Modeling the acquisition of social rank in crayfish: winner and loser effects and self-structuring properties

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Summary

Stable hierarchical structures within groups of crayfish emerge from a series of dyadic encounters among its members. A modeling approach was used to explore the progression in fighting success of individual entities under different behavioral scenarios and the respective outcomes were fitted to empirical data. Changes in the relative magnitude of winner and loser effects influenced the divergence of hierarchical ranks: a few high-ranking despots rapidly emerged when winner effects were dominant, an excess of loser effects quickly produced individuals of distinctly low rank, while a balance of winner and loser effects produced a more gradual divergence of ranks. Comparison with empirical data from the formation of social group structure in crayfish indicated a greater importance for loser effects.

Keywords: winner-loser effects, dominance hierarhy, social rank, self-structuring, aggression.

Introduction

Social relations in many animal groups emerge from repeated agonistic interactions. Aside from relatively fixed, individual differences between contestants (e.g., size), the behavior and the outcome of subsequent dyadic interactions is highly contingent on dynamic variables, such as an individual's previous history of encounters (e.g., Bakker & Sevenster, 1983; Beacham,

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1988; Otronen, 1990; Chase et al., 1994, 2002; Hollis et al., 1995; Beaugrand et al., 1996; Whitehouse, 1997; Hsu & Wolf, 1999; Taylor et al., 2001). Repeated agonistic interactions thereby progressively crystallize the social structures present within the group. Once dominance relationships are established, they are likely to be maintained in subsequent encounters without further prolonged assessment of individual abilities (Winston & Jacobson, 1978). However, it is neither intuitively obvious nor easily predictable in what way repeated applications of simple rules used in the resolution of dyadic interactions give rise to the respective social group patterns. The particular mechanisms that determine individual ranks and structure such groups thus warrant further investigation.

Social dominance, referring to predictable asymmetries in agonistic success between contestants, is typically associated with relative differences in resource holding potential (RHP) (e.g., Parker, 1974; Maynard Smith & Parker, 1976; Dugatkin & Biederman, 1991; Hack, 1997; Stokkebo & Hardy, 2000) or each contestant's assessment of its own RHP (Smith et al., 1994; Whitehouse, 1997; Taylor et al., 2001). In most systems, social dominance is contingent upon previous success, where individuals with previous wins become more likely to win again, while a loss lowers an individual's chances for future wins. Such 'winner-loser effects' (Chase et al., 1994) may reduce actual fighting capabilities, or alter perceptions of associated risks or the odds of winning (Hsu & Wolf, 2001). Effective communication of an individual's aggressive state therefore provides a general mechanism in which information about social status is conveyed independently of the need to ascertain the previous success history with a given opponent (Winston & Jacobson, 1978; Copp, 1986). On a group level, dyadic interactions act as structuring events, and complex social structures emerge from polarities inherent in the resolution of simple dyadic interactions (Vannini & Sardini, 1971; Atema & Cobb, 1980; Issa et al., 1999; Goessmann et al., 2000; but see also Chase et al., 2002, 2003). Hierarchies under such conditions assume a linear structure in most taxa (Wilson, 1975), and individual ranks can be unambiguously determined based on previous successes towards other members of a group. However, the role that combined winner and loser effects play in formation of hierarchies in animal groups cannot be easily inferred from outcomes of respective dyadic encounters alone.

While documenting winner and loser effects in dyads has been fairly straightforward, it remains difficult to examine such variables empirically in larger groups of individuals. Mathematical and computer modeling approaches have frequently been proposed in literature to effectively investigate how various parameters governing dyadic interactions affect the formation of self-organizing hierarchies in larger groups (e.g., Hogeweg & Hesper, 1983; Hogeweg, 1988; Bonabeau et al., 1995, 1997; Hemelrijk, 1996, 1997, 1998, 2000, 2002; Taylor & Elwood, 2003). In a series of models, Hemelrijk and coworkers explored the interdependence between dominance interactions, spatial structure, and other factors such as resource distribution and sex-specific aggression (Hemelrijk et al., 2003; Hemelrijk & Gygax, 2004; Hemelrijk & Wantia, 2005). While these models incorporated varying degrees of aggressive behavior displayed by the participants, for example those of a different sex, they did not focus on the dynamic properties of interactions themselves and their consequences on the emerging social structures. Another model specifically examined the importance of winner and loser effects on the resulting social structure (Dugatkin, 1997; Dugatkin & Earley, 2003). When only winner effects were considered, a clear hierarchical structure emerged, but when only loser effects were important, a single despotic alpha individual emerged. While this model offers insights into the consequences of winner and loser effects, it is not clear how final hierarchical relationships came to be, and how individual decisions to initiate or escalate would affect their emergence.

Though underlying rules from general models can be applied to empirical social systems, few theoretical models have taken advantage of published empirical data to guide the choice of actual values for the various parameters that affect dominance hierarchy formation. The extensive empirical characterization of social interactions in decapod crustaceans, as well as types of decisions involved in these interactions, presents an ideal opportunity for development of just such model. Interactions in Decapoda involve highly stereotyped threat displays that progressively escalate into restrained forms of physical combat, and finally into brief periods of unrestrained fighting where opponents may even inflict injuries on each other (for a characterization of contests, see Huber & Kravitz, 1995). Previous studies have independently ascertained the importance of various parameters on the outcome of interactions in this system, such as the link between altered decision to retreat and intensity of the contests (Huber & Kravitz, 1995), little tendency to form social coalitions (Huxley, 1880), propensity for formation of dominance hierarchies that are linear in nature (Issa et al., 1999; Goessmann et al., 2000), interdependency between levels of aggression, fight escalation, and the resulting outcome (Schroeder & Huber, 2002), and the temporal dynamics of winner effects (Bergman et al., 2003). This wealth of empirically determined parameter values permits construction of a comprehensive model characterizing the role of winner and loser effects in the formation of complex social structures.

The present study thus aims first to provide a case-specific theoretical model by integrating a previously published general theoretic model (Hemelrijk, 2000) with a system where both empirically determined values for key parameters as well as the final outcome are known. Secondly, it explores the effects of contextually-dependent winner and loser effects on dominance hierarchy, and their relative influence on the resulting social structure, when their magnitude is varied independently of each other. Finally, it compares and contrasts characteristics of the social structures generated by computer modeling to the corresponding values obtained in previous empirical investigations of the crayfish system (Goessmann et al., 2000). The comprehensive model proposed in this study thus aids in shedding new light on how combined winner-loser effects resulting from dyadic interactions lead to the emergence of hierarchical structuring observed in social groups.

Methods

A modeling framework was developed using the Java programming language (Java 1.4.1 API) in order to provide a spatially explicit behavioral system where individual entities interacted in a virtual arena implemented as a 2-dimensional spatial constraint.

The non-behavioral parameters of the model, such as the size of the arena and group size, were designed so as to closely match the parameters of an empirical experimental setup published in Goessmann et al. (2000). A continuous wrap-around world representing a space 0.6 × 0.4 m (270 by 180 pixels of coordinate system) provided a spatial constraint, where entities that left the arena at the south or east border automatically reentered it from the north or west border, respectively. This allowed simulated entities to move freely in an open space without altering the number of entities available for interaction. Individuals with a dimension of 1 pixel extent were placed into this space at a random starting location for each run of the model. Each run featured multiple iterations of moves by the agents in the arena (Figure 1). Every individual moved independently of the rest of the group by selecting at random a move from a distribution of 9765 empirically determined moves (Panksepp & Huber, unpubl.). The moves were recorded in four-second intervals as vectors, and involved measuring the distance covered and movement direction of a solitary and freely moving adult crayfish in a two-dimensional space that was devoid of any physical obstacles. Each run of the model consisted of a group of four individuals moving independently in the arena, and each group was allowed to interact for an equivalent of three hours (2700 moves).

The rules governing interactions between individuals were adopted from a model published by Hemelrijk (2000), and modified to reflect the specific behavioral system of interest. Individuals were assigned a variable that represented their aggressive state which in turn determines the relative probability of an individual to win future interactions (DOM). All individuals started with a DOM value set at 0.5, which in turn meant that they were all equally likely to win an initial interaction against a naïve opponent. In order to keep DOM values positive, minimum DOM values were limited at 0.0001. A decision to interact was made each time when two of the contestants came to within a certain critical distance of each other, i.e. when the distance between them was equal to or less than one tenth of a longer side of the arena (27 pixels of coordinate system or an equivalent of 0.06 m). In the present models, all such encounters resulted in an interaction. All interactions were resolved instantly, in that an individual won or lost the interaction in the very same iteration when it came within the critical distance of the opponent. The loser then performed an escape behavior, moving directly away from the winner for a randomly chosen distance between 1 and 3 critical distances, and only then were individuals in a group allowed to resume movement.

The interactions were resolved following the equations in a previously published work (Hemelrijk, 2000) where the relative difference between two contestants' DOM values is compared against a randomly chosen number from zero to one to determine the winner. By comparing the values of the two contestants and determining the resulting outcome, contestant i won an interaction against contestant j if

$$\mathrm{DOM_i}/(\mathrm{DOM_i} + \mathrm{DOM_j}) > \mathrm{RND}(0, 1)$$

Therefore, an individual with a higher DOM value was more likely to win an interaction than its opponent. DOM values of each contestant were then

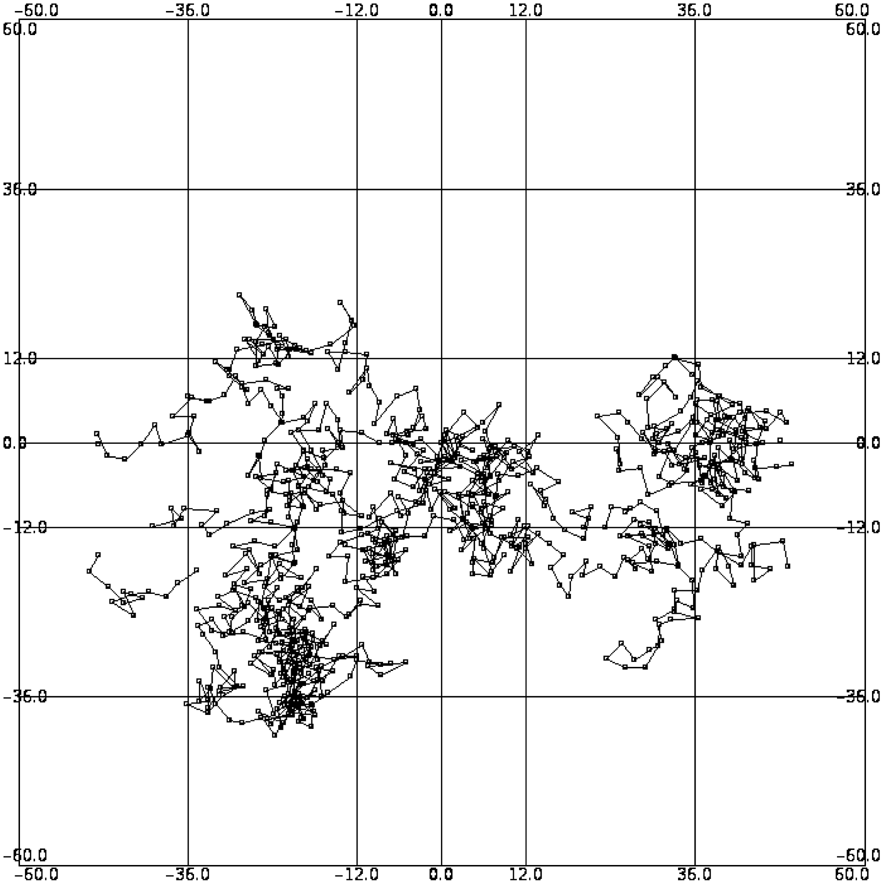

Figure 1. Entities moving in a virtual arena. After initial random assignment of starting locations, entities changed their location in four-second interval equivalents following vectors recorded from live animals. Each dot represents a position of an entity in space at a certain point in time, and the lines connecting the dots represent move vectors performed by the entities.

updated to reflect the outcome of an interaction, that is, by increasing the DOM value of the winner and decreasing DOM value of the loser. Updating of DOM values was done in a following fashion:

$$\mathrm{DOM}_{\mathrm{i(T+1)}} = \mathrm{DOM}_{\mathrm{i(T)}} + (w_{\mathrm{i}} - \mathrm{DOM}_{\mathrm{i(T)}}/(\mathrm{DOM}_{\mathrm{i(T)}} + \mathrm{DOM}_{\mathrm{j(T)}})) \times \mathrm{STEPDOM}$$

$$\mathrm{DOM}_{\mathrm{j(T+1)}} = \mathrm{DOM}_{\mathrm{j(T)}} - (w_{\mathrm{i}} - \mathrm{DOM}_{\mathrm{i(T)}}/(\mathrm{DOM}_{\mathrm{i(T)}} + \mathrm{DOM}_{\mathrm{j(T)}})) \times \mathrm{STEPDOM}$$

where $\mathrm{DOM}_{\mathrm{i(T)}}$ and $\mathrm{DOM}_{\mathrm{j(T)}}$ are DOM values for the two contestants before the interaction that are also used in calculation of the outcome, $\mathrm{DOM}_{\mathrm{i(T+1)}}$ and $\mathrm{DOM}_{\mathrm{j(T+1)}}$ are DOM values updated as a result of the interaction outcome, and w represents the determined outcome of an interaction, where $w_{\mathrm{i}} = 1$ if the individual i won an interaction and $w_{\mathrm{i}} = 0$ if it lost. In other words, the DOM value changed following a damped positive feedback pattern, where winning against an opponent with a comparatively low DOM value yielded less of a change in both contestants' DOM values, and conversely, winning against an opponent with an equal or higher DOM value resulted in a larger change in both DOM values. While this pattern follows from the model postulates themselves (Hemelrijk, 2000), there is also empirical evidence that supports it (Huber & Kravitz, 1995; Beaugrand & Goulet, 2000; Goessmann et al., 2000). As it follows from the equations, the change in DOM value as a result of an interaction additionally depended on a scaling factor STEPDOM, which could assume values between zero and one. In the present model, STEPDOM was used to represent contextually-dependent changes in a DOM value which resulted from characteristics of a fight itself. If STEPDOM value was high, the resulting change in DOM was also high, whereas a low STEPDOM value resulted in a low change in DOM. Therefore, the changes in DOM value were not fixed for every interaction, but rather depended on the value of DOM for each contestant, their relative difference, and the values of STEPDOM.

Previous work (e.g., Huber & Kravitz, 1995) established that conflicts in decapod crustaceans involve a series of stereotyped behaviors that progressively escalate in intensity over time. With each higher intensity level, animals are able to acquire more information about an opponent, and thus assess the probability to win an interaction, which in turn determines their decision about whether to continue fighting. The duration of the interaction is therefore determined by the loser's decision to retreat, and its decision to retreat in turn influences the maximum intensity reached in an interaction. At the same time, the intensity level is an indication of the amount of information gathered by comparing each others' fighting prowess, both because of the time spent collecting the information and because of the escalating nature of the assessment process.

Since conflicts in the model are resolved instantaneously, duration of an interaction was not modeled in absolute terms of time spent interacting. Rather, it was used solely for the purpose of determining the probability of reaching certain maximum intensity in a fight. Since it can be assumed that the aggressive state of the individual with a lower DOM value will determine the point at which it will make a decision to retreat from an interaction and thereby end an encounter, DOM value of the lower ranking individual was used as an estimate for the duration of the interaction. This is consistent with observations that fights involving dominants and subordinates tend to be short and reach low maximum intensities (Huber & Kravitz, 1995), and have less of an effect in terms of impact on the contestants' fighting experience (Beaugrand & Goulet, 2000). In order to simulate the interdependence between the duration and maximum intensity reached in an interaction, a probability to reach each maximum intensity level for a given duration was calculated from previously published results (Huber & Delago, 1998; Stocker & Huber, 2001; Schroeder & Huber, 2002). Thus, the probabilities of reaching certain fight intensity in the present model follow the formulas for the sigmoid curves that describe fight intensity as a function of duration in those studies. Each intensity was then attributed a specific value of STEPDOM, where high intensity fights were attributed with high values of STEPDOM and therefore resulted in a larger degree of change in DOM value, while in turn low intensity fights were ascribed a low STEPDOM value and resulted in comparatively lower changes in DOM. The escalation rate was kept constant for all models presented in this study.

These probabilities were then incorporated into the modeling framework to simulate contextually-dependent changes in aggressive state of the individuals. In other words, if at least one of the contestants in a given interaction had a relatively low DOM value, i.e. aggressive state, that particular interaction was less likely to reach a high maximum intensity, and therefore also less likely to have a high resulting change in DOM value for either contestant regardless of the actual outcome. However, due to the probabilistic interdependency between fight duration (determined by the DOM value of a lower-DOM contestant) and fight intensity (represented as the STEPDOM factors of different magnitude), it was nevertheless possible for a contest between two individuals to result in different changes in DOM from those expected if the changes were made on the basis of the DOM values alone. Thus, it was possible, but not probable, for a contest between two individuals who both had high DOM values to occur at a low intensity, resulting in relatively small subsequent changes in DOM values for the contestants, even though both of them had high DOM values. The opposite was likewise true, in that even an interaction in which at least one of the participants had a low DOM value could have potentially resulted in a high-intensity contest and subsequent relatively large changes in DOM values. Thus, the changes in DOM values were dependent not only on the relative DOM values of the contestants, but also on the nature of the interaction that took place.

The tendency for the change in probability of winning an interaction to revert to its initial state has also been modeled. A study by Bergman et al. (2003) indicated that crayfish that had won an interaction tended to win 10/10 of the interactions against naïve opponents immediately after the winning experience as opposed to the 5/10 wins of the control animals, while they tended to win only 8/10 of the subsequent interactions if the time between the two contests was 40 minutes. Using these results, a formula was derived to adjust for the changes in DOM value that happen over time, where the DOM values altered through interactions tended to revert to the initial value in an exponential fashion, reaching approximately 2/3 of the starting change after an equivalent of 40 minutes had passed. If the DOM value of an agent after any move was different from the starting value of DOM $= 0.5$, before the agent was allowed to interact or move again, its DOM value was adjusted in the following fashion:

$$\mathrm{DOM}_{\mathrm{i(decayed)}} = \mathrm{DOM}_{\mathrm{i(T)}} - 1/3N \times (\mathrm{DOM}_{\mathrm{i(T)}} - \mathrm{DOM}_{\mathrm{i(initial)}})$$

where $\mathrm{DOM}_{\mathrm{i(decayed)}}$ is the decayed value of DOM for agent i used in all post-adjustment calculations, $\mathrm{DOM}_{\mathrm{i(T)}}$ is the DOM value of the agent i after the move T was made, $\mathrm{DOM}_{\mathrm{i(initial)}}$ is the starting value of DOM for agent i ($\mathrm{DOM}_{\mathrm{i(initial)}} = 0.5$ in all calculations), and N is the number of moves performed 40 minutes (effectively, it is the measure of elapsed time; $N = 600$ in all calculations). Thus, the DOM value of an agent will change more rapidly the greater its difference from the starting value of 0.5 is. The resulting decay of positive and negative deviations from the initial value of DOM followed the same pattern, that is, both winner and loser effects followed an identical temporal pattern of decay.

The present study utilized the model described above to explore the importance of winner and loser effects and their context-dependent values on the formation of dominance hierarchies. Previous experiments in Decapoda (Huber & Kravitz, 1995) have characterized four different levels of maximum fight intensity that interactions between individuals can reach: intensity of 0, 1, 2, and 3, respectively. In the present model, a different value of STEPDOM was ascribed to each of these maximum fight intensities. Furthermore, three different sets of STEPDOM values, each comprised of four STEPDOM values, were used in the model. These are: low set (STEPDOM values of 0.03125, 0.0625, 0.125, 0.25 for intensity of 0, 1, 2, and 3, respectively), medium set (STEPDOM values of 0.0625, 0.125, 0.25, 0.5 for intensity of 0, 1, 2, and 3, respectively) and high set (STEPDOM values of 0.125, 0.25, 0.5, 1 for intensity of 0, 1, 2, and 3, respectively). Thus, in any set, interactions reaching the maximum intensity of 1 would have twice as great scaling factor and subsequent changes in DOM value than those reaching the maximum intensity of 0. Likewise, interactions reaching the maximum intensity of 1 which utilized the medium set of STEPDOM values would have twice as great scaling factor and subsequent changes in DOM than those which utilized the low set.

By independently combining the aforementioned sets of STEPDOM values for winner and loser effects in the general modeling framework, nine different model scenarios were constructed in order to explore all the possible combinations between sets. A total of 50 replicates were created for each of the nine scenarios. All the measurements were obtained in regular intervals after 20 interactions occurred across the group irrespective of the identity of the individuals involved in them. Interactions that took place after the last whole 20-interaction interval in a group was completed were not taken into account so as to keep the recording process limited to discrete preset intervals. A choice of data collection in 20-interaction intervals, in combination with selected group and arena sizes, also diminished the probability of getting missing relationships between group members in the early stages of a simulation. Such incomplete results would have been discarded had they occurred, and the respective trial rerun. However, no results needed to be discarded due to missing relationships between group members.

The program recorded each individual's ordinal rank and cardinal rank measured using the Batchelder-Bershad-Simpson (BBS) method (Jameson et al., 1999), as well as the number of overall interactions in a group and the number of elapsed moves. Landau's statistic h (Landau, 1951) was also computed to compare the number of transitive triads to those maximally possible (Appleby, 1983). All the measured parameters were cumulative, i.e. took into account all the previous interactions. The degree of linearity was then plotted as a function of the number of interactions that took place within the group, and the characteristics of slopes for the resulting logarithmic best-fit curves compared across all scenarios. Means and variances of cardinal ranks recorded at the end of each trial for each individual were also compared across scenarios in order to examine the characteristics of the resulting social structures. A two-way analysis of variance (ANOVA) was used to elucidate the role that relative differences in the size of winner and loser effects play in the determination of an individual's final rank. The results from the models were then compared to those obtained in an empirical setup (Goessmann et al., 2000) to examine similarities and differences in patterns of outcomes of the measured parameters for hierarchies observed in virtual and empirical settings.

Results

A total of 14316 20-interaction intervals were recorded in all 450 groups, with a number of interactions per group ranging from 520 to 720, and a median value of 640 interactions per group. In all models, interactions between individuals resulted in clear dominance hierarchies. A degree of linearity approached 1 in a logarithmic fashion with increasing number of interactions within the group. This tendency was more pronounced in models that had comparatively large loser effects. Slopes of logarithmic best-fit lines were invariably shallower and intercepts larger in cases with higher loser effects if winner effects were kept constant. The parameter estimates describing the degree of linearity in a hierarchy (expressed as Landau's statistic h) as a function of number of interactions that took place in a group for all models are presented in Table 1.

When cardinal ranks recorded after the 3-hour period were compared among models, three distinct patterns of their distribution emerged (Figure 2), depending on the relative difference between winner and loser effects. In three models where winner and loser effects were equal, the variance of cardinal ranks was equal for all four ordinal ranks, and the cardinal rank means followed a linear pattern. In the models where the winner effect was comparatively greater than the loser effect, variance for the highest ranking animal's final cardinal rank was larger than variances for any of the remaining three individuals, and final cardinal rank means followed an exponential pattern. However, in the models where loser effects were comparatively greater than the winner effects, it was the variance of the δ individual's final cardinal rank that was greater than the variances of the other three individuals, and final cardinal rank means followed a logarithmic pattern.

Table 1. Parameter estimates for curvilinear best-fit lines (ln(interactions)) describing the degree of linearity (measured as Landau's statistic h) as a function of number of interactions that took place in a group over all model versions. The models are listed according to the magnitude of winner and loser effect used in their generation. The values presented for each model are estimates for intercept and slope and their 95% confidence intervals. All values are given in units of h. For a given magnitude of winner effects, both slope and intercept were invariably lower in models with lower loser effects, while the same is not observed across models with the same magnitude of loser effects.

	Winner effect					
	High		Medium		Low	
	Intercept ±95% CI	Slope ±95% CI	Intercept ±95% CI	Slope ±95% CI	Intercept ±95% CI	Slope ±95% CI
Loser effect						
High	0.734	0.043	0.797	0.03	0.796	0.029
	0.7-0.767	0.037-0.049	0.759-0.835	0.023-0.037	0.756-0.837	0.022-0.036
Medium	0.658	0.048	0.537	0.076	0.586	0.068
	0.602-0.715	0.038-0.058	0.497-0.578	0.067-0.083	0.55-0.622	0.062-0.074
Low	0.495	0.062	0.438	0.085	0.429	0.089
	0.417-0.573	0.049-0.077	0.383-0.494	0.075-0.095	0.376-0.483	0.08-0.099

Three models representing extreme variations in magnitude of winner-loser effects (high winner – low loser or HL, medium winner – medium loser or MM, low winner – high loser effects or LH, respectively) were further analyzed to explore the emergence of social structure over time under these conditions. Individuals' cardinal ranks recorded over the course of three hours were grouped according to the final ordinal rank each individual assumed at the end, and plotted over the number of interactions that took place in the group. The resulting best-fit curves for cardinal ranks are shown in Figure 3. In the HL model, a distinct α individual was present at first, but as the interactions progressed, the difference between α and the remaining ranks slowly decreased, resulting in a hierarchical structure that became less pronounced with time. In the MM model, hierarchical structure was ambiguous at start, with little difference between individual ranks, but later it became progressively more pronounced with all ranks being clearly distinct from each other. In the LH model, the structure was stable from the start, with difference between low ranking animals being more pronounced than

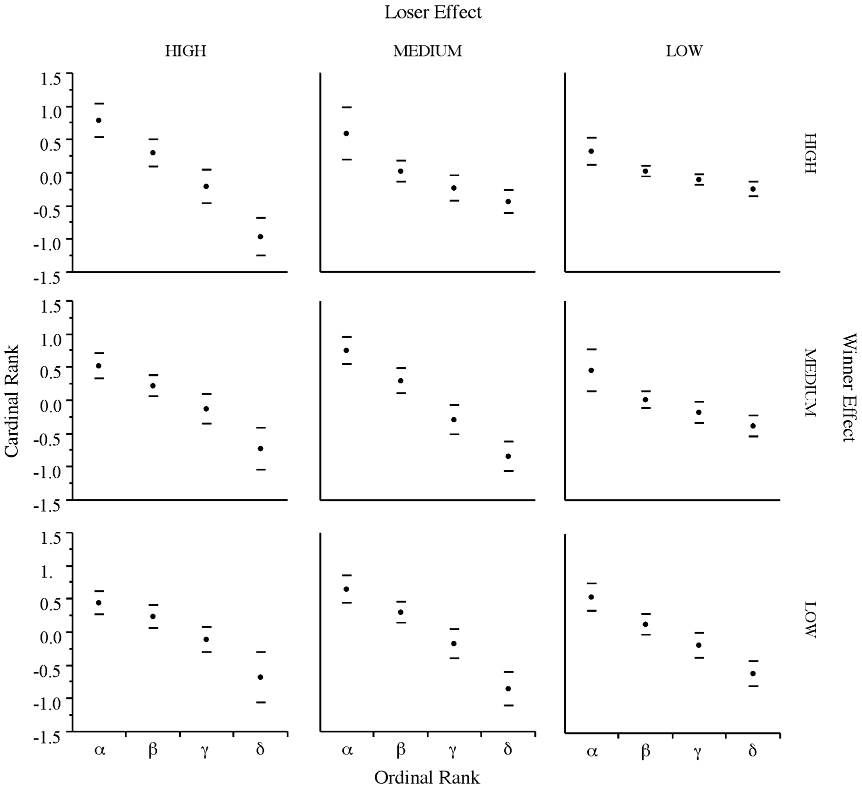

Figure 2. Means and standard deviations of final cardinal ranks (BBS method) plotted for each ordinal rank within a group. Models with equal winner and loser effects exhibit linear distribution of means and homoscedasticity; models in the upper right triangle exhibit exponential distribution of means and in relative terms highly variable cardinal ranks for highest ranking individuals; models in the lower left triangle exhibit logarithmic distribution of ranks and in relative terms highly variable cardinal ranks for lowest ranking individuals.

the difference between α and β, and it remained to be so over the duration of the experiment, the only exception being that the lowest ranking individual experienced further decreases in its respective cardinal rank. For the same three models, the degree of linearity across all groups plotted as a function of number of interactions was examined (Figure 4). The hierarchy structure was most ambiguous in the HL model regardless of the number of interactions that elapsed. The MM model exhibited a markedly logarithmic relationship between the degree of linearity and the number of interactions: the structure became less ambiguous over time. In the LH model, the hierarchy was highly linear and stable from the start and remained so with subsequent interactions.

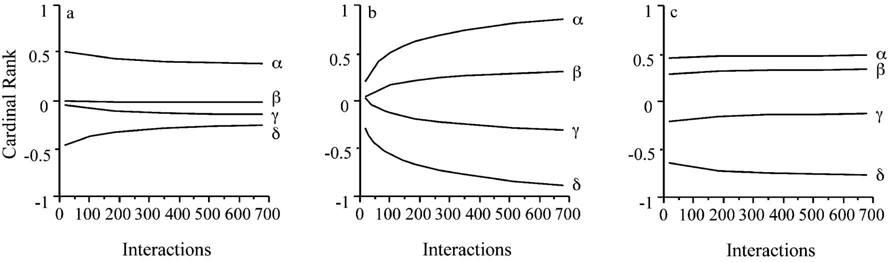

Figure 3. Cardinal ranks separated by an individual's final ordinal rank as a function of the number of interactions for three models: (a) high winner – low loser effects (HL); (b) medium winner – medium loser effects (MM); (c) low loser – high winner effects (LH). In the HL model, the distinction between ranks, apparent for α and δ individuals initially, became less pronounced with subsequent interactions. In the MM model, the hierarchy became less ambiguous and more stable with subsequent interactions, and the cardinal ranks increased for the high ranking individuals and decreased for the low ranking ones. In the LH model, ranks remained stable for all individuals except δ, whose cardinal rank decreased. The difference between high ranking individuals is low, and there is no pronounced difference between α and β individuals.

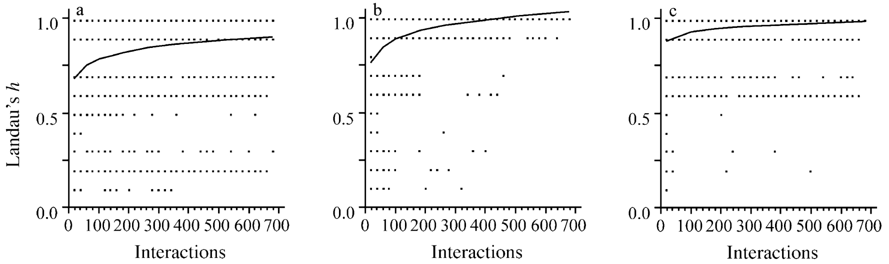

Figure 4. The degree of linearity, measured as the value of Landau's statistic h, as a function of the number of interactions that took place in a group for three models: (a) high winner – low loser effects (HL); (b) medium winner – medium loser effects (MM); (c) low loser – high winner effects (LH). The data points indicate the measure of linearity obtained from each group at a given interaction interval and represent the actual data distribution, while the best-fit curves point to the trends expected from the outcomes. In the HL model, there was a tendency towards linearity, but the intercept was low and the slope was shallow, with cases of low linearity hierarchies even after 500 interactions. In the MM model, the relationship was pronouncedly logarithmic, and the degree of linearity increased as the ranks diverged. In the LH model, the degree of linearity was high from the start, and remained so over time.

A two-factor analysis of variance was performed to test for the effect of size of winner and loser effects on the final cardinal rank of individuals. Both winner and loser effects, as well as the interaction between winner and loser effects, were found to have a significant effect on the final cardinal rank for

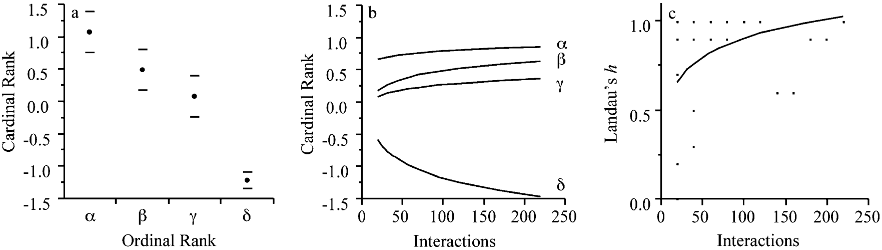

Figure 5. Analysis of hierarchical structures performed on the empirical data (Goessmann et al., 2000). (a) Means and standard deviations of final cardinal ranks (measured by BBS method) plotted for each ordinal rank within a group; although the variance for δ individuals was low, the rank means followed a logarithmic pattern. (b) Cardinal ranks separated by an individual's final ordinal rank as a function of number of interactions; the hierarchy was stable from the start, with ordinal rank for δ individual becoming more negative as interactions progressed, while other individuals exhibited little change from their starting values. (c) The degree of linearity, measured as the value of Landau's statistic h, as a function of number of interactions that took place in a group; the degree of linearity approached 1 (perfectly linear) in a logarithmic pattern. The pattern of outcomes in empirical dataset is similar to those models which have high winner-low loser effects.

α, β and δ individuals (all $p < 0.0001$), while only interaction effects were found to be significant for γ individuals ($p < 0.05$).

Results obtained from an empirical setup (Goessmann et al., 2000) were analyzed in a manner equivalent to the analysis of the model data. Cardinal ranks (calculated through BBS method) and degrees of linearity (in terms of values of Landau's statistic h) obtained from five groups of four animals on the first day of trials were calculated for intervals of 20 interactions in order to make the analysis comparable to the one performed on the models (Figure 5). Although the number of interactions that took place per group was notably lower than in the virtual setup groups, the pattern of outcomes observed in these results indicated that the formation of hierarchical structures in decapod crustaceans emerges from interactions that appear to best fit with results from models which had high loser and low winner effects.

Discussion

Winner and loser effects have been the focus of studies in a variety of taxa and theoretical models (e.g., Dugatkin, 1997). In a review of winner effects, Chase et al. (1994) concluded that the winner effect, if present, tends to reset itself to its resting value fairly rapidly as opposed to a loser effect that is generally longer-lasting. Possible explanations proposed in the literature suggest (1) that it is of greater importance for an individual to recognize its lack of ability to win than it is to memorize previous victories (Hsu & Wolf, 1999), (2) that it could prove more costly for a subordinate animal to behave aggressively during subsequent losses (Van Doorn et al., 2003), or (3) that winner effects cannot evolve without parallel loser effects (Mesterton-Gibbons, 1999). However, while a number of studies suggested that winner effects were either not detected at all (Schuett, 1997), or were short lived (Francis, 1988; Bakker et al., 1989; Bergman et al., 2003), others demonstrate that effects of both winning and losing experiences were not only present but long-lasting (Hsu & Wolf, 1999).

Unlike a model by Dugatkin (1997), the present model utilizes a spatially explicit setup as a stage for social interactions, which more closely resembles true experimental conditions where identities of the participants and the rates at which the interactions occur are determined by movements of the individuals in the experimental arena. At the same time, and unlike the model by Hemelrijk (2000), the present model also examines social dominance without any dependence on spatial grouping rules. In our current setup, each encounter is followed by a change in aggressive motivation and the resulting probability to win future contests, and this change is contingent on both the relative magnitude of the participants' aggressive states and on the nature of interactions that took place, with the latter being itself influenced by the magnitude of the aggressive states. These interrelationships among fight dynamics, dominance status, and associated winner and loser effects, coupled with sequential analysis of hierarchy formation, make the model described in this study a potent tool for examining the parameters that govern social structuring in animal groups.

In this light, the present study thus offers insights into the possible reasons behind the relative importance of winner and loser effects, as well as their temporal dynamics. The magnitude of winner effects plays an important role for the divergence of ranks, especially in the emergence of a prominent alpha individual, while loser effects are important for stability and maintenance of the hierarchy over time and for the prominence of omega individuals. If the return for winning an encounter is large, ranks will diverge rapidly, and individuals that win them will become clear alphas. The rapid increase of aggressive state increases the probability that an individual will have a series of wins initially, as its aggressive state will become more positive in large increments, and thus its probability of winning a second encounter will be greater than in the cases where the change occurred at a lower rate. However, if loser effects are low, the individuals comprising the rest of the group retain a relatively high probability of winning encounters against alphas, effectively attenuating the difference in aggressive state between winners and losers. Furthermore, the high winner effect returns from interactions mean that aggressive state will remain high across the group, since even an occasional win has the potential to negate the effect of a series of losses. Likewise, high aggressive state individuals will be likely to escalate to higher maximum intensities, further amplifying these effects. Thus, the rules in systems with high winner and low loser effects will over time both diminish alpha's ability to dominate, and enable omega individuals to substantially decrease the difference to other participants through an occasional odd win. Therefore, while high winner effects aid in the emergence of high-ranking individuals, systems in which they are not coupled with prominent loser effects will produce unstable hierarchical structures.

Conversely, high loser effects will aid in the emergence of low-ranking individuals in a group. Losing initial encounters in such conditions greatly reduces an individual's ability to win subsequent interactions, and thus these individuals will be more likely to experience a series of losses. They are unable to remain competitive with the dominants, facilitating the maintenance of the social structure once it becomes established. Moreover, coupling high loser effects with low winner effects further aids in stabilizing the hierarchy, due to the inability of low-ranking individuals to regain their status through occasional odd wins. Subordinates become progressively less likely to participate in high-return intense interactions as their aggressive state decreases, and even if they do so, wins in those interactions will have less impact than the losses previously suffered. While such rules may also decrease the ability of high-ranking individuals to further increase their rank and achieve some form of despotism, they will nevertheless be able to retain their status due to the constraints acting on low-ranking members of the group.

When winner and loser effects are of equal magnitude, the structure of the hierarchy is ambiguous at the start, but becomes clear and stable as more interactions take place in a group. The uncertainty of the outcome in initial interactions means that no single win or loss clearly predisposes an individual for a given rank in the hierarchy. Rather, a series of wins or losses is necessary for the ranks to begin substantial divergence. Once this takes place, however, the divergence is ongoing. The ratio of wins and losses will be faithfully reflected in the changes in aggressive state due to the equality of the two effects, and the distribution of rank means will assume a linear pattern in such systems. Thus, while inequality of winner and loser effects facilitates the initial formation of asymmetries, their later reinforcement benefits from both effects acting in synergy.

Empirical analysis of hierarchy formation in decapod crustacean groups (Goessmann et al., 2000) resulted in the emergence of a clearly differentiated omega individual, while the difference between other ranks in a group was less pronounced. This pattern resembles those observed in models where loser effects were comparatively higher than the associated winner effects. These observations are also consistent with the generally more pronounced and longer lasting loser effects described in many taxa (reviewed in Chase et al., 1994; Hsu & Wolf, 1999). However, the number of transitive triads increased at a slower rate than that in the theoretical model with low winner and high loser effects, and the ranks continued to diverge. One possible explanation for these discrepancies is that the ratio of winner to loser effects is likely to be less extreme in crayfish than the one used in the model.

The results of the present study therefore shed light on how the dynamics of winner and loser effects in behavioral systems give rise to social structures that are both stable and unambiguous. Any asymmetry in the magnitude of these effects will aid in the initial divergence of ranks. Depending on the nature of this asymmetry, hierarchies will exhibit either prominent high-ranking or low-ranking individuals. Once the structure is established, loser effects provide a mechanism for its maintenance. Therefore, behavioral effects of wins in individuals who have attained a high status can diminish rapidly after the hierarchy is in place as long as low ranking individuals retain the behavioral changes designating them as losers. By examining the mechanisms that underlie behavioral conventions, it is thus possible not only to explain the characteristics of emergent properties in social structures, but also to provide insight into the processes that shaped them.

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