies exist in nature.

These results indicate that dominant crayfish are better able to exclude other individuals from shelter resources. In turn, less dominant crayfish may disperse away following eviction shelters in order to avoid continued aggression from dominants or to find accessible resources. Computer modeling of such behavioral strategies has produced spatial patterns that resemble the pattern measured in this study. Hemelrijk's (2000) "risk-sensitive" and "obligate attack" strategies both outline patterns of behavior where aggression in a population subsequently decreases as a result of subordinate dispersal away from dominants. The "obligate attack" strategy, in particular, is one where the goal of the action is to acquire dominance rank. Strategies that aim to reduce aggression, such as the "ambiguity reducing" strategy, produce spatial structures where individuals of disparate social rank are closer together than those that are of similar rank. Our results suggest that crayfish use behavioral strategies to increase dominance rank, in addition to gaining knowledge of the fighting abilities of others. Additionally, the correlation between shorter neighbor distance and smaller difference in neighbor social status may reflect that these individuals are less able to defend space as the dominance relationships are more tenuous; in other words, the probability of a dominance reversal increases when individuals are close in hierarchy rank (Pagel and Dawkins 1997).

In crayfish, size (carapace and chelae length) is one of many intrinsic and extrinsic factors that determines or reinforces crayfish social status (Moore and Bergman 2005; Pavey and Fielder 1996; Ranta and Lindstrom 1992). The observed effect of dominance on nearest neighbor distance may be attributable to increased space requirements for large crayfish or size-dependent spacing, rather than size-dependent dominance. Size-dependent spatial distribution has been documented as a reflection of RHP-based decisions to engage in agonistic interactions (Hemelrijk and Kunz 2005) and of the ability of larger males to monopolize females, along with their home ranges (Haenel et al. 2003). Even though size was significantly correlated with dominance in reconstructed hierarchies, behavioral strategies such as size-dependent "risk avoidance" (Hemelrijk and Kunz 2005) may be excluded as crayfish size did not correlate with social spacing.

Shelter ownership is another factor that may contribute to social status in crayfish (Gherardi and Daniels 2004). Shelter eviction by more dominant crayfish may be indicative of territorial behavior or some other mode of competition for space which enforces nearest neighbor distance. We are unable to derive any definitive conclusions concerning crayfish territoriality in this study as resource distribution (shelter and food) was not quantified.

The fact that dominance correlated with spacing but size did not indicates that social dynamics (e.g., winner–loser effects and bystander effects; Chase et al. 2002; Dugatkin 2001) may have greatly contributed to the outcome of dominance interactions in the field. In contrast with many studies examining crayfish hierarchy formation (Fero et al. 2007; Goessmann et al. 2000; Issa et al. 1999), sample site populations in this study exhibited strong asymmetries in RHP (Parker 1974), mainly in terms of size and sex of individuals (refer to "Materials and methods"). Hierarchies, where all individuals possess similar RHP, arise primarily by social dynamics that are stochastic in nature and are not reproducible (Chase et al. 2002). In nature, RHP differs greatly between individuals and resulting social dynamics may build upon these RHP differences in a predictable manner. For example, early winning experiences by larger crayfish may instill strong winner and loser effects, causing hierarchies to differentiate rapidly (Hock and Huber 2006; Hsu et al. 2006). The results from the present study suggest that crayfish, *O. propinquus*, maintain stable and reproducible hierarchies in nature.

Ultimately, dominance in crayfish appears to confer increased control over space as demonstrated by the correlations found between dominance, territorial behavior, and social spacing. Consequently, dominant crayfish may acquire increased access to shelter and food resources. Examining crayfish social dominance has yielded many insights into the neural basis of aggression (Edwards et al. 2003). This study provides an evolutionary context for such insights by revealing potential selection pressures that shape the formation and maintenance of dominance relationships. Future studies should examine factors such as social context, space use, and resource distribution in concert to further elucidate what resource advantage dominance yields for crayfish.

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