The ghost of social environments past: dominance relationships include current interactions and experience carried over from previous groups

Colby J. Tanner1,2,* , Gul Deniz Salali3 and Andrew L. Jackson1

1Department of Zoology, School of Natural Sciences, Trinity College Dublin, Dublin, Republic of Ireland
2Department of Ecology and Evolution, UNIL, Lausanne, Switzerland
3Institut des Sciences de l’Evolution, Centre National de la Recherche Scientifique, UMR 5554, Université Montpellier II, 34095 Montpellier, France

*Author for correspondence (colbyjtanner@gmail.com).

Dominance hierarchies pervade animal societies. Within a static social environment, in which group size and composition are unchanged, an individual’s hierarchy rank results from intrinsic (e.g. body size) and extrinsic (e.g. previous experiences) factors. Little is known, however, about how dominance relationships are formed and maintained when group size and composition are dynamic. Using a fusion–fission protocol, we fused groups of previously isolated shore crabs (Carcinus maenas) into larger groups, and then restored groups to their original size and composition. Pre-fusion hierarchies formed independently of individuals’ sizes, and were maintained within a static group via winner/loser effects. Post-fusion hierarchies differed from pre-fusion ones; losing fights during fusion led to a decline in an individual’s rank between pre- and post-fusion conditions, while spending time being aggressive during fusion led to an improvement in rank. In post-fusion tanks, larger individuals achieved better ranks than smaller individuals. In conclusion, dominance hierarchies in crabs represent a complex combination of intrinsic and extrinsic factors, in which experiences from previous groups can carry over to affect current competitive interactions.

Keywords: aggression; carry-over effects; dominance hierarchy; fission–fusion; social environment

1. INTRODUCTION

Animal societies are characterized by dominance relationships that emerge from repeated competitive interactions. Dominance relationships affect fitness, as high-ranking individuals often have access to resources unavailable to subordinates [1]. Hierarchies are developed and maintained by a combination of intrinsic factors associated with individuals’ physical traits, and extrinsic factors associated with previous interactions among group members [2–5]. The effects of intrinsic and extrinsic factors in hierarchy formation become difficult to predict where the two factors negatively interact (e.g. when one cancels the other) [6,7].

Changes to the social environment, such as group size and composition, can further complicate the effects of intrinsic and extrinsic factors on hierarchy formation. Most studies investigating dominance relationships to date have focused on groups with static composition [8], with the notable exception of mammalian fission–fusion societies [9]. Group composition often fluctuates in natural populations, however, as individuals periodically disperse and re-group [10], and events occurring within one group can have far-reaching effects on social interactions in later groups [11]. Dominance hierarchies should therefore reflect a combination of intrinsic and extrinsic factors operating within the current group, as well as some combination of these factors carried over from previous groups. Although carry-over effects are gaining empirical recognition elsewhere in ecology [12], and the concept has been suggested for dominance relationships [13], there has been little progress made in this area. Results of the few studies investigating dominance hierarchies with changing group composition have been inconsistent [13–15].

Here, we investigate how intrinsic and extrinsic factors affect dominance relationships when group size and composition varies, using a fusion–fission design with the European shore crab, Carcinus maenas. Shore crabs disperse/aggregate with high/low tidal cycles, and group composition during aggregation ranges from predictable (individuals return to previous group) to variable (individuals form new groups) [16]. Additionally, C. maenas individuals develop clear dominance relationships [17]. Therefore, this provides an example of a species that develops and maintains social structure within dynamic groups. We begin with previously isolated crabs forming stable hierarchies in pre-fusion groups. These crabs are then fused into larger groups that form new hierarchies. Finally, individuals are returned to their initial groups to form post-fusion hierarchies. We predict a correlation between individuals’ body sizes (a known intrinsic factor [18,19]) and ranks in pre-fusion conditions, as these individuals do not have recent previous interactions to affect competitive outcomes. Therefore, larger individuals should win early interactions, and the positive feedback associated with winner/loser effects should maintain these initial outcomes within static groups [4] (hypothesis 1). If dominance relationships are reset with a change in group size and composition [14], fights during fusion should be distributed equally among previous group and non-group members, as individuals all re-assess their relative ranks (hypothesis 2). Finally, if previous information carries over with an individual from one group to the next [13], we expect changes among individuals’ rank between pre- and post-fusion conditions to reflect their experiences during fusion (hypothesis 3).

2. MATERIAL AND METHODS

Adult male crabs were labelled and stored (12 C, 12 L; 12 D cycle) in isolation for 7 days [20]. For pre-fusion conditions, four crabs varying in size (mean largest–smallest approx. 7% largest) were placed into 600 cm³ tanks with approximately 5 cm sea water. We video recorded all interactions for 30 min (preliminary trials...
showed that interaction rates declined and stable hierarchies formed within this time). For treatment fusion conditions (four tanks), we combined crabs from pairs of pre-fusion tanks into common fusion tanks (eight crabs per tank). Controls (four tanks) were not fused. We recorded all interactions for 30 min, and then returned crabs from fusion tanks to their initial pre-fusion groups for 30 min of post-fusion recording. To minimize effects of human contact and physical displacement, we omitted the first 5 min of observations prior to analysis.

We recorded winners and losers of all competitive interactions [21] to establish ranks within tanks according to the Elo-rating method [22], which sequentially quantifies hierarchies reflecting individual’s relative strengths within the group. Scores increased/decreased with wins/losses relative to the expected outcome, based on previous results as described in Albers & De Vries [23].

To determine whether post-fusion hierarchies differed from pre-fusion ones, we compared them separately for control and treatment groups, using permutation tests for non-independent data [20]. Randomly permuted rank matrices (10^4, constrained within tank [23]) were created, and the proportion of correlation coefficients from simulated matrices greater than the observed correlation between pre- and post-fusion hierarchies represents the p-value for this statistic. We also compared numbers of aggressive interactions during fusion treatments between pre-fusion same-group and non-group members using a Mann–Whitney test.

Where ranks differed between pre- and post-fusion hierarchies, we used permutation tests to determine correlations between an individual’s change in rank and its: number of losses, number of wins, and total time in aggressive interactions during fusion. We used permutation tests to determine whether body size was correlated with hierarchy status separately for pre- and post-fusion conditions (constrained within tanks), and exact binomial tests (separately for pre- and post-fusion groups), to determine whether winning the first interaction explained dominance relationships within a static group.

3. RESULTS

Individuals’ ranks between pre- and post-fusion were not correlated (i.e. much change; $r = 0.05, p = 0.43$), while individuals’ initial and final ranks in control tanks were significantly correlated (i.e. little change; $r = 0.75, p < 0.01$) (figure 1). As hypothesis 2 predicted, individuals during fusion were equally aggressive to previous group and non-group pre-fusion members ($V = 8, p = 0.20$).

Consistent with hypothesis 3, losing fights during fusion led to a decline in individuals’ ranks between pre- and post-fusion ($r = -0.61, p < 0.01$) (figure 2a), although winning fights during fusion did not significantly improve rank ($r = 0.62, p = 0.16$). Total time being aggressive during fusion, however, was positively correlated with individuals improving rank between pre- and post-fusion ($r = 0.68, p < 0.01$) (figure 2b).

Contrary to hypothesis 1, individuals’ body sizes and ranks were uncorrelated in pre-fusion ($r = -0.08, p = 0.14$), while larger individuals were dominant to smaller ones in post-fusion ($r = -0.51, p < 0.01$; hypothesis 3). In 73 per cent of pre-fusion ($p < 0.01$) and 77 per cent of post-fusion groups ($p < 0.01$), individuals’ first interaction outcomes correctly predicted their relative ranks within that group. After 30 and 90 min in control tanks ($r = -0.31, p = 0.17$; $r = -0.15, p = 0.31$, respectively), body size and rank were uncorrelated.

4. DISCUSSION

Our experiment demonstrates that intrinsic and extrinsic forces play important, yet subtly different, roles in establishing and maintaining dominance relationships in dynamic social environments. Extrinsic factors carried over across social environments, leading to the establishment of hierarchies increasingly influenced by intrinsic factors. Contrary to expectation, initial hierarchies of individuals not influenced by recent external factors (i.e. fight outcomes) were independent of intrinsic ability (i.e. size). As expected, however, initial hierarchies did reflect outcomes of individuals’ early fights. We conclude that external factors via positive feedback [4,6] dictate hierarchy formation within a static group, but these hierarchies do not necessarily reflect intrinsic factors when individuals lack recent competitive interactions. This conclusion is consistent with size-independent hierarchies persisting throughout the experiment in control tanks.

Altering group size and composition led to group members resetting relationships via renewed aggressive interactions [2,14,24], as fusion-group individuals were equally aggressive towards previous group and non-group members. When groups changed, individuals re-assessed their ranks, resulting in the change between pre- and post-fusion hierarchies. Individuals’ post-fusion ranks, unlike their pre-fusion ones, accurately reflected their body sizes.

The negative effects of losing are often more important and/or longer lasting than the positive effects of winning [8], which may explain why losing fights was significant between pre- and post-fusion conditions while winning fights was not. Of particular interest here is the positive effect aggression during fusion had on an individual’s change in rank between pre- and post-fusion conditions. Similarly, Kim & Zuk [25] found that hens with previous social experience were superior to naive individuals, and that fighting (irrespective of outcome) improved subsequent rank.

One possible mechanism for changes in rank between pre- and post-fusion, such that only post-fusion ranks reflected individuals’ body sizes, is that aggressive interactions provide information regarding an individual’s ability [26]. In this way, changes to group size and composition destabilize hierarchy structure previously maintained by external effects [14] and, as individuals re-establish hierarchies through aggressive interactions, they gain information regarding their relative competitive abilities. Alternatively, changes
in hierarchy rank between pre- and post-fusion groups could reflect a discriminatory process by which larger individuals do better as hierarchies become re-established (e.g. smaller crabs in new groups could have been unable to continue fighting to re-assess rank) [27]. Although these two, non-mutually exclusive explanations differ mechanistically, they are functionally similar. In either case, group structure emerging from current competitive interactions must include carry-over effects of interactions from earlier groups. Determining what type of information is collected, how it carries over when individuals switch groups, and how it is used in various contexts, will certainly provide a more full understanding of how group structure emerges from a collection of interacting individuals.

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Figure 2. Relationship among change in rank (vertical axis) between pre- and post-fusion tanks for treatment individuals and the (a) number of fight losses (p < 0.01), and (b) time spent being aggressive (p < 0.01) during fusion (horizontal axes).


