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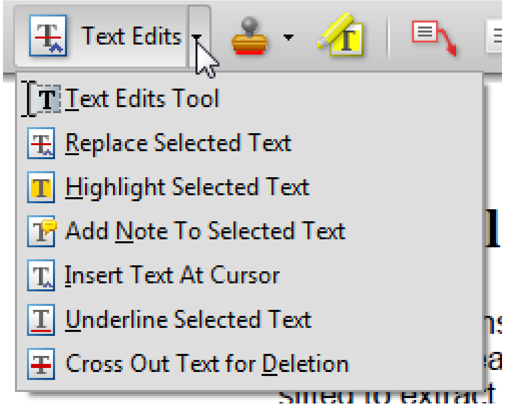

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Spatial structure of hierarchical groups: testing for processes of aggregation, clustering, and spatial centrality in crayfish (*Orconectes rusticus*)

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Competing group members tend to arrange in a social order that governs who will likely submit to whom. In many species the spatial distribution of individuals often reflects social status: dominants tend to occupy central locations while subordinates are often found along the group's periphery. This article explores the emergence of spatial consequences as a result of social rank differentiation. Rather than orienting centripetally, the movements of crayfish (*Orconectes rusticus*) primarily indicated a tendency to remain close to arena walls. Spatial locations were affected by the location of group members; but, rather than actively aggregating or clustering, individuals maintained a minimum distance. Previously established social rank did not affect spatial distributions. High population densities in the field are likely attributed to habitat constraints, rather than any social or centripetal tendencies of individual crayfish.

Keywords: crayfish; *Orconectes rusticus*; group organization; aggregation; centrality; Selfish Herd; dominance hierarchy; wall following

Introduction

Favorable local conditions and high-value resources tend to attract scores of individuals ready and willing to compete for access to those resources. The formation of stable dominance hierarchies is thought to reduce the amount of day-to-day fighting necessary to negotiate access to these resources. An individual rapidly decides whether to challenge an opponent based on information from past agonistic encounters. The resulting social structure, represented by a matrix of each individual's decisions to submit to a particular opponent, forms as the collective result of repeated dyadic agonistic encounters among group members (Francis 1988; Drews 1993). Subordinates begin to retreat from dominants with little or no physical contest giving rise to conspicuous and lasting polarities in the outcomes of future agonistic encounters (Drews 1993). The losing individual is likely displaced from the site, resulting in its spatial exclusion from contested resources

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(Greenberg and Crews 1990; Krause 1994; Hall and Fedigan 1997) or in enhanced dispersal (Ellsworth and Belthoff 1999) and territorial displays (Wiley et al. 1993). Conversely, high social rank endows its bearer with a range of benefits that include reduced danger from predation (O'Neill and Cobb 1979; Ranta and Lindström 1992, 1993), increased feeding rates (Tilson and Hamilton 1984; Alanärä et al. 1998), increased growth and development (Phillips et al. 1993), and mating success (Post 1992; Choe 1994; Hirotani 1994).

Conspecifics competing with each other under crowded conditions must balance conflicting tendencies of aggregation and dispersion, navigate the benefits and risks of proximity to neighbors, negotiate the social demands of aggression, and adopt behavioral decisions that allow them to successfully navigate this social group structure (Hemelrijk 2000).

A number of models have advanced potential mechanisms through which social hierarchical structuring may produce a distinct spatial organization. Enhanced aggregation may arise from a basic tendency of individuals to place themselves toward the geometrical center of a group, as predicted by the Selfish Herd model (Hamilton 1971). This centripetal behavior is based on a presumed increase in predation risk toward the edges of the group. With superior competitive abilities, dominants are better able to attain and defend these "safer" central locations, resulting in a radial gradient of decreasing dominance from center to periphery. Alternatively, a more general bias for individuals to aggregate has been proposed by Hemelrijk's (1998, 1999, 2000) DomWorld simulations. In this model, an animal finding itself distanced from the group will attempt to rejoin it. In a refinement of the MIRROR model (Hogeweg 1988), spatial centrality of dominants results as a simple consequence of social interactions. In this scenario, robust spatial patterns emerged without the explicit need for any inherent positional preference of individuals toward the group center. Spatial distributions simply arose through self-structuring (i.e. self-organization): spatial structure emerges as an individual's tendency to remain close to others is counterbalanced with its tendency to retreat from more dominant individuals.

With natural population densities often exceeding densities of 50 individuals m^{-2} (Davis and Huber 2007), the species of crayfish studied in this article offers a rich environment in which to explore the social context of agonistic interactions in a larger group setting. Individuals readily form dyadic dominance relationships through series of paired encounters (Huber et al. 2001), where social relationships coalesce into largely linear hierarchies (Issa et al. 1999) in both the laboratory (Copp 1986; Goessmann et al. 2000) and the field (Bovbjerg 1953, 1956; Davis and Huber 2007; Fero and Moore 2008). Subordinate crayfish avoid confrontations by retreating from the immediate vicinity of dominants (Huber et al. 2001). However, it is unclear whether a tendency to aggregate and move toward conspecifics exists. While socially naïve crayfish readily engage their opponents in agonistic interactions even in the absence of resources or landscape features (Issa et al. 1999; Huber et al. 2001), it is not clear whether individuals actively seek such confrontations or even simple proximity to conspecifics (aside from potential cannibalistic tendencies; cf. Adams and Moore 2003). Moreover, it is not apparent whether such alternating decisions to interact and retreat will result in a centric distribution of individuals according to rank. High population densities reported in the field (Davis and Huber 2007) may thus simply stem from a high carrying capacity within a constrained habitat, while tendencies to associate with conspecifics may contribute to such crowded conditions.

This article explores an individual's spatial choices and movement patterns in relation to its decisions to engage in or retreat from agonistic encounters. Toward this goal, we tracked the spatial distribution of individuals in order (1) to characterize the effects of social rank on movement patterns relative to other group members and (2) to explore whether spatial patterns emerge that reflect the social status of individuals (e.g. through centripetal tendencies). This study extends a study of social relations in crayfish by providing an explicit spatial context for such encounters.

Materials and methods

Study animals

Adult male crayfish (*Orconectes rusticus*) weighing 4.1–8.0 g were collected from the Portage River, near Bowling Green, OH, USA. Animals were housed in individual opaque plastic containers placed in a tray supplied with filtered, aerated water from a common reservoir kept at 20 ± 1°C. Animals were fed weekly with commercial rabbit food pellets, and maintained on a 16/8 h (light/dark) cycle. All animals were kept in social isolation for at least 1 week prior to experiments. Randomly chosen individuals were examined to insure that they possessed a full complement of intact appendages and showed no signs of an imminent molt. Crayfish were weighed and marked individually by gluing a colored tag onto the dorsal cephalothorax.

Experimental setup

Spatial distributions and movement patterns were obtained in a plexiglass arena ($0.43 \times 0.43\,\mathrm{m}^2$) filled with dechlorinated water to a depth of 100 mm. The bottom of the arena was covered with a layer of gravel. Five groups consisting of five crayfish were selected (<30% maximum weight difference), each group run in its own trial. Individuals in their containers were placed into the arena and allowed to acclimate for 1 hour. The crayfish were then released from their containers into the wider arena and allowed to interact with each other for 24 hours. All groups formed stable, linear dominance hierarchies during this time. Following this 24-hour period, the arena was videotaped from above using a Sony DCR-TR7000 camera for 1 hour to (1) deduce dominance relationships based on dyadic interactions, and to (2) relate it to each individual's utilization of the arena''s space. These 1 h trials were run between 9:00 and 12:00 and timing was such that the weekly feeding did not occur during any part of the experiment.

Determining previously established dominance relations

The identities of initiating and retreating individuals were recorded for each encounter (Huber et al. 2001) and the number of supplants between all pairs of individuals was summarized in the form of a dominance matrix. The matrix obtained for each group was subjected to non-parametric analyses in order to characterize the social relationships within the group. Estimates for the degree of linearity and transitivity (Appleby 1983; deVries 1995), independence of interactions (Hemelrijk 1990a, 1990b), and likelihood of reversals were obtained for each group. Rank of the individuals in the dominance hierarchy of each group was calculated by recording the overall pattern of wins and losses for each individual. Specifically, ordinal ranks were calculated for all members of each group (Theraulaz et al. 1992) with dominance activity indices calculated according to Bartos (1986). While ordinal dominance ranks offer a simple way to compare the ratio of wins and losses, they also sometimes result in ties between individuals who have the same statistics. Such ambiguities in dominance status were resolved using the dominance activity index measure (Bartos 1986) that takes into account the pattern of wins and losses to resolve ties between individuals. All measures were obtained using a set of freeware Java applets (available at http://iEthology.com/). The social profile of individuals distributed in the arena was related to social rank.

Space usage and directionality

For the first 25 min of each trial, one frame at the beginning of each minute was digitized from the video recordings. Within each frame, x- and y-coordinates were obtained for all members of the group using NIH Image (developed at the US National Institutes of Health and available at http://rsb.info.nih.gov/nih-image/). A matrix of geometric distances between all group members, as well as the mean distance of individuals to the group's Euclidian center point, was calculated (Figure 1). Additionally, to account for non-random movement of individuals within the arena, we obtained the relative angle between all sequential moves relative both to the hypothetical center of the group and to the actual center of the experimental arena. This approach was used to distinguish between movements that were directed toward conspecifics and those affected by the arena constraints. To test whether mean movements of animals were significantly directed toward the center of the group, the angles were analyzed using the Rayleigh test for circular uniformity (Mardia and Jupp 2000).

Aggregation, clustering, and spatial centrality

Measures of spatial centrality were derived from (1) the average distance to other group members, and (2) the mean distances to the group's center. Individuals that consistently occupied the center of a group will tend to have lower mean distances to others (and to the group's center) than those pushed to the periphery through agonistic encounters. Within each frame, the distance of every animal to its nearest crayfish neighbor was obtained and summarized with minimum and mean measures. If individuals exhibit a general tendency to approach conspecifics, such as in the Hogeweg/Hemelrijk model, mean and minimum neighbor distances ought to be lower than those obtained by randomly sampling distances from the distribution of all individuals. The mean distance to the Euclidian center of the five individuals in each frame (Figure 1) was used as another measure of spatial proximity. Mean distance to the center should decrease as individuals attempt to remain with or rejoin other group members. A similar result will emerge if individuals actively try to place themselves close to the hypothetical center of the group, analogous to Hamilton's centripetal instinct. Mixed linear model design (JMP software, SAS Institute, NC) was used to test for spatial centrality of dominant individuals, examining the effects of dominance rank on mean and minimum neighbor and mean center distances, while taking into account respective individuals nested within frame and group.

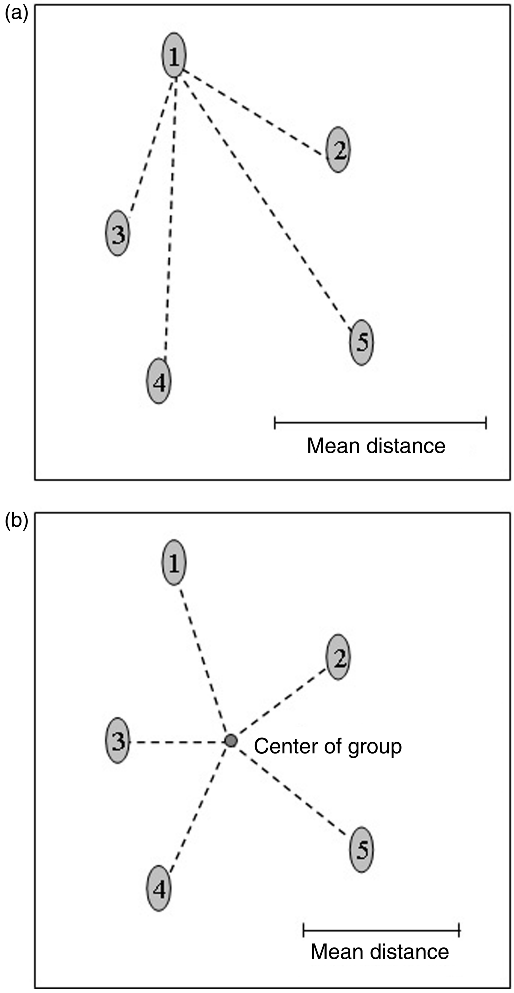

Figure 1. A schematic diagram of a single recorded frame. Within the frame there are five individuals, each marked for identification. (a) Mean and minimum neighbor distances; the distances from each individual to the other four were used to calculate the mean distance between an individual and all the other individuals in the frame, and the value for the nearest neighbor was used to determine minimum neighbor distance. (b) Mean distance to the center of a group; the distances from each individual to the geometric center of the group were used to calculate a mean distance of individuals to the center of the group for each frame. Note that the values for two mean distances (neighbor and center) are not equal in this example.

To determine whether the spatial distribution of crayfish was affected by the presence of other crayfish in the arena, the x- and y-coordinates for each individual within a given trial were randomized to generate null-hypothesis comparisons. Using a randomization approach, probability density functions for measures of mean neighbor and center distances were obtained for each group using Monte Carlo Simulations. A total of 2500 random frames were generated for each group by randomly selecting from a list of actual locations for each individual. If spatial centrality exists, empirical data sets should show significantly smaller mean and minimum distance values than those in the generated data sets. This permutation approach also controls for a crayfish's non-random use of the arena. We used mixed linear models to examine differences in mean center distance between empirical and random measurements while taking into account respective individuals nested within frames and groups.

Results

Dominance

Individuals in all groups were socially embedded within linear dominance hierarchies that formed during the 24-h interaction period. While there was never ambiguity regarding individuals at the highest or second-highest rank, ordinal ranks occasionally showed ambiguity among the lower positions. In cases where two individuals shared the same ordinal rank (Theraulaz et al. 1992), differences in dominance activity index values (Bartos 1986) were used to resolve each individual's relative position in the hierarchy for the purpose of spatial analyses. The interactions from five trials are summarized in Table 1. These results were then used to characterize individuals according to their rank in the hierarchy in spatial analyses.

Directionality of movements

Circular statistics were used to examine whether individuals tended to move toward the center of the group. With all locations included, individuals of all ranks showed directionality toward the group's spatial center (Rayleigh $R = 240.235$, $p < 0.001$; Figure 2a). However, additional analyses indicated that this result is likely an artifact of the arena border's constraints, as individuals located right along the wall cannot further increase their distance to the center. To reduce the effects of this artifact, all captures within 15 mm of the arena wall were dropped from the analysis. After this removal, no remaining significant centrality was evident in any rank (Rayleigh

Table 1. Summary of agonistic interactions that lead to a set of dyadic dominance relationships among group members.

		Losses					
	Rank	1	2	3	4	5	Total
Wins	1		32	21	32	28	113
	2	3		11	13	9	36
	3	1	8		14	13	36
	4	0	5	12		22	39
	5	0	4	3	1		8
	Total	4	49	47	60	72	232

Notes: A total of 232 social interactions were observed across the five trials. The number of wins and losses are grouped according to rank, and represent the cumulative numbers of wins and losses for individuals of a given rank. The upper-right diagonal of the table represents the number of successful attacks initiated by each animal against the other members of the group; the lower-left diagonal of the table represents the number of times each animal retreated from a specific member of the group.

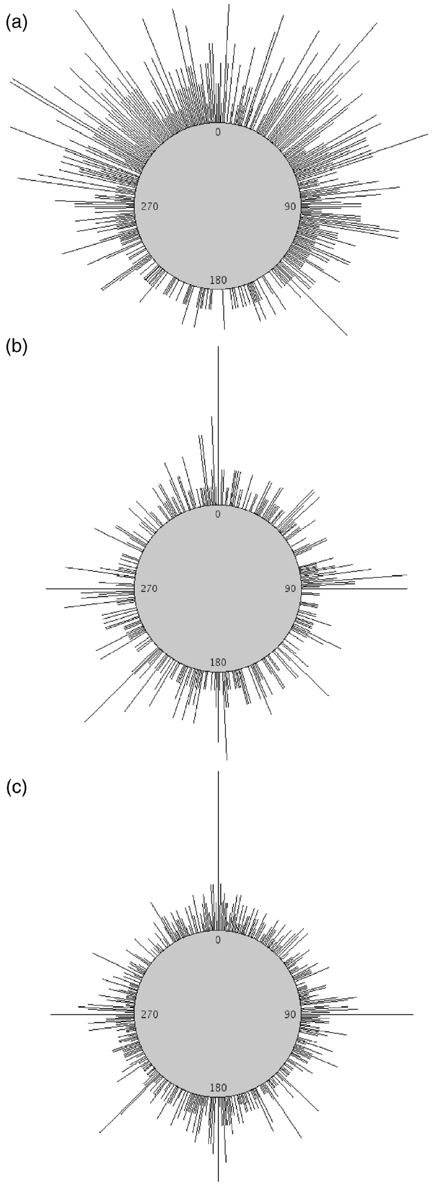

Figure 2. (a) Total movement directions of animals relative to the spatial center of a group. Rays represent the probability of movement at a certain angle from the center of a group. A move directly toward the group center was designated as having a 0° angle. When all movements are taken together, animals appear to significantly move toward the center of the group (i.e. angles <90° and >270° represent centripetal moves). (b) Once movements in close proximity of walls are excluded from the analysis, tendency for centrality disappears, and the proportion of centripetal moves becomes non-significant. (c) Absolute movement directions, i.e. when the movements were analyzed as being relative to the arena orientation rather than relative to the center of a group. In this analysis, a move toward the north of the arena was designated as having a 0° angle. The animals exhibited a pronounced tendency to walk alongside the walls of a rectangular arena (movement directions of 0°, 90°, 180°, and 270°).

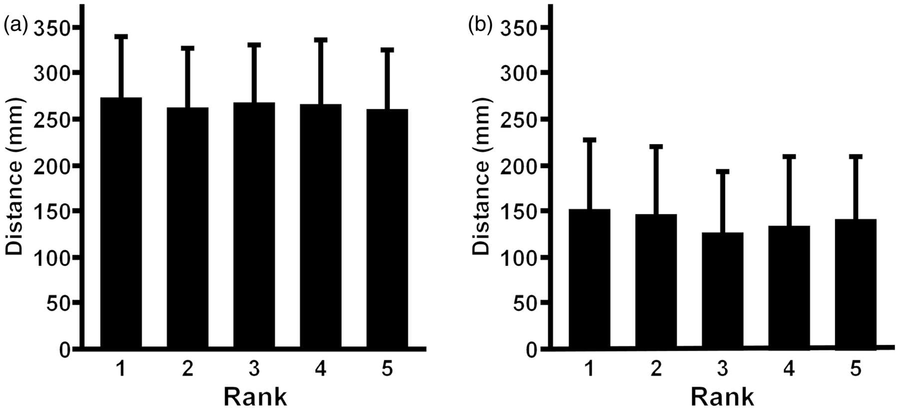

Figure 3. (a) Mean neighbor distances (mm) plotted against rank in the dominance hierarchy for individuals from five trials. (b) Minimum neighbor distances (mm) plotted against rank in the dominance hierarchy for individuals from five trials. When nesting individuals within frame and trial group, neither mean nor minimum neighbor distance significantly influenced by individual's rank. Error bars represent standard deviation from the mean.

$R = 5.674$, $p = 0.918$; Figure 2b). Taking into account the absolute movement directions in relation to a fixed point in the arena, crayfish exhibited movement directions indicative of walking alongside the arena walls (Figure 2c). We conclude that crayfish do not move toward the group center, but rather their movements are primarily affected by a tendency to remain in proximity to the arena walls.

Relative spatial positioning; aggregation and clustering tendencies

We first tested whether social rank has an effect on the relative positioning of an individual crayfish within its group. When individuals nested within frame and trial group were taken into account, there was no significant effect of dominance rank on mean neighbor distance ($F_{[4,620]} = 0.56$; $p = 0.692$; Figure 3a). Minimum neighbor distances (again taking into account individuals nested within frame and trial group) were also not significantly affected by rank ($F_{[4,620]} = 2.099$; $p = 0.08$; Figure 3b). Social rank of animals, therefore, was of little value in explaining relative distances between animals and their neighbors and social rank was not associated with a central to peripheral gradient within the group.

Mean and minimum neighbor distances (±SD), averaged for each individual over 25 frames at 1 min apart, were compared to the values obtained by Monte Carlo simulations on sets of randomized locations (Figure 4). Accounting for individuals nested within groups, empirically determined mean neighbor distances of individuals (268.7 ± 23.5 mm) differed significantly ($F_{[1,24]} = 14.762$; $p < 0.001$) from randomly obtained ones (254.8 ± 22.4 mm).

A comparison of minimum neighbor distances calculated for each individual embedded in its group also illustrated significant difference ($F_{[1,24]} = 32.1$; $p < 0.001$) between actual (139.8 ± 23.8 mm) and randomly generated (98.9 ± 20.2 mm) data sets. This shows that, although neighbor distance may not have been determined by rank, distances to other crayfish in the arena were not random. An active avoidance

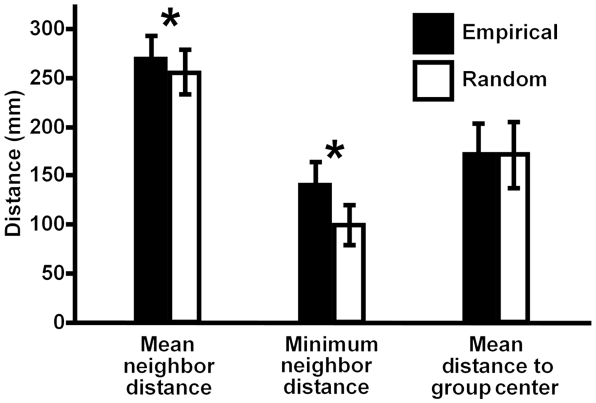

Figure 4. Empirically measured mean and minimum neighbor distances, as well as the distance to the center of group, were compared to identical measures using randomized locations (see "Materials and methods" section for details of randomization). Values were calculated for 25 frames from 5 trials with 5 individuals in each trial. Empirical crayfish put significantly more distance between themselves and their neighbors than predicted by their model counterparts, but they did not cluster around group center. Error bars represent standard deviations from the mean, and values found to be significantly different from one another are marked with an asterisk (*).

of others at close proximity produced greater mean and minimum neighbor distances than would have been predicted had the crayfish been indifferent toward the presence of others.

Crayfish spatial positions also did not gravitate toward the center of the group, as would be predicted if the animals exhibited centripetal tendencies (Figure 4). Comparison of a crayfish's mean distance to the center of the group (170.5 ± 33.9 mm), with distances calculated using randomized locations (171.7 ± 31.3 mm) showed no significant difference between the empirical and randomized results ($F_{[1,124]} = 0.951$; $p = 0.331$). This suggests that crayfish were not clustering around the geometric center of the group and that, after accounting for arena constraints, the moves of crayfish were also not directed towards the group's center.

Discussion

In this study, empirical data in crayfish did not correspond well with predictions that would link spatial association tendencies between crayfish with the hierarchical structure of the group. If central position provided comparative benefits, dominant individuals should adopt a position close to the center of a group, though the mechanisms by which this occurs may vary (Hamilton 1971; Hogeweg 1988; Hemelrijk 1998, 1999, 2000). The results of this study showed no effect of dominance rank on spatial centrality of individuals, which suggests that assumptions of the spatial consequences of dominance structure were not supported in *O. rusticus*. Avoidance of conspecifics or spatial exclusion (repulsion) of others from the immediate space around the individual is consistent with results obtained from other species, where cannibalism amplifies strong intra-specific competition (Barki et al. 1997; Hawkins et al. 2005; Nilsson 2006).

The absence of dominants at the group center, a common prediction for linking dominance and spatial structure of groups, could either be that central tendency is absent in crayfish or that some other mechanisms interfere with its manifestations. For example, a tendency to avoid the close proximity of conspecifics may conflict with the tendency of the dominants to attain centrality. Alternatively, a central position may not offer comparative advantages to dominants, which therefore may be disinclined to seek it. For example, this could happen if the main predatory threats were aimed at the center of the group, such as is the case when threats come from above the group, or with clustering around scattered resources, such as rock shelters. Moreover, such mechanisms could be further affected by the crayfish's avoidance of open spaces and their tendency to stay close to walls.

While the animals did appear to move predominantly toward the center of the group, this largely resulted from the arena's constraints and not from a tendency for centrality. An animal positioned next to the wall had no options but to move away from the wall or alongside it, thus skewing the distribution of moves in favor of those that were centrally oriented. Moreover, crayfish may exhibit the kind of wall-following behavior observed in other taxa, in which the tactile cues are used to stay close to habitat boundaries or other obstacles (Jeanson et al. 2003, 2005; Dussutour et al. 2005; Cowan et al. 2006; Patton et al. 2010). Tactile exploration of environment has been observed in Decapoda (e.g. Basil and Sandeman 2000; McMahon et al. 2005), and such behavior could be an adaptive way to explore novel surroundings, escape from threats, find shelters, or facilitate dispersal. However, once such wall-specific movement patterns were excluded from the analysis, the previously observed central tendency disappeared altogether. This lack of directional preference in movement patterns provides additional evidence that spatial distribution and positioning of individuals was not dependent on the dominance structure of a group.

The results of this study therefore neither supported a tendency toward group centrality through clustering, as exemplified by the centripetal instinct of the Hamilton's (1971) Selfish Herd model, nor a tendency toward spatial proximity of conspecifics, as postulated by the Hogeweg/Hemelrijk MIRROR/DomWorld model (Hogeweg 1988; Hemelrijk 1998, 1999, 2000). If crayfish possessed an analog of a centripetal instinct, we would observe individuals attempting to move toward the center of a group, avoiding the periphery wherever possible. In this study, such a tendency would result in low distances to the center of the group for all individuals as they tried, perhaps with differing degrees of success, to attain a more central position. The mean distances to the center of the group obtained from the trials were not, however, noticeably lower than those generated using randomized locations, providing no evidence that such a tendency exists in crayfish.

Rather than moving centripetally, individuals could also move with no spatial central preference, but non-randomly with respect to one another (e.g. preferring group members at a certain distance). Beyond this distance the tendency to aggregate would come into play, and the individual will move toward the group until the distance is closed. Such an aggregation term, as illustrated by the MIRROR/DomWorld models, suggests that individuals may prefer the close proximity of conspecifics. However, the present results show no evidence that such active aggregation exists in crayfish. While little sign of actual aggregation was detected within the trial arena, the tendency for individuals to avoid close proximity to their immediate neighbors does suggest that there is a distance within which the presence of another crayfish affects the behavior of an individual, though in a pattern more complex than simple aggregation.

Avoidance of conspecifics could be the mechanism to avoid future agonistic interactions. Crayfish tend to readily engage conspecifics in escalated and sometimes dangerous combat, even in the absence of resources such as food or shelter (Issa et al. 1999; Huber et al. 2001). Such contests are frequently preceded by individuals being close to each other. Avoidance of such close proximity would therefore be a general mechanism for reducing potentially costly and injurious fighting. However, the lack of association between neighbor distance and social rank would suggest that such exclusion was not directly based on dominance or interaction history. Rather, such avoidance, or repulsion, of others could be beneficial to all individuals regardless of their dominance status, and complement the benefits of dominance hierarchy as a way to reduce fighting in a group. In addition to visual and olfactory cues, tactile cues likely play an important role in avoidance behavior. Future experiments that look at the contribution of each of these cues (e.g. using blindfolded or individuals with ablated antennae) could determine the importance of each of these cues in spacing between individual animals.

An explanation for this discrepancy may come from observation of dyadic encounters between individual crayfish. Once a dominance hierarchy has been established, as was the case in our trials, interactions between individuals are brief, with the subordinate retreating after little or no contest (Goessmann et al. 2000; Huber et al. 2001). The crayfish in the spatial distribution trials had established dominance hierarchies for 24 h prior to the period used for analysis, and as a result rarely stayed within one body length of one another. Thus, the observed spatial distribution could be result of the active avoidance of conspecifics rather than proximity-seeking behaviors. While crayfish can live in high densities (Davis and Huber 2007), our results suggest that such spatial aggregations could be a necessity arising from habitat constraints, and that crayfish will, given enough room, tend to space out in the habitat, possibly to minimize potential costs of continuous agonistic interactions (Hock and Huber 2009). Nevertheless, while aggregation tendencies have not been observed in our trials, they cannot be completely ruled out, and crayfish may indeed seek out other conspecifics based on the received chemical cues (e.g. Zulandt Schneider et al. 1999; Adams and Moore 2003). However, it is likely that such tendencies could be better interpreted as opportunistic, and associated with tendencies such as cannibalism rather than gregariousness and sociality. The individuals in our trials were free to occupy space and only had to contend with other conspecifics. Clustering around the group center could still occur under a different set of circumstances. Presence of a predator may induce a preference to get closer to the center of the group, and the dominance status could then play a role in who gets the preferential position. While the crayfish could still form a selfish herd when faced with predation pressure, we conclude that in the absence of such external cues they did not exhibit centripetal instincts.

Taken together, the results of this study suggest that crayfish exhibit moves that do not bring them closer to conspecifics or to the group center to be surrounded by the conspecifics. Rather than active aggregation, in a group with established hierarchical structure the crayfish would appear to be avoiding close contact with conspecifics, possibly due to the costs of potential agonistic interactions associated with personal space violations. The high population densities of crayfish in natural environments would therefore be more indicative of superior use of a given habitat's carrying capacity than an actively gregarious species.

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