Behav Ecol Sociobiol (2000) 48:418–428

ORIGINAL ARTICLE

Christoph Goessmann · Charlotte Hemelrijk
Robert Huber

The formation and maintenance of crayfish hierarchies: behavioral and self-structuring properties

Received: 11 November 1999 / Revised: 1 March 2000 / Accepted: 3 May 2000

Abstract Behavioral changes in fighting and the development of dominance relationships were analyzed in groups of juvenile crayfish (*Astacus astacus*) using quantitative behavioral techniques. When individuals were placed into an aquarium, the number of agonistic challenges, their mean duration, and maximum intensity reached were high initially but then decreased steadily as the hierarchy developed. In all groups, linear hierarchies emerged which became increasingly stable over time. Winning influenced subsequent fighting behavior on two distinct time scales. In the short term, recent winners became progressively less likely to retreat. Second, individuals occupying dominant positions for days became increasingly likely to escalate to higher intensities early in the encounter. Both effects biased the outcome of future interactions such that winning enhanced further success and losing decreased an individual's subsequent chances for dominance.

Keywords Self-structuring · Dominance · Winner-loser effect · Rank · Aggression · Agonistic behavior

Communicated by R.F.A. Moritz

R. Huber (✉)
J.P. Scott Center for Neuroscience, Mind and Behavior,
and Department of Biological Sciences,
Bowling Green State University,
Life Sciences Building, Bowling Green,
OH 43403, USA
e-mail: lobsterman@caspar.bgsu.edu
Tel.: +1-419-372-7492, Fax: +1-419-372-2024

C. Goessmann · R. Huber
Department of Zoology, Division of Neuroethology,
University of Graz, Universitaetsplatz 2,
8010 Graz, Austria

C. Hemelrijk
AILab, Department of Information Technology,
University of Zuerich, Switzerland

Introduction

The fighting behavior of clawed decapod crustaceans has attracted considerable interest due to conspicuous visual displays and potentially lethal weaponry (Sastry and Ehinger 1980). In most instances, a meeting between two lobsters or crayfish of similar size leads to agonistic interactions, which progressively escalate until one of the opponents withdraws. A typical escalation advances through several stages of fight intensity, beginning with threat displays, ritualized aggression, and restrained use of the claws, through to brief periods of unrestrained combat (Jachowski 1974; Glass and Huntingford 1988; Huber and Kravitz 1995). Fighting success depends on a variety of factors, such as physical superiority (Ranta and Lindstrom 1992, 1993; Rutherford et al. 1995; Barki et al. 1997), dietary effects (Vye et al. 1997), molt stage (Tamm and Cobb 1978), behavioral strategies (Guiasu and Dunham 1997), knowledge of resource value (Smith et al. 1994), and social experiences such as isolation (Dunham 1972), prior residence (Figler and Einhorn 1983; Evans and Shehadi-Moacdieh 1988; Peeke et al. 1995), or previous agonistic encounters (Rubenstein and Hazlett 1974; Burk 1979).

Established dominance relationships between opponents produce a lasting polarity in the outcome of agonistic bouts (Francis 1988; Drews 1993). Individual recognition, an important mechanism underlying dominance in vertebrates (Wilson 1975; Clutton-Brock and Harvey 1976), produces learned, pair-wise relationships. Although some decapods may communicate dominance in this manner (Vannini and Gherardi 1981; Karavanich and Atema 1998), a recognition of aggressive state undoubtedly represents the more common mechanism (Winston and Jacobson 1978; Copp 1986; Zulandt-Schneider et al. 1999). At a group level, dyadic relationships combine to form dominance hierarchies (Vannini and Sardini 1971; Atema and Cobb 1980) which have generally been found to be stable and (near) linear in most taxa (Wilson 1975; Schein 1975). An ability to dominate is commonly attributed to relatively fixed individual characteristics, including body size or innate aggressive state (Bovbjerg 1953; Hyatt 1983; Dingle 1983). Although such characteristics may play important roles if they vary greatly between individuals, their importance is commonly overshadowed by contextual factors (McBride 1958; King 1965; Francis 1988) and chance events (Landau 1951; Rushen 1982). Individuals frequently assume different ranks when identical groups are repeatedly reconstituted (Guhl 1953; Dugatkin et al. 1994). Furthermore, final social status is strongly contingent upon the order in which individuals are added to the group (Landau 1965; Bernstein and Gordon 1980). A central role appears to be played by social conditioning, where recent winners become more likely to win a subsequent fight (e.g., Burk 1979; Jackson 1991; Hollis et al. 1995; Hsu and Wolf 1999), and chances for future success are reduced in previous losers. Such winner/loser effects, along with evidence for their underlying physiological mechanisms, have been empirically demonstrated in many taxa (e.g., Francis 1983; Chase et al. 1994).

Theoretical models suggest that a repeated application of such a mechanism among initially identical entities will lead to the formation of linear hierarchies through self-assembly (Hogeweg 1988; Bonabeau et al. 1995; Hemelrijk 1996, 1997, 1999). Thus animals losing to an opponent early in hierarchy formation may likely achieve only relatively low ranks, while winning early encounters may predispose individuals to obtain more dominant positions (Theraulaz et al. 1995). In some taxa, rank appears to be determined by the incidence of fighting itself rather than by its outcome (Stamps and Krishnan 1997, 1998). Computer models, in which entities perform self-reinforcing dominance interactions, indicate that the stability of a hierarchy is an automatic consequence of a feedback between spatial structure and the polarization of hierarchical positions (Hemelrijk 1998a, 1999). With the differentiation of ranks, some individuals become permanent losers. As these individuals flee from all others, the group spaces out and the frequency of aggression decreases. Due to increased risks of injury, initiations of attack decline further in these animals, decreasing their opportunities for a rank reversal. A comparison of different offensive strategies demonstrated that a "risk-sensitive strategy" (i.e., increased attacks on opponents with lower rank) will increase the degree of unidirectionality of attack as hierarchies differentiate (Hemelrijk 1998b, 2000). In contrast an "ambiguity-reducing strategy" where individuals preferentially attack opponents of close rank will not lead to such an increase. Self-reinforcing effects of winning and losing may also affect by-standers (Chase 1982a, 1982b, 1985). For example, winners may subsequently dominate unrelated third individuals nearby (double dominance) and losers may submit to by-standers (double subordinance). Sequential patterns of this kind have been observed in social systems with predominant linearity of ranks (Chase 1980; Mendoza and Barchas 1983; Eaton 1984).

We explored the complex dynamic processes acting during hierarchy formation in crayfish. In this system, timing and frequency of stereotyped component behaviors, their temporal structure, decisions delineating different fighting strategies, and the eventual outcome of bouts can be quantified reliably (Bruski and Dunham 1987; Huber and Kravitz 1995; Huber et al. 1997a). In five groups of juvenile crayfish we determined specifically: (1) whether frequency and intensity of fighting decline over time; (2) in what way hierarchies differentiate, stabilize, and become linear; (3) to what extent first encounters affect subsequent fighting and final rank; (4) which particular attack strategies (ambiguity reducing or risk sensitive) are used, and (5) the behavioral correlates of rank. These results will be used to generate hypotheses about proximate, neurochemical processes which presumably are an integral part of such a behavioral system.

Methods

Experimental animals and general laboratory setup

Juvenile crayfish (*Astacus astacus*), 1–1.5 years old, with cephalothorax length of 2–3 cm, were obtained from local commercial suppliers. Eight weeks prior to the experiment, animals with all appendages intact were separated into individual containers providing visual and tactile isolation. All containers and experimental observation chambers were maintained under controlled environmental conditions at a holding facility in the Department of Zoology, University of Graz, under 14 h light:10 h dark. Water was supplied from a central tank (ca 2,000 l) where it was partially recirculated, filtered, aerated, and held at temperatures between 12–16°C. Animals were fed every second day ad libitum with a variety of items including pelleted fish food and live meal worms.

Animals were weighed to the closest milligram the day before experiments began, matched according to body weight and molt state, and assigned to five groups of four animals each. Weight differentials per group ranged from 2.4% to 8.8% (descriptive statistics are summarized in Table 1). To reduce potential disruptions of group structure due to molting, we only used individuals that

Table 1 Descriptive statistics for groups of four crayfish each, used in hierarchy experiments. Groups are listed with their range of weights, the relative size advantage of the largest opponent compared to the smallest (*Diff.*), and the sex composition (*M* male, *F* female) within these pairs. The overall number of interactions quantified during the 2-h observation period on each of the 5 days (*Day 1–Day 5*) are also listed for each group

	Weight (g)	Diff. (%)	Sex	Day 1	Day 2	Day 3	Day 4	Day 5
1	2.155–2.274	5.5	1 F, 3 M	100	141	129	106	104
2	2.581–2.739	6.1	4 M	221	171	138	158	74
3	2.859–3.003	5.0	2 F, 2 M	111	101	86	67	55
4	3.653–3.742	2.4	3 F, 1 M	100	72	50	67	43
5	2.698–2.936	8.8	1 F, 3 M	94	72	75	63	54

had molted at least 7 days and not more than 21 days prior to the start of observations. All animals were marked individually with small plastic symbols glued to the dorsal carapace.

The observation chamber (60 cm wide×40 cm deep×10 cm water level) was constructed from white, non-reflecting plastic with rounded corners. The bottom surface of the arena was spatially homogeneous. Water flowed continuously through the tank via pairs of holes arranged symmetrically along the sides of the tank. Inflows were arranged below the water line to minimize disturbances of the surface during filming. All interactions were recorded using a video camera (Sony CCD-V6000E) mounted centrally above the tank at a distance of 90 cm.

Groups of four individuals were placed together into a container and observed for 2-h periods on each of five consecutive days. At the end of the observation period individuals remained within the experimental chamber but containers were placed over each crayfish to visually and tactily isolate individuals until the following day. Observation periods always began at the same time of day (9:00 a.m.). Our laboratory studies were designed to resemble natural conditions in the field. Local populations of crayfish commonly distribute into series of small rock pools, often with only a few individuals in each. Low water levels result in the disjunction of these habitats, reduced migration between pools, and isolation of small groups within them. In the field, it is not unusual to find groups of four similarly sized individuals in pools the size of our observation arena.

Quantitative behavioral data

In five groups, we observed a total of 2,452 agonistic encounters in 2-h periods on 5 consecutive days (Table 1). Behavioral measures quantified for each bout included its duration, maximum intensity, frequency of escalated fighting with unrestrained use of

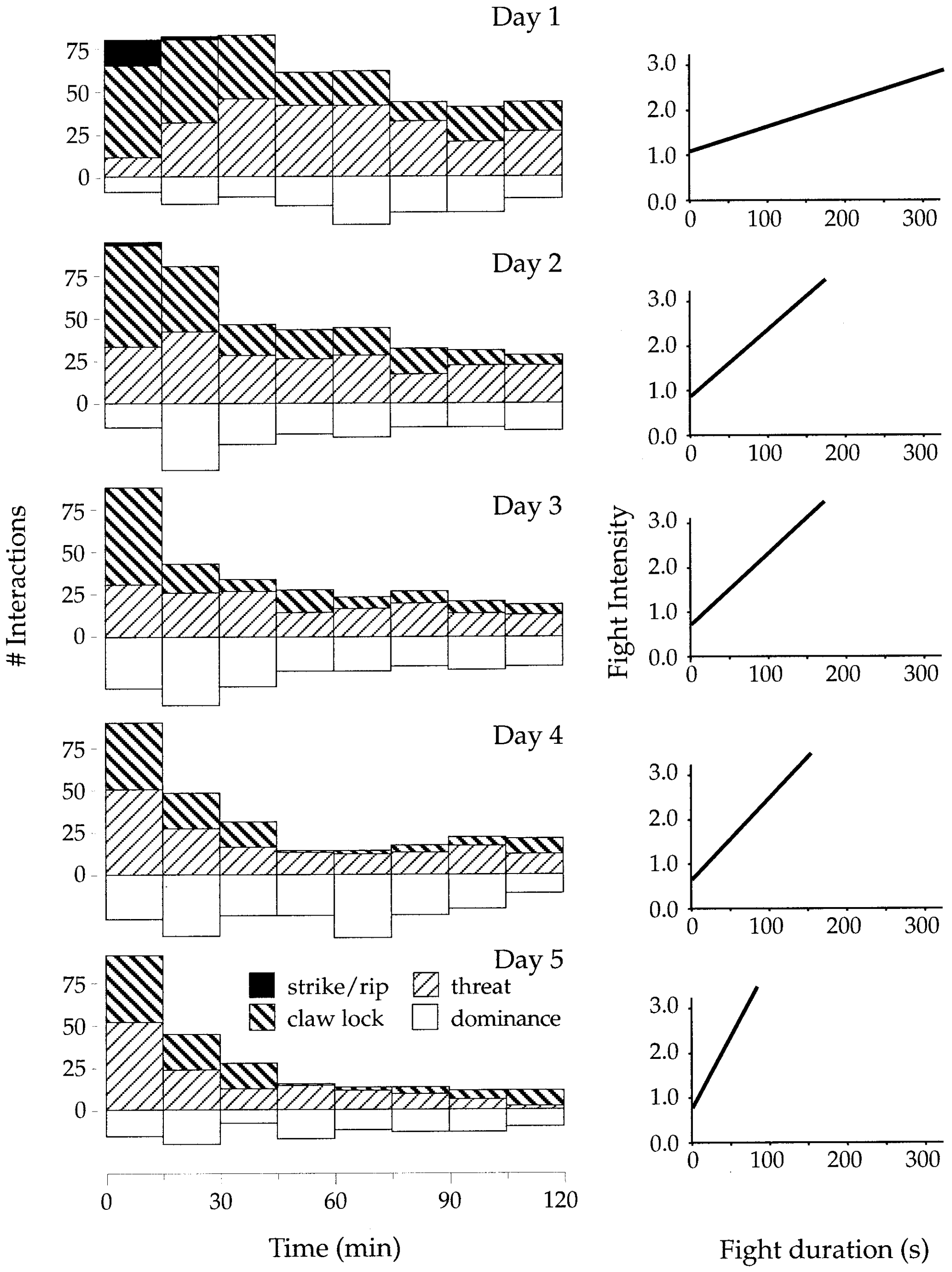

Fig. 1a,b Changes in fighting behavior over time (i.e., 2-h observation periods on days 1–5) pooled across all five groups. **a** Summarized for 15-min intervals. The number of encounters with established dominance relationships are graphed downwards. Fighting (i.e., both individuals contested the interaction) is plotted upwards with increasing levels of intensity. **b** Duration significantly accounted for the maximum intensity of a fight on each day. However, the slope of the regression line (i.e., representing the rate of escalation) differed among days and increased significantly in steepness with each further day. Day 1: y=1.09+0.006x, $F_{1,624}$=76.41 (P≤0.001), R^2=0.11; day 2: y=0.87+0.015x, $F_{1,555}$=81.78 (P≤0.001), R^2=0.13; day 3: y=0.71+0.016x, $F_{1,476}$=34.09 (P≤0.001), R^2=0.07; day 4: y=0.64+0.019x, $F_{1,459}$=76.19 (P≤0.001), R^2=0.14; day 5: y=0.88+0.033x, $F_{1,328}$=55.44 (P≤0.001), R^2=0.15

the claws, and the identities of the initiating and retreating animals (Huber and Kravitz 1995; Huber and Delago 1998). The beginning of an interaction was defined as the point in time when two opponents advanced to within one body length and overtly reacted to each other's presence. The approaching animal was termed the initiator. As the interaction progressed, maximum intensity was noted according to the following criteria: (0) *no fighting*: neither animal attacked its opponent or one animal consistently retreated from the advances of the other; (1) *threat postures:* both animals contested the interaction using threat displays or ritualized fighting without resorting to the use of their claws; (2) *claw lock*: both animals contested the encounter and at least one animal used its claws to grab the opponent; (3) *strike and rip*: both animals contested the encounter and at least one animal made unrestrained use of the claws in an attempt to rip or tear off appendages. The fight ended when an animal turned or walked away from its opponent, increasing the distance between them to more than one body length. The identity of the retreating animal was recorded as the loser. For each group and each day, a dominance hierarchy was constructed from a matrix containing the frequency with which each individual supplanted other group members. Rank order was determined from this matrix by shuffling the position of individuals to minimize the number of wins within the lower triangle of the dominance matrix.

Statistical analyses

An initial descriptive view of the data summarized the number and behavioral characteristics of agonistic interactions across the five groups (Fig. 1). All subsequent analyses treated groups separately with nested, repeated-measures analyses of variance (ANOVAs) or by obtaining results for individual groups and then combining them using Fisher combination tests (Sokal and Rohlf 1981).

Dominance structure is perfectly linear when all component triads are transitive (if A > B, and B > C, then A > C) instead of intransitive/circular (if A > B, and B > C, then A < C). A degree of linearity is obtained (Landau's statistic *h*, Kendall's τ/Appleby's *K*) by comparing the actual number of circular triads to those maximally possible (Appleby 1983). We determined the amount of linearity for each group and day separately (Landau 1951; Appleby 1983; deVries 1995). For each individual on each day we obtained measures for its dominance index [DI=number of wins/(number of wins+number of losses); Theraulaz et al. 1992], and its ordinal and cardinal ranks (i.e., Boyd and Silk 1983; Jameson et al. 1999). The τ_{Kr} statistic was used to test for the degree of unidirectionality of social interactions. This measure compares corresponding rows of an actor and receiver matrix of aggression (Hemelrijk 1990a, 1990b). Negative correlations reflect the degree of unidirectionality (i.e., an inverse relationship between social status and fight initiation). Levels of significance (*P*) are reported as: *$0.01=P<0.05$, **$0.001=P<0.01$, ***$P<0.001$. Analyses of behavioral data were performed using public domain Java Applets for the analysis of behavioral data (available on the Internet at http://caspar.bgsu.edu/~software/java/) or software for the Kr test (Hemelrijk 1990a, 1990b) developed by Hemelrijk and available on request.

Results

Duration and intensity of fighting

Upon release from their containers, juvenile crayfish readily interacted with conspecifics (Fig. 1). Each day began with a roughly equal number of agonistic encounters. The incidence of agonistic challenges then dropped consistently during each 2-h interval. Fight duration declined significantly during observation periods in each group (Fisher combination test combined two-way ANOVA results for separate groups $\chi^2_{10}=56.9$***), with days elapsed ($\chi^2_{10}=76.6$***) and, to a lesser degree, as a function of both ($\chi^2_{10}=30.2$**). Similarly, the highest levels of escalation occurred during the initial days of the

Table 2 Degree of linearity (Kendall's *K*/Appleby's *h*), unidirectionality of attack (τ_{Kr}) and individual dominance status for five groups reconstituted repeatedly on 5 consecutive days. Measures of linearity range from 0 (all circular) to 1 (perfectly linear relationships). Listed for individuals (*A*–*D*) of each group are observed ordinal ranks (α–δ) and cardinal ranks (s_A–s_D)

Group	Day	*h*/*K*	τ_{Kr}	A	B	C	D	s_A	s_B	s_C	s_D
1	1	1	–0.167	α	β	γ	δ	1.124	–0.401	–0.932	–0.554
	2	1	–0.606	β	α	γ	δ	0.639	0.836	–0.894	–1.256
	3	1	–0.367	β	α	γ	δ	0.659	0.891	–0.822	–1.128
	4	1	0.000	β	α	γ	δ	0.169	1.487	–0.447	–1.597
	5	1	–0.367	β	α	γ	δ	0.010	1.398	–0.893	–1.308
2	1	1	–0.087	α	β	γ	δ	1.352	–0.424	–0.519	–0.589
	2	1	–0.437	α	δ	γ	β	1.182	–0.852	–0.414	–0.089
	3	1	–0.367	α	δ	β	γ	1.044	–0.749	–0.053	–0.283
	4	1	–0.606	α	γ	δ	β	1.328	–0.736	–1.074	0.352
	5	1	–0.778	α	γ	δ	β	1.486	–0.226	–0.825	–0.337
3	1	1	–0.473	α	β	γ	δ	1.169	0.143	–0.967	–1.278
	2	1	–0.873	α	β	δ	γ	1.147	–0.223	–1.312	–0.244
	3	1	–0.611	α	β	δ	γ	1.405	–0.162	–1.340	–0.464
	4	1	0.000	α	β	δ	γ	1.212	–0.226	–1.475	–0.509
	5	1	–0.940	α	β	δ	γ	1.445	–0.160	–1.312	–0.472
4	1	1	–0.167	α	β	γ	δ	1.052	–0.057	–0.010	–1.214
	2	1	–0.483	δ	α	γ	β	–1.386	1.160	–0.527	0.357
	3	1	0.000	γ	α	β	δ	–0.671	1.412	0.074	–1.206
	4	1	–0.725	γ	α	β	δ	–1.010	1.245	0.000	–1.029
	5	1	–0.473	δ	α	β	γ	–1.304	1.158	–0.256	–0.684
5	1	1	0.101	α	β	γ	δ	1.398	0.473	–0.518	–1.349
	2	1	–0.367	α	β	γ	δ	1.249	0.202	–0.842	–1.208
	3	1	–0.633	α	β	γ	δ	1.436	0.472	–0.629	–1.370
	4	1	–0.817	α	β	δ	γ	1.356	0.539	–1.378	–0.842
	5	1	–0.667	α	β	γ	δ	1.612	0.317	–0.062	–1.530

experiment (Fig. 1). Fights on subsequent days were resolved more rapidly and at lower intensities. Fight duration significantly accounted for changes in intensity (intensity=0.88+0.01duration; $F_{1,2450}$=245.99***, R^2=0.094) confirming earlier characterizations of fight escalation in related species (Huber and Kravitz 1995; Huber and Delago 1998). The slope of this relationship represents a measure of the rate at which fight intensities escalate (Fig. 1). The rate of escalation did not change within each 2-h observation period, but increased significantly on consecutive days ($F_{4,2432}$=19.76***).

Differentiation, unidirectionality, linearity, and stability of the hierarchy

A repeated-measures ANOVA (JMP 3.0; SAS 1997) of cardinal ranks demonstrated that dominance relationships became increasingly polarized over time. Differences between highest- and lowest-ranking individuals increased over days ($F_{5,15}$=3.222*) with no significant difference evident between groups ($F_{4,15}$=2.409, P=0.2). However, differentiation of hierarchical structures was not accompanied by a significant increase in unidirectionality. This suggests that attacks are preferentially directed toward individuals of similar rank (i.e., ambiguity-reducing strategy; see Hemelrijk 1998a, 1998b, 2000).

Furthermore, within each of the five groups of animals on each of the 5 days of observation, hierarchies proved perfectly linear (Table 2). Although the rank of group members often changed daily (Fig. 2), the stability of the hierarchy (measured by Kendall correlation of ranks between subsequent days) increased from an average τ of 0.42 per group between the first 2 days (equaling a rank change of 1.8 per group per day) to an average τ of 0.80 between the last 2 days (corresponding to an average rank change of 0.8). Differences in DI between upper ranks are greater compared to those between lower ones (Fig. 3), resulting in an exponential function rather than a linear one.

Effects of first encounters

To explore to what degree initial encounters determined final rank, a Kendall concordance test was used to evaluated the associations between behavioral characteristics of fighting for the first ten encounters of each individual. Included were the number of times the animal had competed at different levels of intensity, how long the bout had lasted, how many of these encounters it had initiated, and how often it had remained victorious. All behavioral measures correlated significantly with final rank, with coefficients (Spearman ρ) ranging from 0.597 to 0.912. Fisher combination tests (Sokal and Rohlf 1981), combining the results from different groups, demonstrated that all behavioral measures from these early encounters were tightly linked with final rank as well (number of initiations χ^2_{10}=78.50***; number of wins χ^2_{10}=92.10***; mean duration χ^2_{10}=26.94**; mean intensity χ^2_{10}=48.12***). Thus, early asymmetries in behavior exist and appear to contribute to the rank that an individual will finally attain. The crayfish that would eventually occupy lowest and highest ranks on day 1 were already apparent after the first three interactions of that day (Fig. 4). Considerable rearrangement of ranks between days hinted at the importance of contextual parameters over individual characteristics. Moreover, crayfish that moved up in the hierarchy between days generally had experienced early wins, while early losses by others predis-

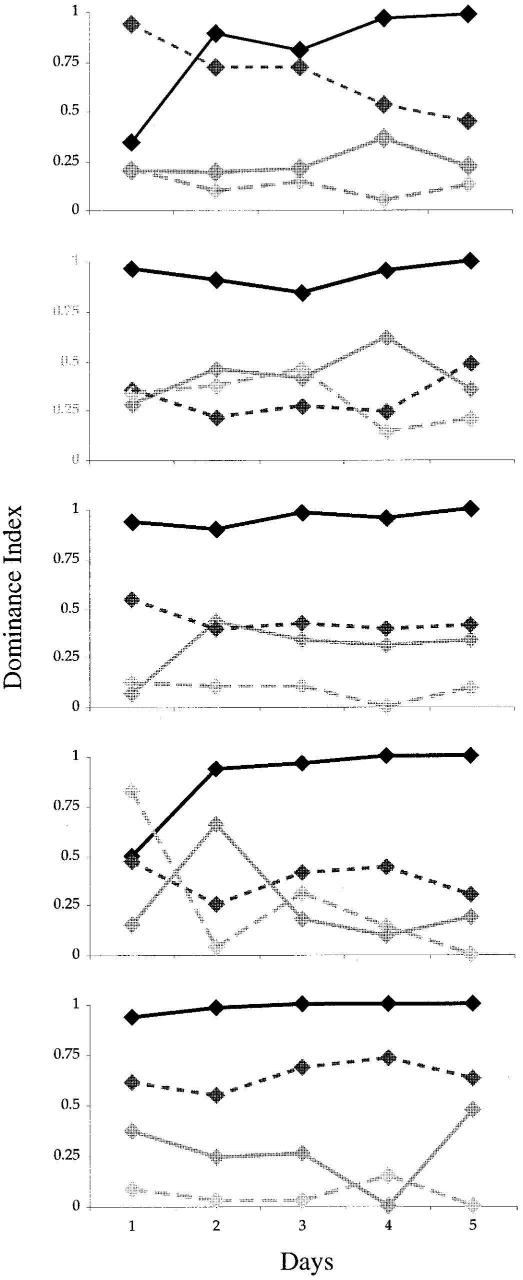

Fig. 2 Dominance index (i.e., number of wins as a proportion of all encounters) for individual crayfish in each group graphed over 5 days. Note that individuals frequently changed ranks between days even though identical groups were reconstituted

Table 3 Frequency distribution and replicated goodness-of-fit tests (*G*-tests) for all seven possible types of interaction sequences in tetrads: win win same (*WWS*) – win twice against same opponent; win lose same (*WLS*) – first win then lose against same opponent; win win different (*WWD*) – win against two different oponents; lose lose different (*LLD*) – lose against two different oponents; win lose different (*WLD*) – win against one individual then lose to another; lose win different (*LWD*) – first lose against one individual then win against another; other pair (*OP*) – different individuals in second interaction. Sequence types differ in the number of individuals involved (n) and their expected probabilities (P). There are four different triadic interactions (WWD, LLD, WLD, LWD) which should occur at equal frequencies under the assumption that animals encounter each other randomly and there is no influence of outcome for subsequent encounters. Sequences which will necessarily lead to transitive triadic relationships (WWD, LLD) occur significantly more often than those sequences which may not lead to linearity (WLD, LWD). An orthogonal set of replicated goodness-of-fit tests illustrated that sequential encounters were not random with regard to their outcome. For each group, overall *G*-statistics (G_T) were partitioned into separate terms representing (pooled) goodness-of-fit (G_P) and heterogeneity among days within a group (G_H). Similarly, total *G* (G_{TT}) is composed of (pooled) goodness-of-fit (G_{PP}) and heterogeneity among groups (G_{HH}) (***$P \leq 0.001$)

Group	WWS n=2 P=1/12	WLS n=2 P=1/12	WWD n=3 P=1/6	LLD n=3 P=1/6	WLD n=3 P=1/6	LWD n=3 P=1/6	OP n=4 P=1/6	Source	*df*	*G*
1	88	11	157	83	70	62	103	G_P	6	124.63 ***
								G_H	24	470.88 ***
								G_T	30	595.51 ***
2	64	16	170	135	100	90	182	G_P	6	103.68 ***
								G_H	24	264.86 ***
								G_T	30	368.55 ***
3	55	10	111	74	48	45	72	G_P	6	73.25 ***
								G_H	24	262.01 ***
								G_T	30	335.26 ***
4	50	4	93	58	23	39	60	G_P	6	103.68 ***
								G_H	24	264.86 ***
								G_T	30	368.55 ***
5	48	3	90	69	44	41	58	G_P	6	74.99 ***
								G_H	24	234.24 ***
								G_T	30	309.22 ***
Σ	305	44	621	419	285	277	475	G_{PP}	6	423.57 ***
								G_{HH}	144	8670.29 ***
								G_{TT}	150	9093.85 ***

Table 4 Association between dominance status and behavior in five groups (*1–5*). The likelihood of initiating encounters depends on an individual's ordinal rank (α–δ). Replicated goodness-of-fit tests (*G*-tests) illustrated that in every group, high-ranking individuals were more likely to engage conspecifics than lower-ranking ones. Overall *G*-statistics (G_T) were partitioned into separate terms representing overall (pooled) goodness-of-fit (G_P) and heterogeneity among groups (G_H). Deviations from the null hypothesis, represented by G_P, are highly significant in every group, with dominant animals three times as likely to initiate encounters compared to their lowest-ranking opponents. In addition, differences in the number of interactions received, or the combined total in which they were involved closely depended on rank. High-ranking individuals participated in more interactions than low-ranking ones and received fewer attacks. Fight duration and intensity varied significantly as a function of (cardinal) rank of the initiating animal, the receiving individual, and on an interaction of both (*$P<0.05$, ***$P \leq 0.001$)

	α	β	γ	δ	Σ	*df*	G_P	*df*	G_H	*df*	G_T
1	233	206	86	55	580	3	169.21***	12	56.82***	15	226.04
2	231	205	163	163	762	3	17.49***	12	35.84***	15	53.32
3	165	139	84	32	420	3	113.60***	12	21.19*	15	134.79
4	165	89	51	27	332	3	128.85***	12	41.93***	15	170.78
5	147	115	59	37	332	3	89.00***	12	24.29*	15	113.29
						15	518.16***	60	180.07***	75	698.23
Σ_{init}	941	754	443	314	2,452	3	410.90***	12	107.26***	15	518.16
Σ_{rec}	456	527	737	732	2,452	3	410.90***	12	107.26***	15	518.16
Σ_{total}	1,397	1,281	1,180	1,046	4,904	3	410.90***	12	107.26***	15	518.16

posed them to a drop in rank. This is evidenced by the fact that all changes in rank proved highly predictable from knowledge about the individual's success (DI) during the first ten bouts of a day (Δrank=–2.83+7.54DI; $F_{1,4}$=14.324***, R^2=0.782).

Triadic effects – the social relationships between all possible combinations of three individuals of a group – were analyzed using a jigsaw puzzle approach (Chase 1985). This method focuses on predictions concerning the first two dominance relationships formed within component triads. Transitive triads (i.e., if A >B and B > C and A > C) will always emerge from two sequential patterns (A > B and A > C; A < B and A < C) irrespective of the outcome of the third interaction. In contrast,

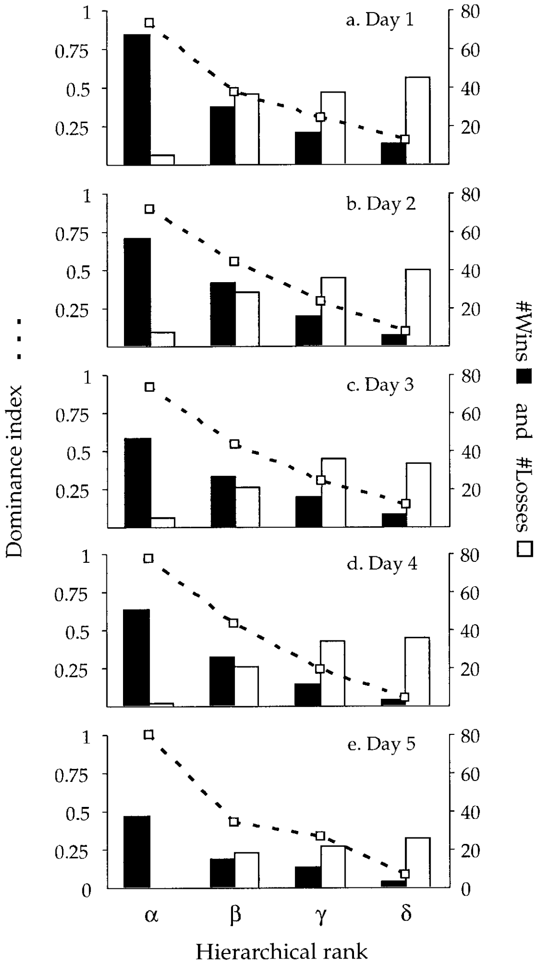

Fig. 3a–e Dominance index (*DI*) and distribution of wins and losses as a function of rank. Differences in DI between the two highest-ranking individuals consistently exceeded those separating the lowest ranks

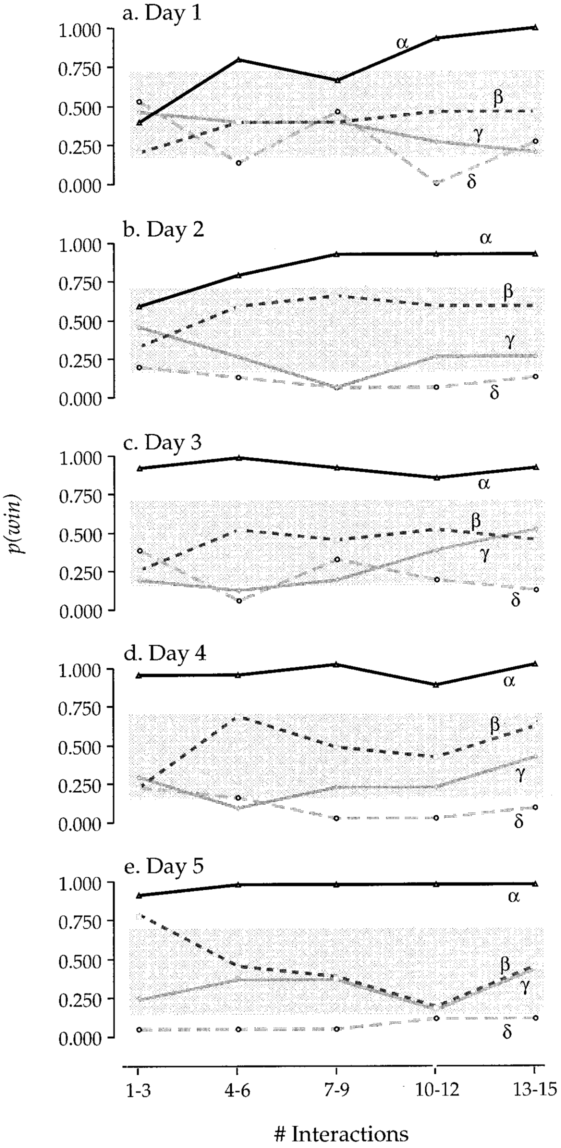

Fig. 4a–e The number of encounters necessary to adequately predict eventual rank. The probability of winning for different final ranks is graphed as a function of previous encounters. The *gray area* along the center indicates ±1 Freeman-Tukey deviates. Points outside this area are considered "large"

transitivity in the two other possible patterns (A > B and A < C; A > B and B > C) is not guaranteed and depends on the third interaction completing the triad. Thus, hierarchies will automatically form in linear fashion when sequences ensuring transitivity greatly outnumber those patterns which do not (Chase 1980, 1985). A non-random distribution of sequential patterns in crayfish confirmed that the outcome of future encounters closely depended on those that had already occurred. Our data identified a significant excess of patterns resulting in transitive triads. 621 double wins (WW=38.76%) and 419 double losses (LL=26.16%) were observed in a total of 1,602 sequential pairs, while wins against previous winners (WL, *n*=285) and wins of previous losers (LW, *n*=277) were less common, with a combined probability of only 35.08%. These frequencies differ significantly (Table 3) from a random distribution where each pattern is expected at equal probability ($P_{WW}=P_{LL}=P_{WL}=P_{LW}=0.25$, $\chi^2_3=184.42^{***}$).

The time course over which winning and losing affected the outcome of subsequent encounters was characterized by evaluating the strength of such effects as a function of time elapsed between these encounters (Fig. 5). Effects of previous success for heightened aggression were pronounced, present immediately, and consistent throughout the experiments. In comparison, the temporal dynamics of loser effects proved more complex. Following a loss, chances for further retreats are significantly higher between 20 s and several minutes following the loss. Data from this study did not permit us to evaluate the time course of winner and loser effects of time intervals exceeding 200 s.

Fighting behavior differed as a function of rank, with dominant animals initiating more interactions (Table 4). Duration and intensity of fighting increased as a function

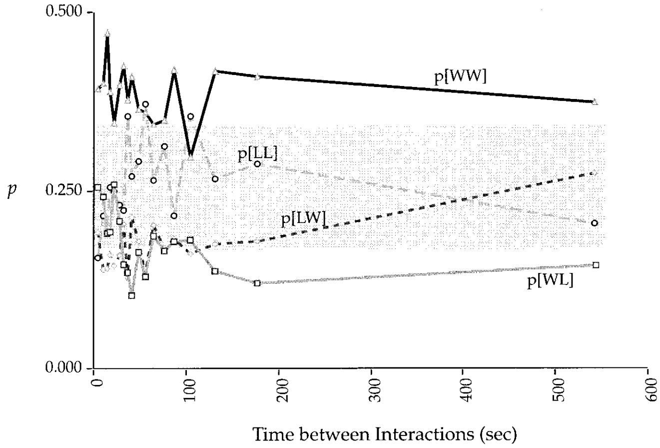

Fig. 5 Temporal dynamics of winner and loser effects. The probability of the first two sequential dyadic patterns in triadic relationships is graphed as a function of the time elapsed between the interactions for two wins ($p_{[WW]}$), two losses ($p_{[LL]}$), a win followed by a loss ($p_{[WL]}$), and a loss followed by a win ($p_{[LW]}$). *Gray areas* indicate ±1 Freeman-Tukey deviates. Points outside this area are considered "large"

of rank of the initiating animal ($F_{2,2436}$=30.09***), rank of the recipient ($F_{2,2436}$=563.61***), and as an interaction of both ($F_{5,2436}$=11.64***), with significant differences between groups ($F_{4,2436}$=72.87***).

Discussion

Initial bouts were often long and intense. The subsequent development of hierarchical structures was accompanied by a reduction in overt aggression. As dominance relationships in groups progressed toward linearity and stability, a variety of concurrent changes in behavior were observed. Dominant animals became increasingly likely to initiate and escalate encounters, and were less likely to retreat. Explanations for enhanced participation in fights traditionally focus on dominants attacking more often due to an increase in aggressive state or a reduction in the risks involved (Theraulaz et al. 1995; Hemelrijk 1996, 1997). Alternatively, computer models indicate that higher rates of initiation may also emerge when dominance status is reflected in spatial distributions (Hemelrijk 1998a, 1999). When dominant entities occupy central positions, they automatically face greater opportunities to encounter opponents from all sides, compared to subordinates located more often at the periphery of the group.

Our data also demonstrated that dominance is associated with specific rates of escalation in this system. Initially, individuals fought conservatively, but as they won more encounters, they appeared to gather less information about the opponent's strength before increasing the stakes of the fight. An opponent's willingness to escalate more rapidly thus contains information about its recent agonistic success and social status; it can thus serve in the recognition of aggressive state alongside status recognition via urine pheromones (Zulandt-Schneider et al. 1999).

Groups of crayfish established linear hierarchies in every instance where they were allowed to repeatedly interact with each other. Although the probability of obtaining apparent linearity due to chance alone is high in such small groups (Kendall 1962; Appleby 1983), the repeated observation of this pattern in multiple groups supports linearity. Linear or near-linear hierarchies have been demonstrated in many taxa (Gorlick 1976; Chase 1985; Bonabeau et al. 1995), including several decapod crustaceans, e.g., hermit crabs (Allee and Douglis 1945; Hazlett 1968; Winston and Jacobson 1978), crabs (Bovbjerg 1960; Vannini and Gherardi 1981), lobsters (Douglis 1946; Fiedler 1965; Scrivener 1971; Cobb and Tamm 1975; Sastry and Ehinger 1980), other crayfish species (Bovbjerg 1953, 1956; Lowe 1956; Copp 1986; Bruski and Dunham 1987), spiny lobsters (Fielder 1965), and palaemonids (Barki et al. 1992). The existence of strict linearity of hierarchical structures despite frequent rank reversals paralleled previous findings (Oliveira and Almada 1996). In contrast to results by Frey and Miller (1972), we found no support for distinct and separate phases of behavioral plasticity associated with initial formation and subsequent maintenance of hierarchies. The degree of unidirectionality did not increase with the differentiation of the hierarchy, which indicates that attacks preferentially occured between crayfish of similar rank (as in an ambiguity-reducing strategy; Hemelrijk 1998a, 1998b, 2000).

Self-reinforcing effects of fight success on subsequent encounters have been demonstrated in a variety of taxa (van de Poll et al. 1982) including crayfish (Lowe 1956; Hazlett 1966; Copp 1986), and their importance for hierarchy formation has been recognized (Theraulaz et al. 1995; Dugatkin 1997; Hemelrijk 1999). Aggressive state depends on previous agonistic success (Stamps and Krishnan 1994a, 1994b), a property which defines the differentiation and stability of dominance ranks in models (Hemelrijk 1998a, 1998b). However, a conceptual difficulty arises when we attempt to separate aggressive state, fighting, and agonistic success, as these properties do not vary independently. The work presented here is consistent with a dynamic view of hierarchies, where aggressive state, fighting success, and social status represent self-structuring, and self-differentiating processes of feedback loops rather than being static, individual qualities. In this study, behavioral polarities are based on a combination of initial asymmetries, contextual biases, and random conditions, which are amplified with each further iteration and thereby lead to the development of individual ranks.

Our behavioral characterization uncovered evidence for the existence of at least three behavioral patterns in need of a physiological explanation. Winner effects follow two distinct time courses. Recent winners continue to escalate normally but become less likely to retreat in subsequent encounters (effect 1). This fight-boosting effect appears within seconds of a win and lasts for more than 10 min. In contrast, those changes in which high-ranking individuals begin to escalate more rapidly occur at longer time scales ranging from hours to days (effect 2). Social conditioning associated with previous losses produce an increased likelihood of retreat (effect 3). A more complex time course distinguishes it from being simply a negative version of effect 1. Such a multi-causal view of decapod aggression matches changes in fighting that result from either a reduction in retreat (Lang et al. 1977; Huntingford et al. 1995; Huber and Delago 1998), or increased escalation (Tamm and Cobb 1978; Steger and Caldwell 1983).

The challenge ahead lies in linking neurochemistry to the observed changes in fighting within a framework of dynamic behavioral mechanisms (e.g., see Antonsen and Paul 1997; Huber et al. 1997a, 1997b; Huber and Delago 1998).

Acknowledgements We thank Moira van Staaden, Jaak Panksepp, Antonia Delago, Amy Dalgleish, Becky Zulandt-Schneider, Alisdair Daws and all members of the Huber laboratory for helpful suggestions and critique of the manuscript. All animal experiments comply with Austrian and US laws governing research protocols. This work was supported by the National Science Foundation (IBN-9874608).

References

Allee WC, Douglis MB (1945) A dominance order in the hermit crab, *Pagurus longicarpus*. Say. Ecology 26:411–412

Antonsen BL, Paul DH (1997) Serotonin and octopamine elicit stereotypical agonistic behaviors in the squat lobster *Munida quadrispina* (Anomura, Galatheidae). J Comp Physiol A 181: 501–510

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

Atema J, Cobb JS (1980) Social behavior. In: Cobb JS, Phillips BF (eds) The biology and management of lobsters. Academic Press, New York, pp 409–450

Barki A, Karplus I, Goren M (1992) Effects of size and morphotype on dominance hierarchies and resource competition in the fresh-water prawn *Macrobrachium rosenbergii*. Anim Behav 44:547–555

Barki A, Harpaz S, Karplus I (1997) Contradictory asymmetries in body and weapon size, and assessment in fighting male prawns, *Macrobrachium rosenbergii*. Aggress Behav 23:81–91

Bernstein IS, Gordon TP (1980) The social component of dominance relationships in rhesus monkeys (*Macaca mulatta*). Anim Behav 28:1033–1039

Bonabeau E, Theraulaz G, Deneubourg JL (1995) Phase-diagram of a model of self-organizing hierarchies. Physica A 217: 373–392

Bovbjerg RV (1953) Dominance order in the crayfish *Orconectes virilis* (Hagen). Physiol Zool 26:173–178

Bovbjerg RV (1956) Some factors affecting aggressive behavior in crayfish. Physiol Zool 29:127–136

Bovbjerg RV (1960) Behavioral ecology of the crab *Pachygrapsus crassipes*. Ecology 41:668–672

Boyd R, Silk JB (1983) A method for assigning cardinal dominance ranks. Anim Behav 31:45–58

Bruski CA, Dunham DW (1987) The importance of vision in agonistic communication of the crayfish *Orconectes rusticus*. I. An analysis of bout dynamics. Behaviour 63:83–107

Burk TE (1979) Analysis of social behavior in crickets. Oxford University Press, Oxford

Chase ID (1980) Social process and hierarchy formation in small groups: a comparative perspective. Am Sociol Rev 45:905–924

Chase ID (1982a) Behavioral sequences during dominance hierarchy formation in chickens. Science 216:439–440

Chase ID (1982b) Dynamics of hierarchy formation: the sequential development of dominance relationships. Behaviour 80: 218–240

Chase ID (1985) The sequential analysis of aggressive acts during hierarchy formation: an application of the ‘jigsaw puzzle’ approach. Anim Behav 33:86–100

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

Clutton-Brock TH, Harvey PH (1976) Evolutionary rules and primate societies. In: Bateson PPG, Hinde RA (eds) Growing points in ethology. Cambridge University Press, Cambridge, UK, pp 195–239

Cobb JS, Tamm GR (1975) Dominance status and molt order in lobsters (*Homarus americanus*). Mar Behav Physiol 3:119–124

Copp NH (1986) Dominance hierarchies in the crayfish *Procambarus clarkii* (Girard, 1852) and the question of learned individual recognition (Decapoda, Astacidea). Crustaceana 51: 9–24

deVries H (1995) An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Anim Behav 50:1375–1389

Dingle H (1983) Strategies of agonistic behaviour in crustacea. In: Rebach S, Dunham DW (eds) Studies of adaptation: the behavior of higher crustaceans. Wiley, New York, pp 85–111

Douglis MB (1946) Some evidence of a dominance subordinate relationship among lobsters, *Homarus americanus*. Anat Rec 94:57

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, Alfieri MS, Moore AJ (1994) Can dominance hierarchies be replicated – form-reform experiments using the cockroach (*Nauphoeta cinevea*). Ethology 97:94–102

Dunham PJ (1972) Some effects of group housing upon the aggressive behavior of the lobster *Homarus americanus*. J Fish Res Board Can 29:598–601

Eaton GG (1984) Aggression in adult male primates: a comparison of confined Japanese macaques and freeranging olive baboons. Int J Primatol 5:145–160

Evans DL, Shehadi-Moacdieh M (1988) Body size and prior residency in staged encounters between female prawns, *Palaemon elegans* Rathke (Decapoda: Palaemonidae). Anim Behav 36:452–455

Fielder DR (1965) A dominance order for shelter in the spiny lobster *Jasus lalandei* (H. Milne-Edwards). Behaviour 24:236–245

Figler MH, Einhorn DM (1983) The territorial prior residence effect in convict cichlids (*Cichlasoma nigrofasciatum* Günther): temporal aspects on establishment and retention, and proximate mechanisms. Behaviour 85:157–181

Francis RC (1983) Experiential 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

Frey DF, Miller RJ (1972) The establishment of dominance relationships in the blue gourami *Trichogaster trichopterus* (Pallas). Behaviour 42:8–62

Glass CW, Huntingford FA (1988) Initiation and resolution of fights between swimming crabs (*Liocarcinus depurator*). Ethology 77:237–249

Gorlick DL (1976) Dominance hierarchies and factors influencing dominance in the guppy *Poecilia reticulata* (Peters). Anim Behav 24:336–346

Guhl AM (1953) Social behavior of the domestic fowl. Kansas Agric Exp Stat Tech Bull 73:3–48

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

Hazlett BA (1966) Factors affecting the aggressive behavior of the hermit crab *Calcinus tibicen*. Z Tierpsychol 23:655–671

Hazlett BA (1968) Size relationships and aggressive behavior in the hermit crab *Clibanarius vittatus*. Z Tierpsychol 25:608–614

Hemelrijk CK (1990a) A matrix correlation test used in investigations of reciprocity and other social interaction patterns at group level. J Theor Biol 143:405–420

Hemelrijk CK (1990b) Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. Anim Behav 39:1013–1029

Hemelrijk CK (1996) Reciprocation in apes: from complex cognition to self-structuring. In: McGrew WC, Marchant LF, Nichida T (eds) Great ape societies. Cambridge University Press, Cambridge, pp 185–195

Hemelrijk CK (1997) Cooperation without genes, games or cognition. In: Husbands P, Harvey I (eds) Fourth european conference on artificial life. MIT Press, Cambridge, Mass, pp 511–520

Hemelrijk, CK (1998a) Spatial centrality of dominants without positional preference. In Adami C, Belew R, Kitano H, Taylor C (eds) Artificial Life VI. MIT Press, Los Angeles, pp 307–315

Hemelrijk CK (1998b) Risk sensitive and ambiguity reducing dominance interactions in a virtual laboratory. In: Pfeifer R, Blumberg B, Meyer J, Wilson SW (eds) Proceedings of the fourth international conference on simulation of adaptive behavior: from animals to animats. MIT Press, Cambridge, Mass, pp 255–262

Hemelrijk CK (1999) An individual-oriented model on the emergence of despotic and egalitarian societies. Proc R Soc Lond B 266:361–369

Hemelrijk CK (2000) Towards an integrative approach to social dominance and spatial structure. Anim Behav 59:1035–1048

Hogeweg P (1988) Mirror beyond mirror, puddles of life: artificial life, SFI studies in the sciences of complexity. Adisson-Wesley, Redwood City, Calif, 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 Psychol 109:123–133

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

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 Evol 46:72–83

Huber R, Orzeszyna M, Pokorny N, Kravitz EA (1997a) Biogenic amines and aggression: experimental approaches in crustaceans. Brain Behav Evol 50:60–68

Huber R, Smith K, Delago A, Isaksson K, Kravitz EA (1997b) Serotonin and aggressive motivation in crustaceans: altering the decision to retreat. Proc Natl Acad Sci USA 94:5939–5942

Huntingford FA, Taylor AC, Smith IP, Thorpe KE (1995) Behavioral and physiological studies of aggression in swimming crabs. J Exp Mar Biol Ecol 193:21–39

Hyatt GW (1983) Qualitative and quantitative dimensions of crustacean aggression. In: Rebach S, Dunham DW (Eds) Studies in adaptation: the behaviour of higher crustacea. Wiley, New York, pp 113–139

Jachowski RL (1974) Agonistic behaviour of the blue crab, *Callinectes sapidus* Rathbun. Behaviour 50:232–253

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

Karavanich C, Atema J (1998) Individual recognition and memory in lobster dominance. Anim Behav 56:1553–1560

Kendall MG (1962) Rank correlation methods. Griffin, London

King MG (1965) The effect of social context on dominance capacity of domestic hens. Anim Behav 13:132–133

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

Landau HG (1965) Development of structure in a society with a dominance relation when new members are added successively. Bull Math Biophys 27:151–160

Lang F, Govind CK, Costello WJ, Green SI (1977) Developmental neuroethology: changes in escape and defensive behavior during growth in the lobster. Science 197:682–685

Lowe M (1956) Dominance-subordinance relationships in the crayfish *Cambarellus shufeldti*. Tulane Stud Zool 4:139–170

McBride G (1958) The measurement of aggressiveness in the domestic hen. Anim Behav 6:87–91

Mendoza SD, Barchas PR (1983) Behavioural processes leading to linear status hierarchies following group formation in rhesus macaques. J Hum Evol 12:185–192

Oliveira RF, Almada VC (1996) On the (in)stability of dominance hierarchies in the cichlid fish *Oreochromis mossambicus*. Aggress Behav 22:37–45

Peeke HVS, Sippel J, Figler MH (1995) Prior residence effects in shelter defense in adult signal crayfish (*Pacifastacus leniusculus* (Dana)) – results in same-sex and mixed-sex dyads. Crustaceana 68:873–881

Poll NE van de, Jonge F de, Oyen HG van, Pelt J van (1982) Aggressive behaviour in rats: effects of winning or losing on subsequent aggressive interactions. Behav Proc 7:143–155

Ranta E, Lindstrom K (1992) Power to hold sheltering burrows by juveniles of the signal crayfish, *Pasifastacus leniusculus*. Ethology 92:217–226

Ranta E, Lindstrom K (1993) Body-size and shelter possession in mature signal crayfish, *Pacifastacus leniusculus*. Ann Zool Fenn 30:125–132

Rubenstein DL, Hazlett BA (1974) Examination of the agonistic behaviour of the crayfish *Orconectes virilis* by character analysis. Behaviour 50:193–216

Rushen J (1982) The peck orders of chickens: how do they develop and why are they linear? Anim Behav 30:1129–1137

Rutherford PL, Dunham DW, Allison V (1995) Winning agonistic encounters by male crayfish *Orconectes rusticus* (Girard) (Decapoda, Cambaridae) – chela size matters but chela symmetry does not. Crustaceana 68:526–529

SAS (1997) JMP 3.1.5. SAS Institute, Cary, NC

Sastry AN, Ehinger RE (1980) Dominance hierarchies among communally held juvenile lobsters *Homarus americanus*. Mar Behav Physiol 7:85–94

Schein H (1975) Aspects of the aggressive and sexual behavior of *Alpheus heterochaelis* Say. Mar Behav Physiol 3:83–96

Scrivener JCE (1971) Agonistic behaviour of the American lobster *Homarus americanus* (Milne-Edwards). Fish Res Bd Can 235:1–126

Smith IP, Huntingford FA, Atkinson RJA, Taylor AC (1994) Strategic decisions during agonistic behavior in the velvet swimming crab, *Necora puber* (L). Anim Behav 47:885–894

Sokal RR, Rohlf FJ (1981) Biometry. Freeman, New York

Stamps JA, Krishnan VV (1994a) Territory acquisition in lizards. I. First encounters. Anim Behav 47:1375–1385

Stamps JA, Krishnan VV (1994b) Territory acquisition in lizards. II. Establishing social and spatial relationships. Anim Behav 47:1387–1400

Stamps JA, Krishnan VV (1997) Functions of fights in territory establishment. Am Nat 150:393–405

Stamps JA, Krishnan VV (1998) Territory acquisition in lizards. IV. Obtaining high status and exclusive home ranges. Anim Behav 55:461–472

Steger R, Caldwell RL (1983) Intraspecific deception by bluffing: a defense strategy of newly molted stomatopods (Arthropoda: Crustacea). Science 221:558–560

Tamm GR, Cobb SJ (1978) Behavior and the crustacean molt cylce: changes in aggression of *Homarus americanus*. Science 200:79–81

Theraulaz G, Gervet J, Thon B, Pratte M, Senenoff-Tian-Chansky S (1992) The dynamics of colony organization in the primitively eusocial wasp *Polistes dominulus* (Christ). Ethology 91:177–202

Theraulaz G, Bonabeau E, Deneubourg JL (1995) Self-organization of hierarchies in animal societies – the case of the primitively eusocial wasp *Polistes dominulus* Christ. J Theor Biol 174:313–323

Vannini M, Gherardi F (1981) Dominance and individual recognition in *Potamon fluviatile* (Decapoda, Brachyura): possible role of visual cues. Mar Behav Physiol 8:13–20

Vannini M, Sardini A (1971) Aggressivity and dominance in river crab *Potamon fluviatile* (Herbst). Monit Zool Ital 5:173–213

Vye C, Cobb JS, Bradley T, Gabbay J, Genizi A, Karplus I (1997) Predicting the winning or losing of symmetrical contests in the American lobster *Homarus americanus* (Milne-Edwards). J Exp Mar Biol Ecol 217:19–29

Wilson EO (1975) Sociobiology. Belknap, Cambridge, Mass

Winston ML, Jacobson S (1978) Dominance and effects of strange conspecifics on aggressive interactions in the hermit crab *Pagurus longicarpus* (Say). Anim Behav 26:184–191

Zulandt-Schneider RA, Schneider RWS, Moore PA (1999) Recognition of dominance status by chemoreception in the red swamp crayfish, *Procambarus clarkii*. J Chem Ecol 25:781–794