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Effects of fighting decisions on formation and structure of dominance hierarchies

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Abstract
The characteristics of complex social systems often cannot be predicted from exploring individual agonistic interactions in isolation. In a series of models, this study linked the decision-making processes that govern dyadic interactions with the emergent properties of hierarchical structures in social groups. Contrary to the intuitive expectation that resolution of ambiguities in fighting between closely matched opponents effectively promotes the formation of a social hierarchy, engagement in contests with opponents of dissimilar status lead to a faster emergence of hierarchical structures. The increased certainty of outcome in such asymmetric contests both reinforced the previously established dominance, and allowed for an indirect resolution of existing ambiguous relationships. High-return fights also resulted in a more rapid hierarchy formation, while escalating in fights decreased the costs of maintaining hierarchical relationships and increased their stability.

Keywords: *Dominance hierarchy, aggression, initiation, contest dynamics*

Introduction

Dyadic interactions represent the primary structuring events in the formation of even the most complex social group structures. Hierarchical relationships thus emerge from an iterative occurrence of dyadic interactions (Issa et al. 1999; Goessmann et al. 2000; but see also Chase et al. 2002). Establishment of a clear structure of social ranks brings about a decrease in aggression among contestants (Francis 1988), and a reduction of potentially damaging behaviors in species that can inflict injury upon each other (e.g. Enquist and Leimar 1990; Huber and Kravitz 1995; Neat et al. 1998). The assessment of the opponent's aggressive motivation appears to guide decisions made in conflicts, the resulting certainty for one's social position, and the levels of aggression within a group (Parker 1974; Clutton-Brock and Albon 1979; Parker and Rubenstein 1981; Hack 1997; Halperin et al. 1998; Neat et al. 1998). However, the way in which such dyadic interactions

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influence the emergence and properties of complex social structures is neither intuitively apparent nor easily predictable.

"Winner–loser effects" refer to a change in the likelihood of winning that is contingent upon an individual's past agonistic success: recent wins increase chances for future wins, while losses reduce this probability (Francis 1988; Drews 1993; Chase et al. 1994). Such phenomena have been studied with empirical experiments and theoretical models (Francis 1983; Beacham 1988, 2003; Otronen 1990; Chase et al. 1994, 2002; Hollis et al. 1995; Beaugrand et al. 1996; Dugatkin 1997; Whitehouse 1997; Hsu and Wolf 1999, 2001; Taylor et al. 2001; Dugatkin and Earley 2003; Hock and Huber 2006). The resulting behavioral changes are dynamic, and indicate that an individual's actual fighting capability may not be diminished, but rather that its own perception of or confidence in it is reduced (Hsu and Wolf 2001). In one explanation, subordinate individuals may comply with behavioral conventions when submitting in future contests so as to avoid future aggression from dominants (Van Doorn et al. 2003a, 2003b).

Fighting progress critically depends on a series of decisions made by the contestants, including whether and when to initiate, escalate, retaliate, or withdraw. Previous experience appears to impact such decisions (e.g. Jackson 1991; Drews 1993; Chase et al. 1994; Hack 1997; Neat et al. 1998; Hsu and Wolf 1999, 2001; Maan et al. 2001; Van Doorn et al. 2003a, 2003b; Huber et al. 2004). Recent winners frequently become more likely to initiate future conflicts (Jackson 1988, 1991), while a delay in decisions to retreat increases fight intensities (Huber and Kravitz 1995). The sequential assessment model (Enquist and Leimar 1983; Enquist et al. 1985, 1990) suggests that longer contests will involve more costly behaviors in which dominants are more likely to participate. While escalation rate could depend on a variety of factors (e.g. Taylor et al. 2001; Maan et al. 2001; Schroeder and Huber 2002; Van Doorn et al. 2003b), increased escalation is primarily a result of having experienced past wins (Turner and Huntingford 1986; Beacham and Newman 1987; Hack 1997; Hsu and Wolf 2001). Interaction history should therefore not only determine an individual's success, but also the characteristics of the ensuing encounters.

Despite the considerable attention paid to predictors and consequences of dyadic dominance, there have been few attempts to elucidate these properties in more complex social settings. Because of the emergent nature and inherent complexities of hierarchy formation within social groups, computer-modeling approaches have played a prominent role in attempts to ascertain the importance of individual variables (e.g. Hogeweg 1988; Hemelrijk 2000; Dugatkin and Earley 2003). Computer models allow us to independently vary all constituent variables, thus alleviating the inherent difficulties of studying such a multivariate system. Moreover, their outcome may serve as a null hypothesis in subsequent empirical studies. In one such model, Hemelrijk (2000) proposed that particular sets of conditions will result in an uneven spatial distribution of individuals from which agonistic opponents are selected. When conspecifics are encountered, individuals may employ a variety of strategies: they may engage in every opportunity to increase their own rank, attack only when they are reasonably certain beforehand that they will win an interaction, or fight only when encountering animals close to their own rank in order to reduce ambiguities in social status (Pagel and Dawkins 1997; Hemelrijk 2000). With different scaling factors for winner and loser effects (i.e. high or low return fights), individual spatial distributions emerged as a function of the interaction history of the participants. A reduction in the number of aggressive encounters within the group is supported by another published model (Beacham 2003), where spatial proximity of individuals with similar rank facilitated the emergence of transitive triads, and thus, of linear hierarchies.

While Hemelrijk's models are suited to explain the relationship between spatial and social structure, they can, however, neither be easily applied to scenarios lacking spatial centrality, nor to those where hierarchies are formed through series of escalating contests. In the latter scenarios, the cost of fighting varies not only with respect to the frequency of agonistic interactions, but it also depends on the characteristics of the contests themselves. Moreover, characteristics of bouts in most species are not likely to remain constant as ranks in the hierarchy diverge. Addressing these questions requires that we extend previous models with methods that dissociate spatial parameters from those that govern dyadic interactions, while, at the same time, take into account the changes in nature of escalating contests and their associated costs.

Agonistic interactions in most decapod crustaceans feature escalating sequences of highly stereotyped behaviors (Huber and Kravitz 1995; Guiasu and Dunham 1997; Huber et al. 2004), which result in lasting polarities in pairs, and social hierarchies at a group level (Issa et al. 1999; Goessmann et al. 2000). Fighting in decapod dyads is most intense and frequent when individuals are closely matched in size, and is likely to develop with heightened dynamics if both contestants have a history of winning (Daws et al. 2002). Different escalation rates can also depend on the body size and allometric growth of claws (Schroeder and Huber 2002). Escalation rates change over time in size-matched groups of individuals, with consistent winners becoming more prone to escalate to higher intensity levels in conflicts (Goessmann et al. 2000). Under such conditions, dominant individuals initiated more interactions in a group, and participated in more interactions than lower ranking ones. As groups of crayfish exhibit no tendency for spatial aggregation and centrality (Daws and Huber submitted), and seem to lack the ability to form social coalitions (Huxley 1880), decapod crustaceans are an ideal system for an exploration using individual-agent-based models.

In order to examine the consequences of decisions made in contests on hierarchy formation and to link them with empirical observations, an existing model (Hemelrijk 2000) was modified and extended to account for the specific characteristics of dyadic decapod interactions. This allowed for development of a comprehensive model to explore: (1) the effects of individual decisions underlying dyadic interactions (i.e. rules that determine fight initiation, rates of escalation, and retreat) on social structure; (2) the changes in the characteristics of dyadic interactions that occur during hierarchy formation for a given set of rules; and (3) the potential benefits of such decisions for conflict resolution in animal groups.

Methods

Non-behavioral parameters

A modeling framework (Figure 1) was developed using the Java programming language (Java 1.4.1 API). The virtual setup was constructed to resemble an experimental arena described in Goessmann et al. (2000). Individuals interacted in a two-dimensional space with dimensions of 270 × 180 pixels, corresponding to an actual space of around 0.6×0.4 m. The arena was implemented to wrap-around in both dimensions (i.e. entities leaving the arena at the south border automatically reentered from the north, or from east to west). This allowed for movement patterns that were not restricted by arena walls. Individuals were represented by a single center pixel. Initially, all entities were assigned random starting locations and identical behavioral states. For each move, a vector was chosen randomly from a non-parametric distribution constructed of 9765 actual

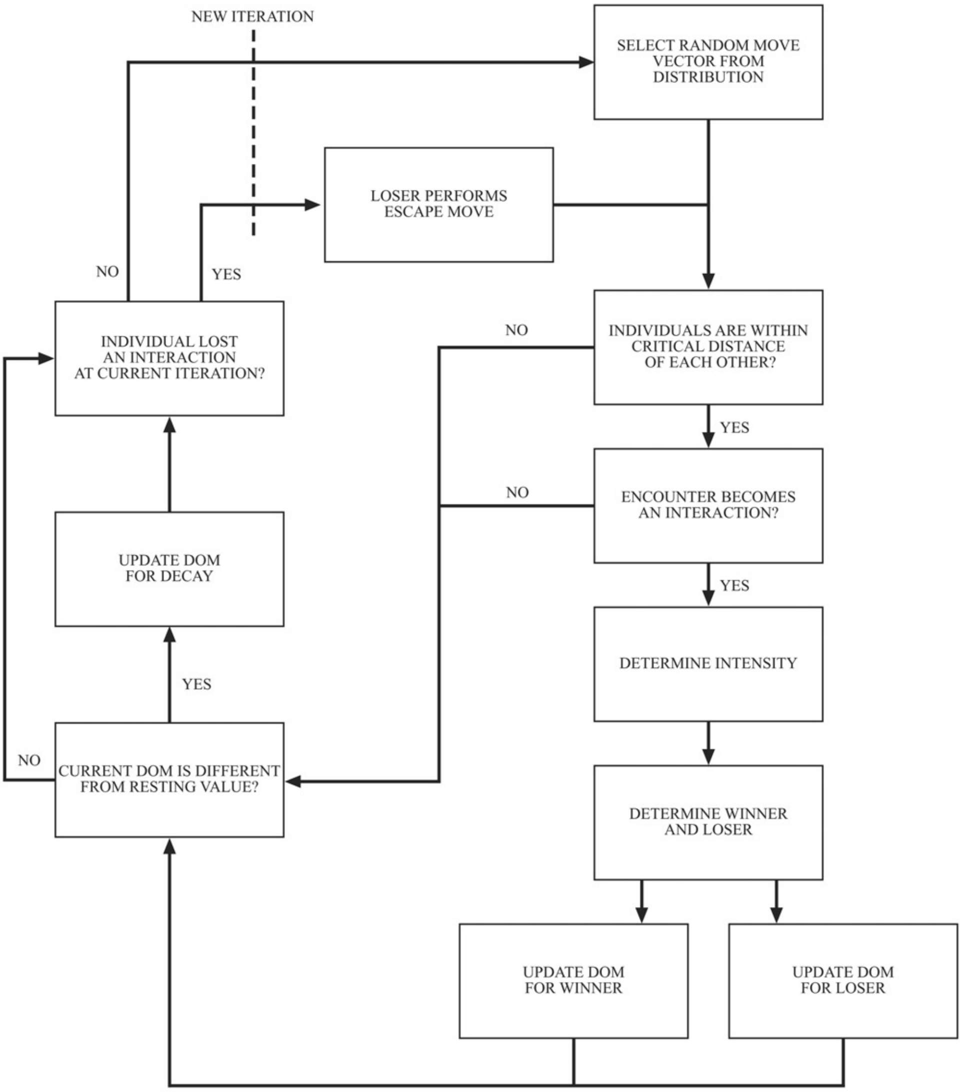

Figure 1. A schematic depiction of the all possible algorithms that can be used within a single iteration of the model. While the general flow of the statements is the same for all models, the difference between scenarios stems from the various strategies used to determine the onset of an interaction (initiation strategies) and interaction intensity (contest dynamics strategies).

moves of adult crayfish moving freely in a two-dimensional open space (Panksepp and Huber 2004). Locations and behavioral states were updated for all entities at once at a timeframe equivalent to actual 4 s intervals. The individuals thus moved simultaneously and in ‘leaps’. Spatial proximities (i.e. simple Euclidian distances) were calculated for all members following each iteration. In the models presented here, groups were composed of four individuals, and were allowed to interact for an equivalent of 3 h (2700 moves).

Interaction rules

General rules that model the basic processes during agonistic interactions were adopted from previously published work (Hemelrijk 2000). Each individual's ability to win future interactions was represented by a variable (DOM), representing "aggressive motivation". All individuals started with the same DOM value, arbitrarily set at 0.5, thus giving them an equal chance to win in interactions against another naïve opponent. Values of DOM were always positive, with its minimum limited at 0.0001. When two entities approached to within a critical distance (DIST) of each other, a decision was made as to whether an encounter was contested, i.e. whether a fight took place. The effects of different strategies for selecting to do battle were tested in this model. If a fight ensued, it was played out in model time (i.e. 4 s intervals) and resolved instantly before the next scheduled move of all contestants. The loser of the interaction performed an escape behavior as its next move away from its opponent for a randomly selected distance between one and three values of DIST. The outcome of a fight was determined based on a comparison of DOM values (Hemelrijk 2000). The probability for winning of contestant i (p_W) was obtained relative to that of contestant j using a ratio of respective starting DOM values (Equation 1).

$$p_w = \frac{\mathrm{DOM}_i}{\mathrm{DOM}_i + \mathrm{DOM}_j} \tag{1}$$

A random number (RND) ranging from zero to one was used to determine the winner. Contestant i won the interaction against contestant j if $\mathrm{DOM}_i/(\mathrm{DOM}_i + \mathrm{DOM}_j) > \mathrm{RND}(0, 1)$. Based on this outcome, the DOM value of the winner was increased (Equation 2) while that of the loser was lowered (Equation 3) in the following way:

$$\mathrm{DOM}_{i(T+1)} = \mathrm{DOM}_{i(T)} + \left\{ w_i - \left[\frac{\mathrm{DOM}_{i(T)}}{\mathrm{DOM}_{i(T)} + \mathrm{DOM}_{j(T)}} \right] \right\} \mathrm{STEPDOM} \tag{2}$$

$$\mathrm{DOM}_{j(T+1)} = \mathrm{DOM}_{j(T)} - \left\{ w_i - \left[\frac{\mathrm{DOM}_{i(T)}}{\mathrm{DOM}_{i(T)} + \mathrm{DOM}_{j(T)}} \right] \right\} \mathrm{STEPDOM} \tag{3}$$

where $\mathrm{DOM}_{i(T)}$ and $\mathrm{DOM}_{j(T)}$ were DOM values for the two contestants before the interaction, and $\mathrm{DOM}_{i(T+1)}$ and $\mathrm{DOM}_{j(T+1)}$ were DOM values updated as a result of the interaction outcome. The interaction outcome (w_i) was $w_i = 1$ if individual i was the winner, and $w_i = 0$ if individual i was the loser of the contest. It follows that winning against an opponent with a much lower DOM value from its own resulted in a comparatively smaller increase in DOM for the winner than winning over an opponent with greater DOM value; the opposite was true for losing.

As more intense fights may have a greater impact, an additional scaling factor (STEPDOM) was used to implement contextual changes in DOM resulting from fights with different maximum intensities. In decapod crustaceans, interactions escalate with increasing chances for injury. Discrete intensity levels (0–3) of such behavioral sequence have been characterized in previously published work (Huber et al. 2004). In the present model, this increase in fight intensity was simulated by attributing different values of STEPDOM to each intensity level (a STEPDOM value of 0.125, 0.25, 0.5, and 1 for intensities 0, 1, 2, and 3, respectively). The magnitude of winner and loser effects was kept equal (Hock and Huber 2006).

Winner and loser effects decay over time. The effects of winning decrease to about two-thirds of its initial value after a period of 40 min (Bergman et al. 2003). In the model,

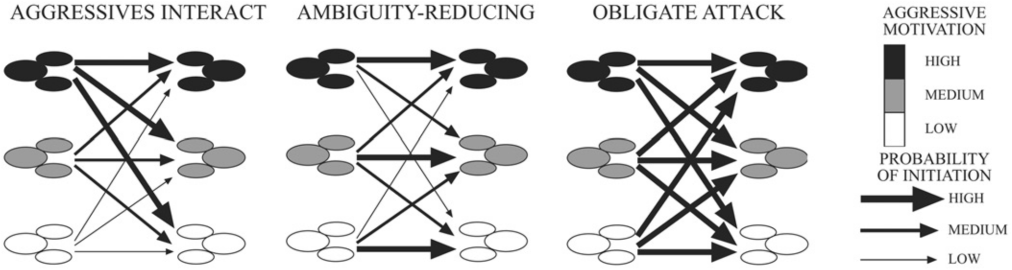

Figure 2. A diagram depicting three different initiation strategies used in the design of the models. It should be noted that this diagram has been simplified for the sake of easier presentation: in the actual models, the levels of aggressive motivation in all scenarios, as well as the probability of initiation under "aggressives interact" and "ambiguity-reducing" strategies, were continuous rather than categorical variables.

DOM values decayed at this rate over time to the starting state of a naïve animal. Between moves, DOM values for all agents were adjusted as shown in Equation 4.

$$\mathrm{DOM}_{\mathrm{decayed}} = \mathrm{DOM}_{(t)} - \frac{\mathrm{DOM}_{(t)} - 0.5}{3N} \tag{4}$$

with N being the total number of 4 s intervals and $\mathrm{DOM}_{(t)}$ as the agent's DOM value right after the move at time t has been made. Without further interactions, the decayed estimate for DOM ($\mathrm{DOM}_{\mathrm{decayed}}$) thus gradually returned to the starting value of 0.5 representing the DOM value of a naïve individual.

Initiation strategies

If two individuals approached each other to within a critical distance of each other, three different strategies for conflict initiation were explored to examine their effects on hierarchy formation and maintenance (Figure 2). Regardless of the initiation strategy used, the decision on whether an encounter resulted in an interaction was made at a level of a pair. In "obligate attack" strategy (OA), individuals inevitably interacted in every encounter, and made use of every opportunity to increase their own rank. In "aggressives interact" strategy (AI), the decision to interact was proportional to the level of aggressive motivation of the individual with a greater DOM value in the pair. Thus, if individual i came within a DIST of j, the program first determined whether $\mathrm{DOM}_i > \mathrm{DOM}_j$, or $\mathrm{DOM}_j > \mathrm{DOM}_i$. If the case was that $\mathrm{DOM}_i > \mathrm{DOM}_j$, then the condition $\mathrm{DOM}_i > \mathrm{RND}(0,1)$ needed to be true for the interaction to develop, whereas if $\mathrm{DOM}_j > \mathrm{DOM}_i$ then $\mathrm{DOM}_j > \mathrm{RND}(0,1)$ condition was used as a criterion for the decision. In "ambiguity-reducing" strategy (AR), individuals featured a high probability to interact with opponents of similar aggressive motivational state. Thus, if individual i ended up within a DIST of j, the comparison was made to determine whether $\mathrm{DOM}_i > \mathrm{DOM}_j$ or $\mathrm{DOM}_j > \mathrm{DOM}_i$. If $\mathrm{DOM}_i > \mathrm{DOM}_j$, then the interaction ensued if $\mathrm{DOM}_i - \mathrm{DOM}_j < \mathrm{RND}(0,1)$ was true, else $\mathrm{DOM}_j - \mathrm{DOM}_i < \mathrm{RND}(0,1)$ needed to be true for the individuals to interact.

Strategies of contest dynamics

Independent of decisions as to whether, and between whom, an agonistic encounter would take place, a set of rules governed the characteristics with which contests proceeded. In the

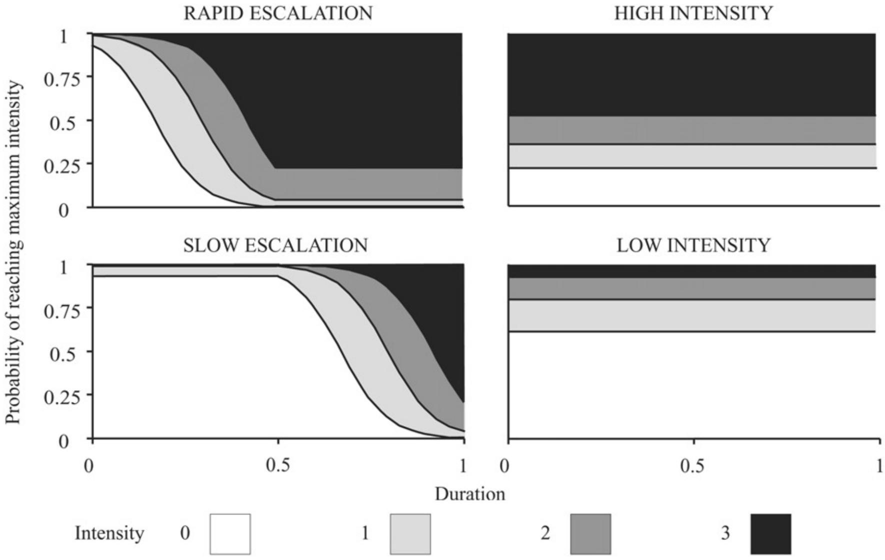

Figure 3. Timing of an individual's decision to retreat (i.e. the DOM value of the lower ranking individual) determines the probability of reaching maximum interaction intensities. The patterned areas represent probability to reach a certain maximum intensity, with darker patterns representing higher intensities.

present models, fight duration was not modeled explicitly in terms of time spent interacting as all interactions in the models were resolved instantly before the next move. Rather, an indirect approach was used in the model to implement the dependence of fight intensity as a function of duration. An interaction will continue to escalate until one of the contestants decides to retreat. The individual with the lower level of aggressive motivation should reach this decision point sooner than its opponent. The model thus links maximum fight intensity to the DOM value of the individual with the lower aggressive motivational state. If individuals i and j interacted and if $\mathrm{DOM}_i > \mathrm{DOM}_j$, the value of DOM_j was used to estimate both duration and maximum intensity of a given fight, else DOM_i was used as a criterion.

Due to the interdependence between fight duration and intensity, decisions to escalate and retreat from fights were modeled jointly as four different strategies of contest dynamics (Figure 3). In "rapidly escalating" scenarios (RE), contests reached higher intensities more rapidly for a given duration. Moreover, fights among dominants had a high probability to progress to the highest intensities. In "slowly escalating" scenarios (SE), contests progressed to higher intensities more slowly with time. Thus fights involving at least one low-DOM individual had a low probability to reach high intensities. In the last two strategies, the probabilities to reach any given intensity were independent of duration. The opponents in the "high-intensity" scenario (HI) were likely to reach high intensities, while opponents in the "low-intensity" scenario (LI) escalated only rarely. The logistic regression curves for the probabilities to reach certain maximum intensities in escalating scenarios were obtained from the pooled results collected on dyadic interactions in pairs of crayfish (Huber and Delago 1998; Stocker and Huber 2001; Schroeder and Huber 2002). The intensities of non-escalating strategies (HI and LI) were matched to those from the corresponding escalating ones (e.g. in Figure 3, the shaded areas of RE and HI are equal in size to those of SE and LI, respectively). Such design allowed comparison of fights of different overall intensity with those where fights escalated at a faster or slower rate.

Program output

Factorial sets of three initiation and four escalation strategies (i.e. 12 different model scenarios) were constructed in order to explore the effects of different decision-making strategies. A total of 50 replicates were created for each of the 12 scenarios, with each replicate consisting of a separate group of four individuals, and a DIST value set at 27 pixels. Descriptive measures of hierarchy structure were obtained at every 20 interactions across the group, irrespective of the identity of the individuals involved in them. The output of the program consisted of each individual's ordinal ranks and cardinal ranks measured using the Batchelder–Bershad–Simpson (BBS) method (Jameson et al. 1999). The values of Landau's statistic *h* (Landau 1951) were also recorded at a group level to compare the number of transitive triads to those maximally possible (Appleby 1983). The values of Landau's statistic *h*, as well as ordinal and cardinal ranks, were cumulative for all previous interactions up to the point of measurement. The proportion of fights ending at various intensities within each 20 interaction interval and the DOM values of the participants of each fight were recorded.

Results

The modeling approach identified a variety of distinct group patterns that emerge as a consequence of individual fighting decisions. Different scenarios of fight initiation produced different overall rates of agonistic interactions, ranging from 600–720 (median 660) for the four OA strategy scenarios to 100–160 (median 100) for the AR strategies (Table I). Ambiguity-reducing strategy reduced the total number of recorded interactions. In all AR models, interactions were contingent on the probability to encounter a matched opponent, and this probability decreased with the divergence of the hierarchy. In AI models with low overall fight intensity, the number of moves per interaction interval decreased with time due to the slow resolution of ranks and slow, but steady, emergence of the aggressive individuals. Obligate attack scenarios had low and constant interaction intervals. With substantial variability in the total number of interactions across models, only the initial 100 interactions were used for a detailed analysis of behavioral characteristics.

Fight intensities were primarily contingent on strategies of contest dynamics. Despite matching overall probabilities to reach a given maximum intensity, in models featuring escalating encounters (RE and SE) the overall intensity of fighting (Figure 4) was effectively reduced in comparison to those models that did not feature escalation (LI and HI). This pattern was consistent across initiation strategies. Fight durations were also compared across models (Figure 5). In slow escalation scenarios (SE models), individual fights lasted longer and their duration decreased more slowly as the hierarchy formed when compared to rapid escalation fights (RE models). Such patterns were less pronounced in models without escalation (HI and LI). Thus, escalation reduced the intensity of future fights and progressively shortened their duration, while a greater likelihood of intense fighting was offset by a further decrease in duration.

The degree of linearity in a hierarchy, expressed as the value for Landau's statistic *h*, was compared to the number of interactions that took place within the group (Figure 6). In all models where asymmetric contests were likely (AI and OA models), linearity approached 1 (i.e. perfectly linear). However, in models with less intense fighting (SE and LI), it did so

Table I. Median number of total recorded interactions (with minimum and maximum), mean number of moves needed to reach the first 100 interactions ± SD, mean number of moves per 20 interaction interval for the first 100 interactions ± SD, mean number of moves per 20 interaction interval after 100 interactions ± SD, and the interaction interval trend ("+" – increasing trend, longer intervals with time; "–" – decreasing trend, shorter intervals with time) for all models.

Total interactions Moves to 100 interactions Moves per interval < 100 Moves per interval > 100 Interaction interval trend	Aggressives interact	Ambiguity reducing	Obligate attack
Rapid escalation	360 (280–420)	200 (160–240)	680 (600–740)
	690 ± 83	1235 ± 145	386 ± 47
	138 ± 37	247 ± 67	77 ± 21
	152 ± 49	272 ± 77	80 ± 20
	+	+	+
Slow escalation	400 (320–480)	260 (200–300)	660 (600–740)
	720 ± 128	884 ± 151	338 ± 43
	144 ± 49	176 ± 69	78 ± 19
	126 ± 37	220 ± 64	81 ± 20
	–	+	+
High intensity	340 (280–440)	100 (100–120)	660 (560–740)
	723 ± 121	2203 ± 264	403 ± 47
	145 ± 49	452 ± 170	81 ± 21
	157 ± 56	499 ± 113	81 ± 21
	+	+	+
Low intensity	380 (300–440)	180 (140–220)	640 (580–720)
	701 ± 99	1307 ± 198	407 ± 50
	140 ± 44	261 ± 94	81 ± 21
	136 ± 45	317 ± 86	81 ± 20
	–	+	+

more slowly than in models with higher intensity fights (RE and HI). When contests were largely conducted between evenly matched opponents (AR models), hierarchies were considerably less linear. In particular, the combination of one of the two non-escalating models (LI and HI) with the AR strategy produced a lower degree of linearity.

Different scenarios showed little variation in final cardinal ranks after the first 100 interactions, irrespective of the strategies involved or the costs associated with them (Figure 7). A roughly linear distribution of final cardinal ranks in all cases suggests that, under given sets of conditions, no individuals were able to achieve especially prominent high or low status in the hierarchy. Although final results were similar among strategies, the patterns, by which mean cardinal ranks emerged from a series of structuring events, were different (Figure 8). Most notably, when fighting included higher maximum intensities (i.e. RE and HI models), cardinal ranks diverged more rapidly. The presence of escalation, as well as different strategies for fight initiation, influenced rank divergence to a lesser degree.

Discussion

Future fighting behavior depends on an individual's past interaction history (e.g. Jackson 1991; Goessmann et al. 2000; Hsu et al. 2006). This not only reflects current behavior and

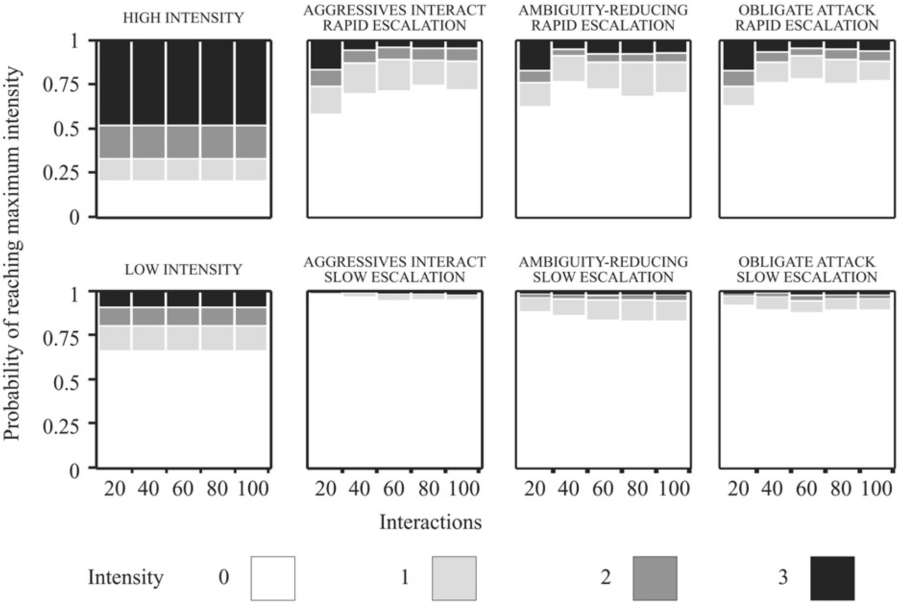

Figure 4. Proportion of fights in each 20 interaction interval that ended at a given maximum intensity. The pattern of probabilities in the two non-escalating models, HI and LI, is identical for all initiation strategies. Bars represent probabilities to reach a certain maximum intensity (higher intensities have darker shading).

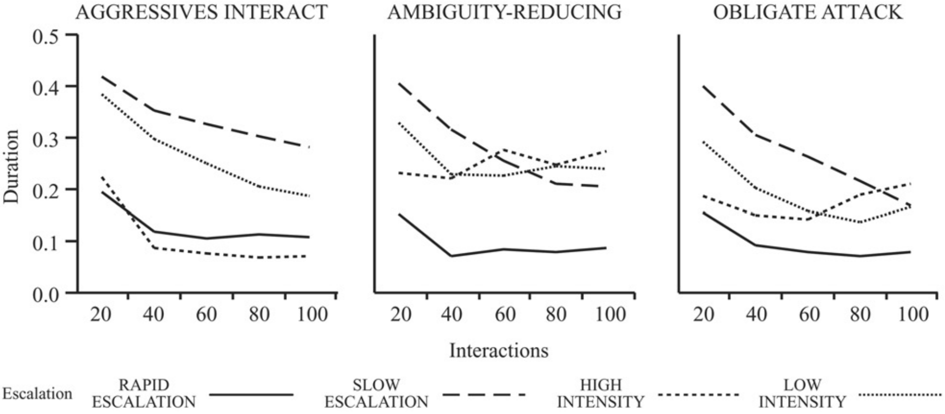

Figure 5. Mean fight duration in each 20 interaction interval for all scenarios. The duration is estimated and expressed as the DOM value of the lower-ranking contestant in the interacting pair, and is therefore dimensionless. The value of 0.5 corresponds to all participants having the initial value of DOM. Initiation strategies are separated as different graphs, while the dashed lines on those graphs represent four associated strategies of contest dynamics.

social status, but also critically determines future agonistic success. Status-dependent likelihood of fight initiation (e.g. Jackson 1991; Issa et al. 1999; Schneider et al. 2001; Song et al. 2006; May and Mercier 2006; but see also Gherardi and Daniels 2003) and context-dependent changes stemming from fight characteristics in contests between individuals of

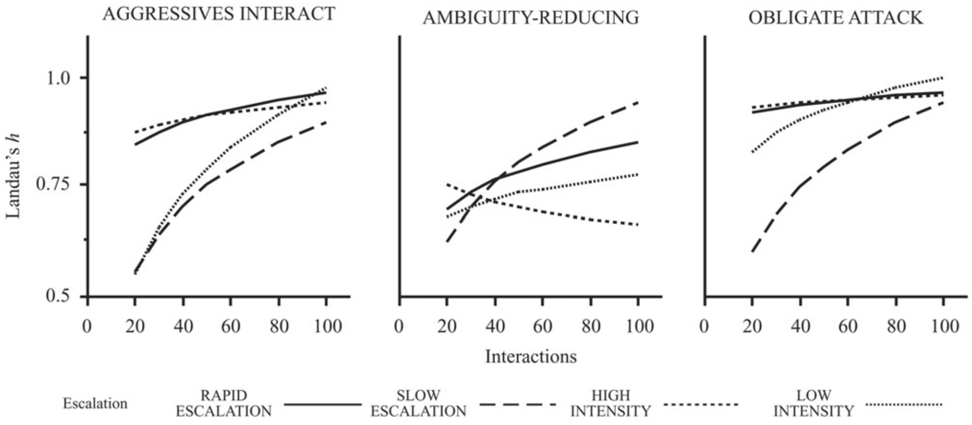

Figure 6. The degree of linearity, measured as the value of Landau's statistic *h*, as a function of the number of interactions for all scenarios. Each graph represents a different initiation strategy, and features the dashed curves for four associated strategies of contest dynamics.

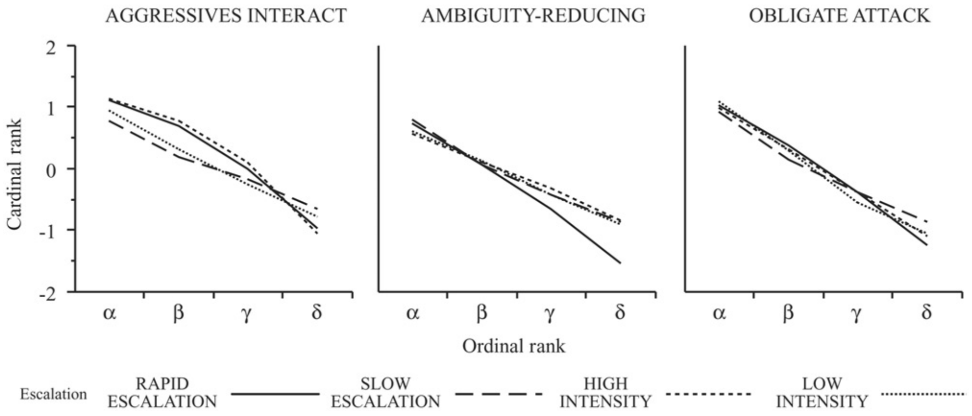

Figure 7. Means of final cardinal ranks (BBS method) after the initial 100 interactions plotted for every ordinal rank within a group. Different initiation strategies are shown as different graphs, while strategies of contest dynamics are represented as different dashed lines on those graphs.

different status (Beaugrand and Goulet 2000; Jennings et al. 2005) exist in a variety of taxa. Moreover, dominance hierarchies formed by repeated agonistic interactions reduce overall levels of aggression in groups of animals (Issa et al. 1999; Goessmann et al. 2000; Obermeier and Schmitz 2003; Delgado-Morales et al. 2004). By modulating its decisions with respect to its interaction history, an individual can therefore maximize the respective net gains in future dyadic interactions directly, while at the same time indirectly minimizing the costs of hierarchy formation and of attaining its social status. By implementing the interaction rules at the level of dyads, it is therefore possible to discern the effects of particular decision-making processes in fights on the properties of emergent social structure. The results of this study offer further insights on the intricate ties between these phenomena.

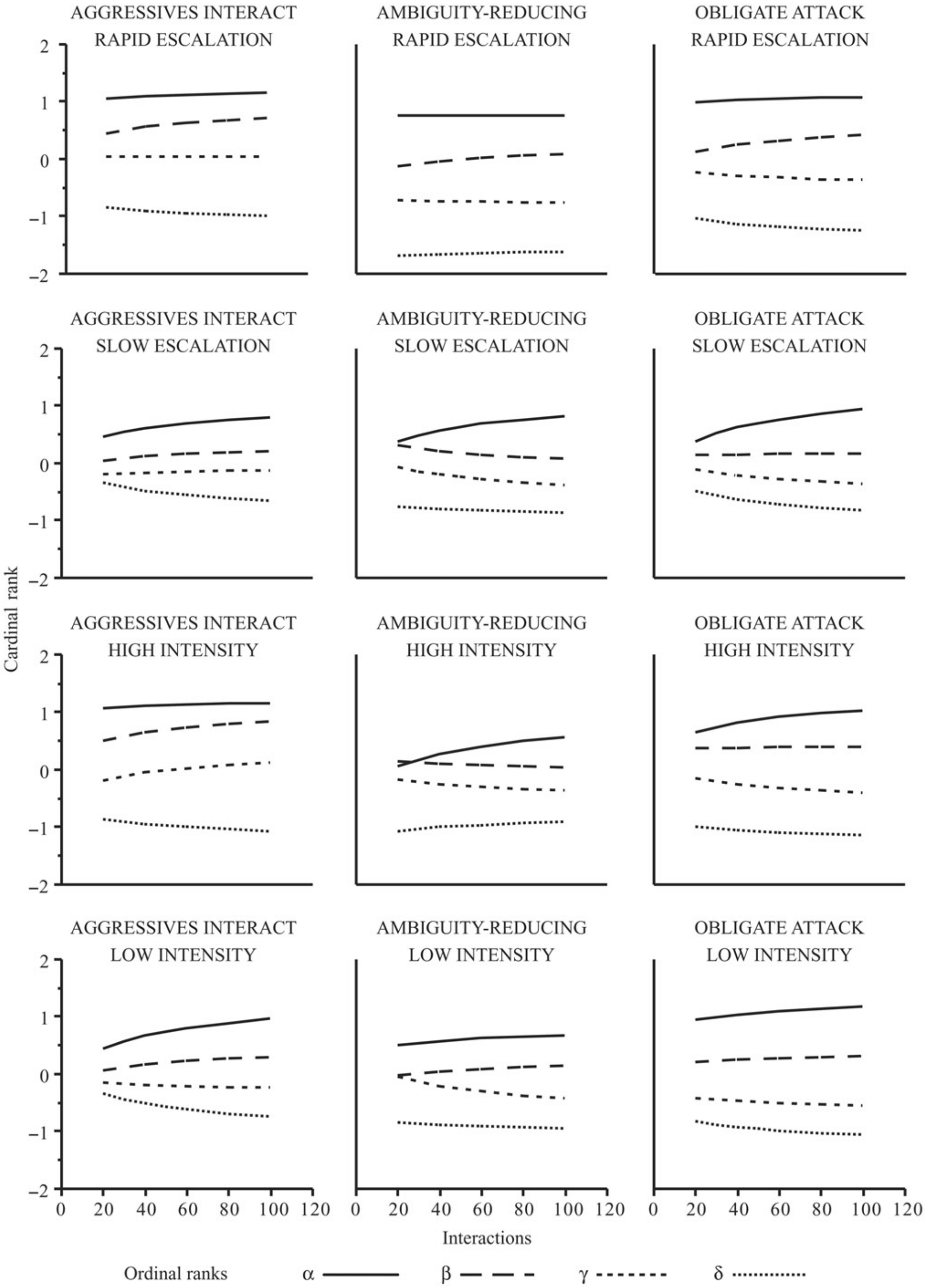

Figure 8. Cardinal ranks separated by individual's final ordinal rank as a function of number of interactions. All models in a given row have the same escalation-retreat strategy, while all models in a given column have the same initiation strategy. Ordinal ranks are represented as different dashed lines.

An increased likelihood of being the target of an attack in asymmetric contests effectively reduced the overall ambiguity of dominance relationships among individuals. In contrast, in scenarios where individuals preferably interacted with opponents of similar aggressive motivation level (i.e. symmetrical contests), hierarchical structures were both less distinct and slower to emerge. While such strategy may reduce the ambiguity in the immediate interacting pair, it is ultimately less effective in crystallizing dominance relationships within a group. The inherent uncertainty of outcome in fighting between closely matched individuals will make it considerably more difficult for such individuals to attain and defend a particular position in the hierarchy. Under such conditions, individuals will have a lower probability of achieving the series of wins (or losses) needed for rapid rank divergence. Such effects will be further exacerbated in systems with non-escalating contests where individuals experience discrete changes in aggressive motivation regardless of rank, and are thus more likely to feature individuals with ambiguous social status. Furthermore, eventual dominants will have few opportunities to reinforce their status due to the lack of suitable opponents, while subordinates will be able to remain competitive through successful interactions with other subordinates. Thus, while the AR strategy may be adequate for the resolution of immediate uncertainties in status for a given pair, it is less effective in producing hierarchically structured groups within a broader social context.

In the other two initiation strategies, where individuals were more likely to fight in asymmetric contests, hierarchical structures emerged more rapidly. Moreover, as a result of such contests fights in groups will be less costly and social status will be reinforced, further decreasing the need to interact. A tendency to participate in contests with a greater certainty of outcome aids in the propagation and reinforcement of dominance relationships by fostering series of wins or losses. Additionally, existing ambiguous relationships in matched pairs will be further reduced indirectly, through interactions with other members of a group. Once established, hierarchical relationships are also more likely to be maintained under such conditions, since the dominants will be able to reinforce their aggressive motivation through repeated interactions with subordinates, while at the same time subordinates will be less likely to achieve surprise upsets. This mechanism is further augmented by the presence of high-return, intense fighting, as such encounters will lead to a more rapid divergence of social status. Low fight intensity will eventually bring forth linearity, but more interactions will be needed for this to occur. Additionally, fights may become more frequent due to the slower promotion of both dominants and subordinates in systems where initiation is contingent upon the high levels of aggressive motivation. The overall level of aggressive motivation in such systems will remain relatively high, and therefore the increase in initiation by the dominants will not be counterbalanced by a corresponding decrease in initiation in pairs of subordinates.

Although initiation strategies generally exerted little effect on characteristics of fights, decisions pertaining to contest dynamics greatly impacted the behavioral parameters of fighting during formation and maintenance of group relations. While a greater intensity of initial fighting benefits in a rapid emergence of hierarchies, such fighting behavior is inherently more dangerous. Escalation strategies, by which individuals slowly acquire information about the opponent's strength in a stepwise fashion, reduce these costs considerably. Even though the overall probability of participating in intense fighting was identical in escalating and non-escalating scenarios, contests were resolved at shorter durations and lower levels of intensity in the presence of escalation strategies. This is likely due to the early emergence of subordinates, which will retreat early and at lower levels of intensity. Since rapid escalation in dyadic fights further facilitated the emergence of hierarchical relationships within the group, it also follows that success during initial intense contests will be particularly effective in determining the individual's eventual social status. This is supported by empirical evidence (Issa et al. 1999; Goessmann et al. 2000), where initial success served as a particularly strong predictor of final social status.

The results of this study therefore suggest that the number of interactions needed to form a hierarchy drops if those interactions are likely to be asymmetric, escalating, and intense, especially at the early stages of hierarchy formation. However, in species with dangerous weapons such as crayfish where the main costs are incurred through intense fighting, the strategies of this nature are associated with considerable risks. The employment of ritualized, slowly escalating fighting effectively decreases such inherent risks, but does so at the expense of longer durations and a slower emergence of the hierarchy. Conversely, in behavioral systems where the main costs are incurred by the time spent fighting, such as those where contestants suffer from an increased exposure to predation while interacting (e.g. Soderback 1994; Roth and Kitchell 2005), rapid escalation will lead to a faster emergence of the hierarchy and shorter bouts, while giving opponents less opportunity to assess the precise risks of injury. This is consistent with observations that juvenile crayfish, with a lower potential to injure each other because of their smaller claws and at a greater predation risk, will escalate more rapidly and fight more intensely for shorter durations than adults (Schroeder and Huber 2002).

In light of such considerations, individual decision-making processes in fighting ultimately result in a favorable cost-to-benefit ratio with respect to the formation and maintenance of hierarchical relationships in groups. By choosing to attack more often, to escalate to higher intensities more readily, and not to retreat, dominants are able to clearly control resources. Conversely, by opting to retreat early and at lower intensity levels, subordinates will be able to retain capacities that would otherwise likely be spent on unsuccessful fighting. These findings are consistent with game theory predictions (Maynard Smith and Parker 1976; Maynard Smith 1982), where a mixed strategy becomes an evolutionary stable strategy (ESS) in a population. In this case, the group forming the hierarchy would act as an analogue of a population in which a strategy of choice for each individual should depend on its relative social status. A stable ratio of strategies, where a portion of individuals who at some point become dominants behave aggressively and a portion of those who become subordinates avoid further intense contests, would thus translate into a stable hierarchical structure while minimizing the costs of its formation and maintenance. While the present simulation applied behavioral interaction rules independent of the participant's current social status, the challenge ahead lies in further elucidating dynamic contextual changes and their effect on social structuring.

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References

Appleby MC. 1983. The probability of linearity in hierarchies. Anim. Behav. 31:600–608.

Beacham JL. 1988. The relative importance of body size and aggressive experience as determinants of dominance in pumpkinseed sunfish, *Lepomis gibbosus*. Anim. Behav. 36:621–623.

Beacham JL. 2003. Models of dominance hierarchy formation: Effects of prior experience and intrinsic traits. Behaviour 140:1275–1303.

Beacham JL, Newman JA. 1987. Social experience and the formation of dominance relationships in the pumpkinseed sunfish (Lepomis gibbosus). Anim. Behav. 35:1560–1563.

Beaugrand JP, Goulet C. 2000. Distinguishing kinds of prior dominance and subordination experiences in males of green swordtail fish (*Xiphophorus helleri*). Behav. Process. 50:131–142.

Beaugrand JP, Payette D, Goulet C. 1996. Conflict outcome in male green swordtail fish dyads (*Xiphophorus helleri*). Interaction of body size, prior dominance/subordination experience, and prior residency. Behaviour 133:303–319.

Bergman DA, Kozlowski C, McIntyre JC, Huber R, Daws AG, Moore PA. 2003. Temporal dynamics and communication of winner-effects in the crayfish, *Orconectes rusticus*. Behaviour 140:805–825.

Chase ID, Bartolomeo C, Dugatkin LA. 1994. Aggressive interactions and inter-contest interval – how long do winners keep winning. Anim. Behav. 48:393–400.

Chase ID, Tovey C, Spangler-Martin D, Manfredonia M. 2002. Individual differences *versus* social dynamics in the formation of animal dominance hierarchies. Proc. Natl. Acad. Sci. USA 99:5744–5749.

Clutton-Brock TH, Albon SD. 1979. The roaring of red deer and the evolution of honest advertisement. Behaviour 69:147–170.

Daws AG, Grills J, Konzen K, Moore PA. 2002. Previous experiences alter the outcome of aggressive interactions between males in the crayfish, *Procambarus clarkii*. Mar. Freshw. Behav. Phy. 35:139–148.

Daws AG, Huber R. Dominance hierarchies and spatial distributions of crayfish, *Orconectes rusticus*. Manuscript submitted.

Delgado-Morales G, Hernandez-Falcon J, Ramon F. 2004. Agonistic behaviour in crayfish: The importance of sensory inputs. Crustaceana 77:1–24.

Drews C. 1993. The concept and definition of dominance in animal behavior. Behaviour 125:283–313.

Dugatkin LA. 1997. Winner and loser effects and the structure of dominance hierarchies. Behav. Ecol. 8:583–587.

Dugatkin LA, Earley RL. 2003. Group fusion: The impact of winner, loser, and bystander effects on hierarchy formation in large groups. Behav. Ecol. 14:367–373.

Enquist M, Leimar O. 1983. Evolution of fighting behavior – decision rules and assessment of relative strength. J. Theor. Biol. 102:387–410.

Enquist M, Leimar O. 1990. The evolution of fatal fighting. Anim. Behav. 39:1–9.

Enquist M, Plane E, Roed J. 1985. Aggressive communication in fulmars (*Fulmarus glacialis*) competing for food. Anim. Behav. 33:1007–1020.

Enquist M, Leimar O, Ljungberg T, Mallner Y, Seferdahl N. 1990. A test of sequential assessment game: Fighting in the cichlid fish *Nannocara anomala*. Anim. Behav. 40:1–14.

Francis RC. 1983. Experimental effects on agonistic behavior in the paradise fish, *Macropodus opercularis*. Behaviour 85:292–313.

Francis RC. 1988. On the relationship between aggression and social dominance. Ethology 78:223–237.

Gherardi F, Daniels WH. 2003. Dominance hierarchies and status recognition in the crayfish *Procambarus acutus acutus*. Can. J. Zool. 81:1269–1281.

Goessmann C, Hemelrijk CK, Huber R. 2000. The formation and maintenance of crayfish hierarchies: Behavioral and self-structuring properties. Behav. Ecol. Sociobiol. 48:418–428.

Guiasu RC, Dunham DW. 1997. Initiation and outcome of agonistic contests in male form I *Cambarus robustus* Girard, 1852 crayfish (Deacpoda, Cambaridae). Crustaceana 70:480–496.

Hack MA. 1997. Assessment strategies in the contests of male crickets, *Acheta domesticus* (L). Anim. Behav. 53:733–747.

Halperin JRP, Giri T, Elliott J, Dunham DW. 1998. Consequences of hyper-aggressiveness in Siamese fighting fish: Cheaters seldom prospered. Anim. Behav. 55:87–96.

Hemelrijk CK. 2000. Towards the integration of social dominance and spatial structure. Anim. Behav. 59:1035–1048.

Hock K, Huber R. 2006. Modeling the acquisition of social rank in crayfish: Winner and loser effects and self-structuring properties. Behaviour 143:325–346.

Hogeweg P. 1988. MIRROR beyond MIRROR, puddles of LIFE. In: Langton C, editor. Artificial life, SFI studies in the sciences of complexity. Redwood City: Addison-Wesley. pp 297–316.

Hollis KL, Dumas MJ, Singh P, Fackelman P. 1995. Pavlovian conditioning of aggressive behavior in blue gourami fish (*Trichogaster trichopterus*) – winners become winners and losers stay losers. J. Comp. Pscychol. 109:123–133.

Hsu YY, Wolf LL. 1999. The winner and loser effect: Integrating multiple experiences. Anim. Behav. 57: 903–910.

Hsu YY, Wolf LL. 2001. The winner and loser effect: What fighting behaviours are influenced?. Anim. Behav. 61:777–786.

Hsu YY, Earley RL, Wolf LL. 2006. Modulation of aggressive behaviour by fighting experience: Mechanisms and contest outcomes. Biol. Rev. 81:33–74.

Huber R, Delago A. 1998. Serotonin alters decisions to withdraw in fighting crayfish, *Astacus astacus*: The motivational concept revisited. J. Comp. Physiol. A 182:573–583.

Huber R, Kravitz EA. 1995. A quantitative analysis of agonistic behavior in juvenile American lobsters (*Homarus americanus* L). Brain Behav. Evolut. 50:60–68.

Huber R, Daws A, Tuttle SB, Panksepp JB. 2004. Quantitative behavioral techniques for the study of crustacean aggression. In: Wiese K, Schmidt M, editors. Physiology of the crustacean nervous system. Berlin: Springer. pp 186–201.

Huxley TH. 1880. The crayfish: An introduction to the study of zoology. New York: D. Appleton and Company.

Issa FA, Adamson DJ, Edwards DH. 1999. Dominance hierarchy formation in juvenile crayfish *Procambarus clarkii*. J. Exp. Biol. 202:3497–3506.

Jackson WM. 1988. Can individual differences in history of dominance explain the development of linear dominance hierarchies? Ethology 79:71–77.

Jackson WM. 1991. Why do winners keep winning? Behav. Ecol. Sociobiol. 28:271–276.

Jameson KA, Appleby MC, Freeman LC. 1999. Finding an appropriate order for a hierarchy based on probabilistic dominance. Anim. Behav. 57:991–998.

Jennings DJ, Gammell MP, Carlin CM, Hayden TJ. 2005. Win, lose or draw: A comparison of fight structure based on fight conclusion in the fallow deer. Behaviour 142:423–439.

Landau HG. 1951. On dominance relations and the structure of animal societies: I: Effect of inherent characteristics. Bull. Math. Biophys. 13:1–19.

Maan ME, Groothius TGG, Wittenberg J. 2001. Escalated fighting despite predictors of conflict outcome: Solving the paradox in a South American cichlid fish. Anim. Behav. 62:623–634.

May HY, Mercier AJ. 2006. Responses of crayfish to a reflective environment depend on dominance status. Can. J. Zool. 84:1104–1111.

Maynard Smith J. 1982. Evolution and the theory of games. Cambridge: Cambridge University Press.

Maynard Smith J, Parker GA. 1976. The logic of asymmetric contests. Anim. Behav. 24:159–175.

Neat FC, Taylor AC, Huntingford FA. 1998. Proximate costs of fighting in male cichlid fish: The role of injuries and energy metabolism. Anim. Behav. 29:221–240.

Obermeier M, Schmitz B. 2003. Recognition of dominance in the big-clawed snapping shrimp (*Alpheus heterochaelis Say 1818*) part I: Individual or group recognition? Mar. Freshw. Behav. Physiol. 36:1–16.

Otronen M. 1990. The effect of prior experience on the outcome of fights in the burying beetle, *Nicrophorus humatio*. Anim. Behav. 40:980–1004.

Pagel M, Dawkins MS. 1997. Peck orders and group size in laying hens: 'Future contracts' for non-aggression. Behav. Process. 40:13–25.

Panksepp JB, Huber R. 2004. Ethological analyses of crayfish behavior: A new invertebrate system for measuring the rewarding properties of psychostimulants. Behav. Brain Res. 153:171–180.

Parker GA. 1974. Assessment strategy and the evolution of fighting behaviour. J. Theor. Biol. 47:223–243.

Parker GA, Rubenstein DI. 1981. Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. Animal Behav. 29:221–240.

Roth BM, Kitchell JF. 2005. The role of size-selective predation in the displacement of Orconectes crayfishes following rusty crayfish invasion. Crustaceana 78:297–310.

Schneider RAZ, Huber R, Moore PA. 2001. Individual and status recognition in the crayfish, *Orconectes rusticus*: The effects of urine release on fight dynamics. Behaviour 138:137–153.

Schroeder L, Huber R. 2002. Fight strategies differ with size and allometric growth of claws in crayfish, *Orconectes rusticus*. Behaviour 138:1437–1449.

Soderback B. 1994. Interactions among juveniles of 2 fresh-water crayfish species and a predatory fish. Oecologia 100:229–235.

Song CK, Heberholz J, Edwards DH. 2006. The effects of social experience on the behavioral response to unexpected touch in crayfish. J. Exp. Biol. 209:1355–1363.

Stocker AM, Huber R. 2001. Fighting strategies in crayfish *Orconectes rusticus* (Decapoda, Cambaridae) differ with hunger state and the presence of food cues. Ethology 107:727–736.

Taylor PW, Hasson O, Clark DL. 2001. Initiation and resolution of jumping spider contests: Roles of size, proximity, and early detection of rivals. Behav. Ecol. Sociobiol. 50:403–413.

Turner GF, Huntingford FA. 1986. A problem for game-theory analysis–assessment and intention in male mouthbrooder contests. Anim. Behav. 34:961–970.

Van Doorn GS, Hengeveld GM, Weissing FJ. 2003a. The evolution of social dominance I: Two-player models. Behaviour 140:1305–1332.

Van Doorn GS, Hengeveld GM, Weissing FJ. 2003b. The evolution of social dominance II: Multi-player models. Behaviour 140:1333–1358.

Whitehouse MEA. 1997. Experience influences male-male contests in the spider *Argyrodes antipodiana* (Theridiidae: Araneae). Anim. Behav. 53:913–923.