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Towards the integration of social dominance and spatial structure

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My aim was to show how individual-oriented (or artificial life) models may provide an integrative background for the development of theories about dominance by including effects of spatial structure. Dominance interactions are thought to serve two different, contrasting functions: acquisition of high rank and reduction of aggression. The model I present consists of a homogeneous virtual world inhabited by artificial agents whose actions are restricted to grouping and dominance interactions in which the effects of winning and losing are self-reinforcing. The two functions are implemented as strategies to initiate dominance interactions and the intensity of aggression and dominance perception (direct or memory based) are varied experimentally. Behaviour is studied by recording the same behavioural units as in real animals. Ranks appear to differentiate more clearly at high than at low intensity of aggression and also more in the case of direct than of memory-based rank perception. Strong differentiation of rank produces a cascade of unexpected effects that differ depending on which function is implemented: for instance, a decline in aggression, spatial centrality of dominants and a correlation between rank and aggression. Insight into the origination of these self-organized patterns leads to new hypotheses for the study of the social behaviour of real animals.

Peck orders in birds were first described by Schjelderup-Ebbe (1922) and since then social dominance has been considered of overwhelming social importance by some, but of little explanatory value by others (Gartlan 1968; Rowell 1974; Drews 1993). Polemics arise partly because functional and structural perspectives are not properly distinguished, and because implicitly different definitions are used, which describe dominance as a feature of either an individual, or an attribute of an interaction, or of a relationship or of a group (Drews 1993). Central to the debate is the relationship between dominance and aggression (Francis 1988). There are two opposing functional views. On the one hand, high rank is believed to offer optimal access to resources and, therefore, individuals should seize every opportunity to increase in rank (e.g. see Popp & DeVore 1979). On the other, the function of a dominance hierarchy is thought to reduce costs associated with aggression and, therefore, individuals should avoid conflicts as soon as relationships are clear. In some species rank and aggression are correlated, but this is not a consistent feature of animal societies and a coherent framework that integrates theories and observations is still needed (Francis 1988).

My aim in the present paper is to show how individual-oriented or artificial life models may provide such an integrative framework. These models represent behavioural acts and their feedback relations with their spatial and social context and they allow us to experiment with different behavioural rules. By recording what happens in the model, one can see how complex behavioural patterns may arise by self-organization. These patterns are unanticipated because they are not designed in the behavioural rules of the agents, but they are essential for understanding the integration of behavioural patterns.

I illustrate this with a model on bumblebees by Hogeweg & Hesper (1983, 1985). In colonies of bumblebees the queen is the only member that reproduces for most of the season, because she suppresses reproduction in workers. About 2 weeks before the season ends, however, the workers start laying eggs and the queen switches from producing workers to producing drones. According to the generally accepted view, the fixed timing of the switch is adaptive and regulated by an external cue. Hogeweg & Hesper, however, showed how such an invariable switchpoint emerges in an individual-oriented model without any external signal. In their model, the queen inhibited oviposition by workers via dominance interactions that were self-reinforcing. This implies that victory (and defeat) increased the chance of victory (and defeat) in subsequent interactions. As a consequence, two rank categories of workers developed: the so-called elite and the common workers. By the end of the season, the colony had grown and then, by sheer force of numbers, it

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became impossible for the queen to suppress all individual workers completely. Workers climbed in rank and some started to lay eggs. Simultaneously, the queen was defeated more often and this made her produce more drones. When Hogeweg & Hesper changed life history variables to generate slow- and fast-growing nests, the switch to producing more drones occurred at about the same time in both types of colony. Thus they showed how this switch and its invariance arise as an emergent aspect of the integration of demographic effects with dominance suppression.

In a later, minimal model of group-living agents that are performing only dominance interactions, Hogeweg (1988) suggested the presence of another unexpected interrelationship, a mutually reinforcing relationship between the development of a dominance hierarchy and a spatial structure (i.e. with dominants in the centre and subordinates at the periphery). In a subsequent, related model, I have shown that such a spatial structure arises only if the dominance hierarchy is steep, but not if it is weak (Hemelrijk 1998b). Thus, spatial centrality emerges in the model from the combined effects of fierce dominance interactions and grouping, but is not implemented in the behavioural rules of aggregation, that is to say the agents lack an innate preference for a spatial location within the group. Agents do not even avoid being located on the group's borders. Such avoidance of being at the periphery of a group is assumed in the main explanatory model for spatial centrality, 'the selfish herd theory' of Hamilton (1971). Hamilton supposed that animals evolved such a 'centripetal instinct' in order to protect themselves against predators approaching from the outside of the group. This centripetal instinct entails that animals seek to have others between them and the group's border. This model shows, however, that assuming such a centripetal instinct as Hamilton did is not required. Thus, the model presents a new, and parsimonious, explanation for the occurrence of centrality of dominants among animals. Instead of the centripetal instinct of Hamilton, in this model, it is the centrifugal force of dominance interactions that, if strong enough, may cause such structure (Hemelrijk 1998b, 1999a).

I use this interdependence between behaviour and spatial structure as a new starting point for understanding the complicated interrelationship between dominance and aggression. To this end, I have built a model similar to that of Hogeweg (1988) and use it as a virtual laboratory (Epstein & Axtell 1996) by tracing the behavioural patterns that emerge among groups of agents endowed with different behavioural rules (see also Hemelrijk 1998a). The model features only a few essentials of group life (i.e. the habit of remaining in the vicinity of others and of executing dominance interactions). It consists of a homogeneous virtual world that is inhabited by group-living, artificial agents that, upon encountering others, may perform self-reinforcing dominance interactions. Such self-reinforcing effects have broad biological relevance, because they have been empirically established in many animal species, such as spiders (Whitehouse 1997), insects (e.g. Hoffman 1990; Theraulaz et al. 1992), crustaceans (Caldwell 1992; Karavanich & Atema 1998), fish (e.g. Beaugrand et al. 1996; Hsu & Wolf 1999), reptiles (e.g. Schuett 1997), birds (e.g. Chase 1985; Drummond & Canales 1998) and mammals, such as mice (Ginsburg & Allee 1942), rats (Van de Poll et al. 1982), deer (Thouless & Guinness 1986) and primates (Mendoza & Barchas 1983; Barchas & Mendoza 1984), including humans (e.g. see Mazur 1985). There are indications that winning and losing are mediated by changes in hormones, such as testosterone in primates (e.g. see Bernstein et al. 1974; Mazur & Booth 1998) and other hormones in other taxa (e.g. see Huber et al. 1997a, b).

Although some investigators assume that dominance is heritable (Ellis 1994), others have shown how it depends on context and the order of introducing individuals into a group (e.g. see Bernstein & Gordon 1980; Dugatkin et al. 1994). Although in reality both nature and nurture may well affect dominance, my model concerns only the effects of differential experiences among agents. This is realized by starting identical agents with the same tendency to win. Subsequent diversification of dominance values is completely due to various experiences of winning and losing.

Many animal fights are ritualized and do not involve physical matching of forces. Instead, individuals recognize each other's capability of winning (i.e. dominance) and this and chance determine the outcome of the conflict. In Hogeweg's model, such a judgement was based on recognizing the identity of the opponent and remembering its power in past encounters (so called memory-based dominance perception, as is found in primates and lobsters; e.g. see Karavanich & Atema 1998). The majority of animal species, however, lack individual recognition of others. Instead, individuals of these species observe rank of others directly from dominance-related cues, such as body posture and, in insects, pheromone composition (Drews 1993). Such direct rank perception is central in the present paper, but for comparison I add a model of agents using memory-based perception.

Furthermore, I implement the two functions of dominance interactions mentioned above (i.e. gaining high rank and aggression reduction) as mechanisms in three ways. When the function is striving for power, animals should continuously seek to obtain the highest possible rank (e.g. Datta & Beauchamp 1991). They may either use all opportunities to interact even if risks seem high or enter into fights only if risks seem low (e.g. see Barnard & Burk 1979; Jackson 1991; Pagel & Dawkins 1997). The first strategy is referred to as the Obligate attack strategy, in which agents invariably initiate fights. The second strategy is represented as the Risk-sensitive strategy in the model, whereby agents are more likely to attack when their chance of winning is greater. When the function is to reduce aggression, individuals perform dominance interactions simply to clarify their own relationships in order to avoid losing energy in useless fighting (Pagel & Dawkins 1997). Here, agents follow an Ambiguity-reducing strategy in which the probability of attacking others decreases with the rank distance of ego to its opponent.

Instead of a functional approach to dominance, Thierry (1985a, b, 1990) followed constraint-oriented

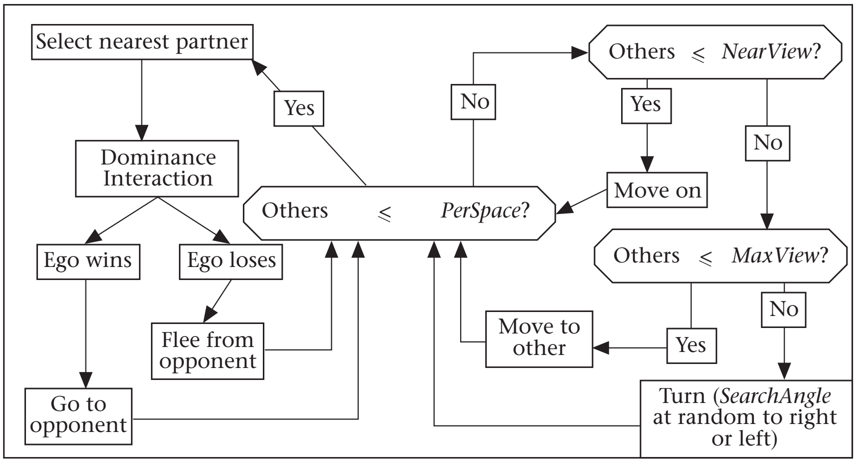

Figure 1. Flow chart for the behavioural rules of the agents in the model. See text for explanation.

considerations to explain the interaction patterns. On the basis of comparative studies of dominance interactions in egalitarian and despotic macaque species, he argued that in intensely aggressive species, individuals are inhibited from counterattacking because of high risks. Consequently, their aggression becomes more unidirectional and less symmetrical than in mildly aggressive species. Accordingly, I trace the consequences of high- and low-intensity aggression in the model.

Furthermore, apart from studying aggression and spatial structure, I analyse in the model other patterns that are usually studied by ethologists, for instance, the correlation between rank and attack and the stability and gradient of the hierarchy (a steep gradient characterizes a despotic society, a weak one an egalitarian society; Vehrencamp 1983). I use the results to unify and explain some contradictory findings on dominance and to provide parsimonious hypotheses for certain functionalistic theories. Because of the observational complexity of these models, they may be used as guidance in empirical studies on real animals.

METHODS

The Model and its Timing Regime

The model is individual oriented and event driven (see Hogeweg & Hesper 1979; Villa 1992; Judson 1994). It is written in object-Pascal, Borland Pascal 7.0 and consists of the ‘world’ with its interacting agents, its visualization and special agents that collect and analyse data on what happens in the world (cf. the ‘recorders’ and ‘reporters’ of Hogeweg 1988). The world consists of a continuous space of 200 × 200 units and its form is toroidal to exclude disturbing border effects; agents are able to move in any direction. They have an angle of vision of 120° and their maximum perception distance (*MaxView*) is 50 units. Parallel simulations cannot be run on most computers and, therefore, activities of agents are regulated by a timing regime. Studies have shown that a specific timing regime influences the results of the simulation (Huberman & Glance 1993). Often a random regime is applied in which each agent receives a random waiting time from a uniform distribution and the one with the shortest waiting time is activated first. Here, I combine a random regime with a biologically plausible timing regime that is locally controlled by other agents (Hogeweg & Hesper 1974; Goss & Deneubourg 1988). The locally controlled timing regime reduces the waiting time of an agent if a dominance interaction occurs within the agent’s *NearView* (24 units). A nearby dominance interaction is thus considered as a kind of ‘disturbance’ that increases the chance that the agent is activated. This reflects observations on real animals, whereby dominance interactions are likely to activate individuals nearby (compare social facilitation; Galef 1988). For the small group size studied here, the results are similar when the locally controlled regime is omitted, but at larger group sizes, this does matter. Agents group and perform dominance interactions according to sets of rules described below (Fig. 1).

Grouping rules

Ecological conditions are implicitly present in the model via grouping tendency and competitive interactions. In the real world the tendency to return to the group is thought to be moulded by predator pressure, because it is safer to be in a group. Competitive interactions depend, among other things, on the degree of clumping of the food sources (e.g. van Schaik 1983).

In the model the forces leading to aggregation and spacing are represented by the following set of rules (inspired by Hogeweg 1988).

(1) If an agent observes another within a critical distance, its ‘personal space’ of 4 units (parameter *PerSpace*), it may perform a dominance interaction depending on the interaction strategy involved. If several agents are within *PerSpace*, the nearest interaction partner is chosen. If the agent wins the interaction, it moves towards its opponent, otherwise it makes a 180° turn and moves away under a small random angle.

(2) If nobody is observed in *PerSpace*, but an agent notices others at a greater distance, but still within *NearView*, it continues moving in its original direction. (3) If its nearest neighbours are outside *NearView*,

but within its maximum range of vision (*MaxView*), the agent moves towards them.

(4) If an agent does not perceive any other agent within *MaxView*, it looks around for group members by turning a *SearchAngle* of 90° at random to the right or left.

Dominance interaction

Dominance interactions denote competitive interactions about resources over which most group-living animal species compete, such as food, sexual partners and spatial location. These resources are, however, not specified in the model.

Two types of agents (Perceivers and Estimators) are distinguished: Perceivers are simple agents endowed with direct rank perception; Estimators are the cognitively more sophisticated agents with memory-based dominance perception (Hemelrijk 1997, 1998b).

Direct perception by 'Perceivers'. The interaction between agents with direct perception of dominance rank (i.e. Perceivers) is modelled after Hogeweg & Hesper (1983) and Hemelrijk (1996b, 1997, 1998a, b) as follows.

P(erceiver)1. Each agent has a variable *Dom* (representing the capacity to win a hierarchical interaction).

P2. After meeting one another in *PerSpace*, agents observe each other's *Dom* value. Agent *i* displays its capacity of winning, Dom_i, agent *j* displays Dom_j. At the start of each run, initial *Dom* values of all agents are arbitrarily set at 15; their minimum value, in order to keep *Dom* values positive, is 0.001. Depending on the attack strategy a dominance interaction may take place. In the case of the Obligate attack strategy a dominance interaction follows inevitably. Subsequent winning and losing are determined by chance and by values of *Dom*,

whereby $w_i=1$ if

$$\frac{Dom_i}{Dom_i+Dom_j} > \mathrm{RND}(0,1), \tag{1}$$

otherwise $w_i=0$

where w_i is the outcome of a dominance interaction initiated by agent *i* (1=winning, 0=losing). In other words, if the relative dominance value of the interacting agents is larger than a random number (drawn from a uniform distribution), then agent *i* wins ($w_i=1$); otherwise it loses ($w_i=0$). Thus, the probability of winning is larger for the one higher in rank. Coming back to the type of attack strategy, in the case of the Risk-sensitive strategy, agents will attack only if they expect victory, that is, a mental dominance interaction as described above takes place and, after winning this, the agent starts a 'real' interaction and, when losing, it flees. The Ambiguity-reducing strategy implies that the probability of attacking is lower the greater the rank distance between the two is. Thus, it is a symmetrical dominance rule. If the relative dominance value is less extreme than both the random number and its complement (i.e. larger than the smaller one of the random number and its complement and smaller than the larger one of both), ego will start a real interaction. Otherwise, it will remain nonaggressively near. For instance, if the random number and its complement were 0.8 and 0.2, respectively, then, if the relative dominance value were 0.5 (because both agents have the same *Dom* value), ego would not attack. If, however, the relative dominance value were 0.9 (e.g. if $Dom_1=9$ and $Dom_2=1$) then ego would start an interaction.

P3. Dominance values are updated by increasing the dominance value of the winner and by decreasing that of the loser:

$$\begin{aligned} Dom_i &= Dom_i + \left(w_i - \frac{Dom_i}{Dom_i+Dom_j}\right) \times StepDom \\ Dom_j &= Dom_j - \left(w_i - \frac{Dom_i}{Dom_i+Dom_j}\right) \times StepDom \end{aligned} \tag{2}$$

In other words, if $Dom_1=1$ and $Dom_2=2$, then the relative dominance value=1/3. This implies that the probability of winning for agent 1 is 1/3 and for agent 2 is 2/3. If agent 2 indeed wins, its *Dom* value changes from 2 to 2.33 and the *Dom* value of agent 1 drops from 1 to 0.67. If, however, unexpectedly, agent 2 loses, its *Dom* value drops to 1.33 and that of agent 1 rises to 1.67. Thus, this system behaves as a damped positive feedback, in which the change in *Dom* value is not fixed, but depends on the interaction. If the higher-ranking agent wins, its relative *Dom* value is only slightly increased, whereas if the lower-ranking one wins, it gives rise to a relatively large change in *Dom* values. Furthermore, for the sake of simplicity the winner and loser effects are assumed to be of equal size (as reflected in the identical subscripts in the bracketed part of both equations). The consequence is that, within a single dominance interaction, the amount by which the *Dom* value of the loser is decreased is equal to that by which that of the winner is increased. Note that the Risk-sensitive and Ambiguity-reducing attack strategies interfere with the damped positive feedback. As the hierarchy becomes more differentiated, the Risk-sensitive strategy will tend to limit the tendency to interact upon encounter towards those interactions that are easily won and are of low risk and, thus, of low impact. The Ambiguity-reducing attack strategy, on the other hand, will do the opposite; it will increase the probability of dominance interactions among agents of equal rank and thus will bias interactions towards those of large impact. Furthermore, 'innate' differences in intensity of aggression (independent of the relative *Dom* values of both partners) are represented as a scaling factor called *StepDom* that varies between 0 and 1. High values imply a large change in *Dom* value after updating, and as a consequence single interactions strongly influence the future outcome of conflicts. Conversely, low *StepDom* values represent low impact.

P4. Victory entails chasing the opponent over a distance of one unit. The loser responds by fleeing over a predefined *FleeingDistance* of two units and, thus, usually gets outside the range of attack of the winner. During this interaction both the winner and loser often turn over a small random angle (45°) to right or left. This change in the orientation angles of both agents decreases the chance of repetition of interactions with the same opponent, because both agents are more likely to move out of each other's sight in subsequent activities.

Indirect perception by 'Estimators'. For indirect, memory-based rank perception, the agents (i.e. Estimators) have to recognize other individuals and to remember their personal experience with each of them. Dominance interactions are based on the model of so-called SKINNIES of Hogeweg (1988) and the three strategies (Hemelrijk 1998a, b).

E(stimator)1. In the case of the Obligate attack strategy, whenever an agent meets another in its *PerSpace*, it immediately starts a dominance interaction.

If, however, it follows the Risk-sensitive strategy, it first consults its memory to establish whether it will win or lose a dominance interaction with this particular opponent. To this end, it performs the same dominance interaction as described in equation (1) under P2 and equation (2) under P3 for the Perceivers, but now in the 'mind' and based on the 'mental impressions' it has of its own rank and that of the other. If it loses this 'mental battle', it moves away without challenging the opponent. It then has a lowered 'opinion' of its own rank and an increased one of its opponent, but since these interactions occurred only in its 'mind' and nothing really happened to the opponent, they do not change how the opponent 'thinks' about itself and leave the *Dom* records of the opponent about the opponent itself and others unchanged. If ego wins, it updates its own records and initiates a 'real' fight (see E2). The Ambiguity-reducing strategy is a symmetrical rule. The less extreme the relative *Dom* value is, the more likely it is that ego will start a real interaction. Otherwise, it will remain nearby without aggression.

E2. An Estimator initiates a 'real' fight by displaying its 'expectancy to win' (which in humans might be reflected by self-confidence) in the form of its updated relative dominance rank (D_i) and the partner displays its value in return (D_j), that is:

$$D_i = \frac{Dom_{i,i}}{Dom_{i,i} + Dom_{i,j}}$$

$$D_j = \frac{Dom_{j,j}}{Dom_{j,j} + Dom_{j,i}}$$

The double subscripts of the *Dom* values in these equations indicate that each agent keeps a list of impressions of *Dom* values of all the other agents. For instance, in a group of 10 agents, agent number 1 saves its records of its own winning tendency under $Dom_{1,1}$ and that of its group members numbers 2 to 10 under, respectively, $Dom_{1,2}$, $Dom_{1,3}$, . . ., $Dom_{1,10}$. Similarly, agent number 2 registers $Dom_{2,2}$ of itself and $Dom_{2,1}$, $Dom_{2,3}$, . . ., $Dom_{2,10}$ of the other group members. To return to the 'self-confidence' displayed by the agents, note that this varies depending on the experience ego has had of a particular partner. The variability of the display is not a strategic option (such as e.g. dishonest signalling in a typical game-theoretical setting), but a direct consequence of the experiences of an agent, as are described by behavioural studies of the winner and loser effects.

E3. Winning is decided as described above under equation (1) of Perceivers, but using D_i and D_j instead of Dom_i and Dom_j.

E4. Updating of the experiences of each agent happens as described for Perceivers, but involves two sets of registrations, one for the agent itself and one for that of the opponent. For instance, for agent *i* this involves updating its record of itself ($Dom_{i,i}$) and of its opponent, agent *j* ($Dom_{i,j}$) as follows:

$$Dom_{i,i} = Dom_{i,i} + \left(w_i - \frac{Dom_{i,i}}{Dom_{i,i} + Dom_{i,j}} \right) \times StepDom$$

$$Dom_{i,j} = Dom_{i,j} - \left(w_i - \frac{Dom_{i,i}}{Dom_{i,i} + Dom_{i,j}} \right) \times StepDom$$

Similarly, agent *j* updates its record of itself ($Dom_{j,j}$) and its registration of its partner ($Dom_{j,i}$).

From now on, the initiation of a dominance interaction is referred to as 'attack' for short.

Experimental Set-up and Data Collection

I use a similar parameter setting (*NearView*=24, *Search Angle*=90°, *FleeingDistance*=2 units) as in a former study (Hemelrijk 1998a, b), but for a greater *PerSpace* (=4) and a slightly larger group size (10 instead of 8). In separate runs, I study two types of agents differing in rank perception. Each type is studied under three different attack strategies and for low and high intensity of aggression, represented by *StepDom* of 0.1 and 1.0, respectively. For each combination of rank perception, attack strategy and value of *StepDom*, I conducted 10 replicates, resulting in $2 \times 3 \times 2 \times 10 = 120$ runs.

During a run, every change in spatial position and heading direction of all agents is recorded. The data analysis is performed over certain time units. One time step consists of 200 activations of agents. After every time step the distance between agents is calculated. Dominance interactions are continuously monitored by recording: (1) the identity of the attacker and its opponent; (2) the winner/loser; and (3) the updated *Dom* values of the agents.

Measurements

Every second time step, dominance differentiation is measured by the coefficient of variation (standard deviation divided by the mean; Sokal & Rohlf 1981) of *Dom* values (i.e. dominance representations for Estimators). A larger coefficient of variation of *Dom* values indicates greater dominance differentiation. In studies on animals stronger dominance differentiation is also referred to as a steeper hierarchy.

The degree of stability of the dominance hierarchy is expressed as the relative number of rank reversals. This is established by calculating the correlation between dominance values of agents at successive time intervals of two time steps (i.e. 400 activations of agents). For Perceivers, the Kendall rank correlation is used, but for Estimators dominance representations of each agent over every group member are cast in matrices and correlations between matrices are tested by the τ_{Kr} matrix test (Hemelrijk 1990a, b). This statistic measures the correlation between the corresponding rows of two social interaction matrices. The method to establish statistical significance is based on the statistical dependence that arises from recurrent observations of the same individual in the same row and column (Hubert 1987).

Unidirectionality of attack is calculated as a τ_{Kr} correlation between an actor and receiver matrix of attack. A stronger negative τ_{Kr} value corresponds to higher unidirectionality and lower symmetry of attack.

The degree to which dominants occupy the centre of the group is measured by a correlation between ego's *Dom* value and the mean spatial direction of others around ego. For each scan the centrality of each agent is calculated by means of circular statistics (Mardia 1972) by drawing a unit circle around ego and projecting the direction of other group members (as seen by ego) as points on the circumference of this circle. The connection of these points with the origin results in vectors (see individual vectors in Fig. 4a in the Results). The length of the mean vector represents the degree to which group members relative to ego form a cluster. Thus, longer mean vectors indicate a more peripheral and thus less central location of ego. It follows that clearer centrality of dominants is represented by a stronger negative correlation between rank and the length of mean vector indicating the mean direction of others (see Fig. 4a in the Results).

To exclude, in comparisons between conditions, a possible bias brought about by transient values, the correlations for centrality of dominants, unidirectionality of attack and the correlation between rank and attack frequency are calculated on data collected after time step 200.

I combined correlation results of 10 runs using the improved Bonferroni method from Hochberg (1988).

RESULTS

The partly opposite assumptions of performing dominance interactions to increase rank (portrayed in the Obligate and Risk-sensitive strategies) or to clarify relationships (represented in the Ambiguity-reducing strategy) are screened on a number of behavioural effects. First, I summarize behavioural patterns among agents with direct rank perception. Next, I compare these to those of agents with memory-based rank perception.

Direct Rank Perception (Perceivers)

Function: improving rank

Starting from the assumption that individuals always strive for higher rank, agents are designed that either always attack (Obligate) or are more likely to attack when the risk is not too great (Risk-sensitive strategy).

Obligate attack strategy. What happens to the supposed aggression-reducing function of a hierarchy? Unexpectedly, aggression declines in the model in the Obligate attack strategy with time (although less than in the Ambiguity-reducing strategy), but only at high *StepDom* when a steep hierarchy develops (Fig. 2b). Lessening of interactions is surprising because it has not explicitly been implemented. To explain this, note that at high *StepDom*, a single event of victory (or defeat) influences the outcome of interactions strongly. Consequently, starting from completely identical agents, ranks differentiate faster at high than at low *StepDom* (Fig. 3). Such a steep hierarchy entails that some unfortunates become permanent losers. When defeated again and again, these ‘underdogs’ move further and further away from others (Fig. 2a). This results in larger average distances. By thus cutting down the frequency of encounter, aggression diminishes (Fig. 2b). Thus, waning of aggression results as an emergent phenomenon from social–spatial structuring.

While agents space out, simultaneously spatial centrality of dominants sets in (as represented by the significant negative correlation in Fig. 4b). This is not a consequence of the behavioural rules for aggregation (see Grouping rules above). The rules cause agents to take care only that they have someone else in *NearView*. Once this requirement is fulfilled, the agents do not distinguish whether they are located in the centre or at the periphery of the group. Instead, spatial centrality of dominants proceeds via a steep hierarchy (which develops only at high *StepDom*) as follows. The larger the rank distance between two opponents, the higher the probability that a dominant will beat and chase away a subordinate. Thus, within the dyad, behaviour will be more asymmetrical. In addition, both agents will be treated differently by others. Consequently, they will not remain close together, but the physical distance of lower-ranking agents from higher-ranking ones will eventually reflect their rank distance. The lowest-ranking agents are chased away by almost everyone and thus will end up at the periphery. This leaves the dominants automatically in the centre. Only the closest-ranking agents will have an approximately equal probability of winning and losing fights with each other and, therefore, an equal probability of chasing away or being chased. Since they are also treated in a nearly identical way by other agents, close-ranking agents are likely to remain in each other's proximity.

Furthermore, a steep hierarchy develops at high *StepDom* via a mutual reinforcement between the differentiation of dominance values and spatial centrality of dominants, in the following way (Fig. 5). When dominance values differentiate, they strengthen hierarchical stability in two ways, directly and indirectly. They do so directly, because dominance differentiation implies greater differences in winning tendency among agents, which makes the outcome of fights more predictable (Pearson correlation between dominance differentiation and stability: $r_{125}=0.88$, $P<0.01$), and indirectly, because

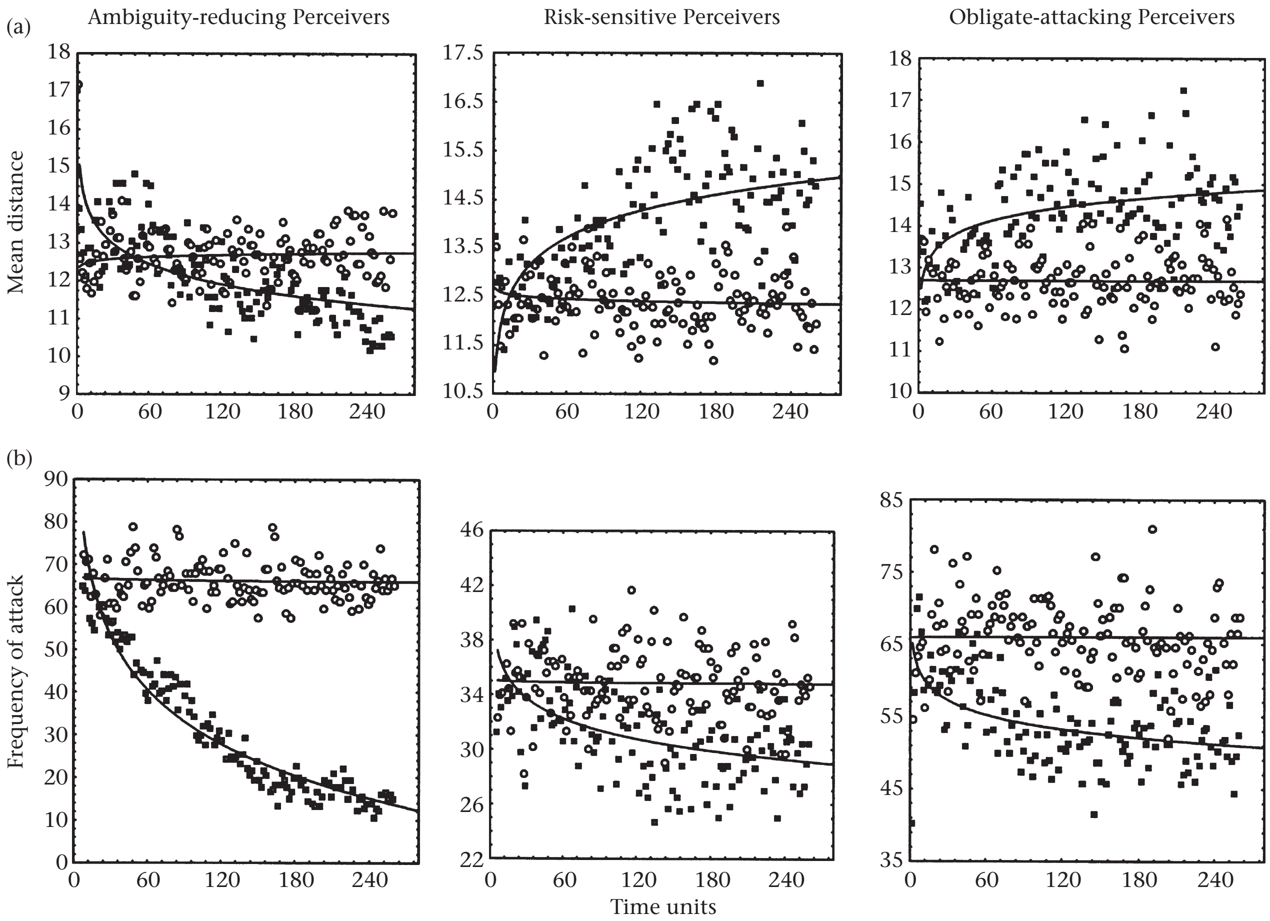

Figure 2. Development over time of (a) mean distance and (b) frequency of aggressive interactions among agents for different attack strategies and intensities of aggression (logarithmic line fitting). Aggression intensity (*StepDom*) ○: 0.1; ■: 1.0.

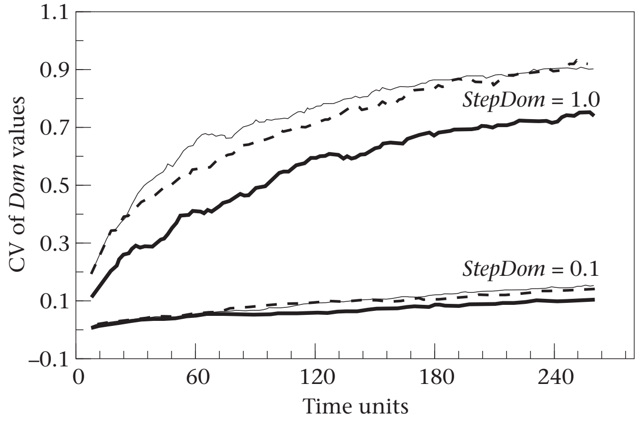

Figure 3. Development of coefficients of variation of dominance values (CV of *Dom* values) of various attack strategies and intensities of aggression (*StepDom*; averaged over 10 runs). – – – –: Obligate attack strategy; ——: Ambiguity-reducing strategy; ——: Risk-sensitive strategy. Note that as the CV of *Dom* values increases, the dominance hierarchy becomes more pronounced.

dominance differentiation causes agents to space out and this, in turn, lowers the frequency of interaction and so increases the stability of the hierarchy (Pearson correlation between stability of ranks and frequency of attack: $r_{125} = -0.67$, $P<0.01$; Fig. 5). The ensuing higher stability and the greater differentiation of dominance enhance spatial centrality of dominants as is indicated by the stronger negative correlations (Pearson correlation between rank stability and the measurement of spatial centrality: $r_{125} = -0.25$; dominance differentiation and the measurement of spatial centrality: $r_{125} - 0.23$, $P<0.01$). Once it has arisen, spatial centrality of dominants maintains itself. Because agents of similar dominance are spatially next to each other, incidental rank reversals mostly take place among similar *Dom* values, and, therefore, are small. Thus spatial structure stabilizes hierarchy and keeps its differentiation intact. In turn a stable hierarchy reinforces the spatial configuration. At low *StepDom*, dominance differentiation per interaction is small; consequently, the effects described above are virtually absent (Figs 2–6).

Spatial centrality of dominants also causes a correlation between rank and attack frequency, because dominants, being central, have more interaction opportunities (Fig. 6). Furthermore, in the Obligate attack strategy, whatever the severity of aggression, attack remains similarly bidirectional because the agents in question attack without any regard for dominance positions of others (Fig. 7).

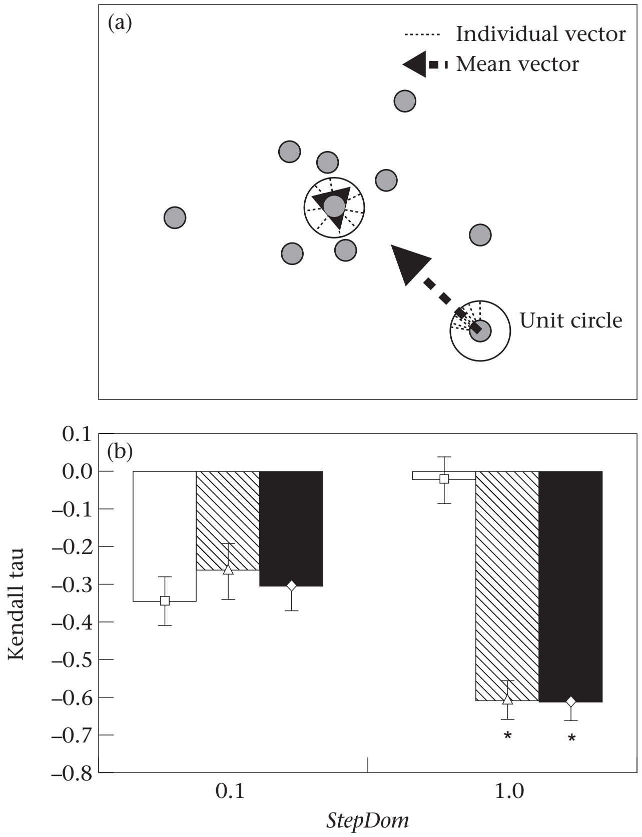

Figure 4. Spatial structure. (a) Calculation of mean vector of direction of other group members. Filled circles represent agents. Unit circles are drawn around a central and a peripheral agent. On these circles the directions of all other agents are projected by individual vectors. For agents in the centre of the group the length of the vector of mean direction of others is small (because vectors in opposite directions cancel each other out); for agents at the periphery of the group it is large. (b) Kendall rank correlation (τ; $\bar{X}\pm$SE) between the dominance value (*Dom*) of each agent and the vector of mean direction of others. The correlation is shown for Perceivers (with direct rank perception) for various attack strategies and intensities of aggression (*StepDom*). □: Ambiguity-reducing strategy; ▧: Risk-sensitive strategy; ■: Obligate attack strategy. Note that stronger negative correlations represent clearer spatial centrality of dominants. *Improved Bonferroni method $P<0.05$.

Risk-sensitive strategy. Results among Risk-sensitive agents have been described elsewhere (Hemelrijk 1999b); they are very similar to those of the Obligate attack strategy. Aggression reduction and spatial centrality arise at high *StepDom* as an emergent phenomenon, by a positive feedback between the developing hierarchy and spatial structure (Figs 2–5). Furthermore, the correlation between rank and aggression emanates not only from the greater number of interaction opportunities for dominants because of their spatial centrality, but also from the internal mechanism of attack (agents are more likely to attack the greater their chance of winning). Thus, dominant agents will attack others more easily even at low *StepDom*, but particularly if *Dom* values are more differentiated (Fig. 6). The same internal, victory-oriented attack mechanism causes lower-ranking agents, because of their lower chance of beating higher-ranking ones, to attack higher-ranking agents less often than vice versa. It follows that the Risk-sensitive system is associated with stronger unidirectionality if the rank differentiation is greater, although unidirectionality does not become statistically significant (Fig. 7; in contrast to the Obligate attack strategy, where it is accompanied by symmetry of attack). Note that unidirectionality strengthens not only the stability of the hierarchy (Pearson correlation between unidirectionality and stability: $r_{125}=-0.54$, $P<0.01$; Fig. 5), but also the spatial structure (unidirectionality and spatial centrality: $r_{125}=0.33$, $P<0.01$), since agents mostly attack and chase lower-ranking partners that are already peripheral to them.

Function: aggression reduction

Ambiguity-reducing strategy. The function of aggression reduction through clarification of relations is explicitly implemented in the Ambiguity-reducing agents: they are more likely to avoid conflicts with opponents the larger the rank distance with the opponents is. As a result, when the differentiation of the hierarchy is weak, as happens at low *StepDom* (Fig. 3), the attack frequency remains approximately constant (Fig. 2). When the hierarchy is strongly differentiated, however, at high *StepDom*, the aggression clearly decreases as ranks differentiate and, simultaneously, the agents 'huddle' closer together (Fig. 2). This huddling happens because, during the differentiation of the hierarchy, Ambiguity-reducing agents more and more meet partners that are distant in rank and these are the ones they nonaggressively tolerate to remain close by. Thus, hierarchical differentiation affects spatial structure, but the greater tolerance among rank-distant than among rank-close agents impedes the development of spatial centrality of dominants (Fig. 4b), as it implies spending more time near rank-distant than rank-close agents, whereas in a configuration with centrally located dominants, close-ranking agents should be in close proximity and agents of decreasing dominance at increasing distances from them. This explains too why clearer hierarchical differentiation, at higher *StepDom*, reduces spatial centrality (Fig. 4b).

No significant correlation between rank and attack frequency is found (Fig. 6). This is to be expected because agents with medium *Dom* values have vaguer dominance relations with more group members and, therefore, the Ambiguity-reducing rules cause these agents to act aggressively towards more group members than agents with extreme *Dom* values (both high and low) do.

Owing to the symmetry of the rule to attack others of both higher and lower rank, unidirectionality of attack is absent. At high *StepDom*, attack even becomes significantly symmetrical (Fig. 7). This stronger symmetry may be due to the weaker spatial structuring compared with that found at low *StepDom* (see Fig. 4). This presents different agents with more equal chances of meeting others. Equal meeting opportunities contribute to increased symmetry of interactions. In other words, at low *StepDom*, because subordinates are slightly more peripheral than higher-ranking ones, they have fewer

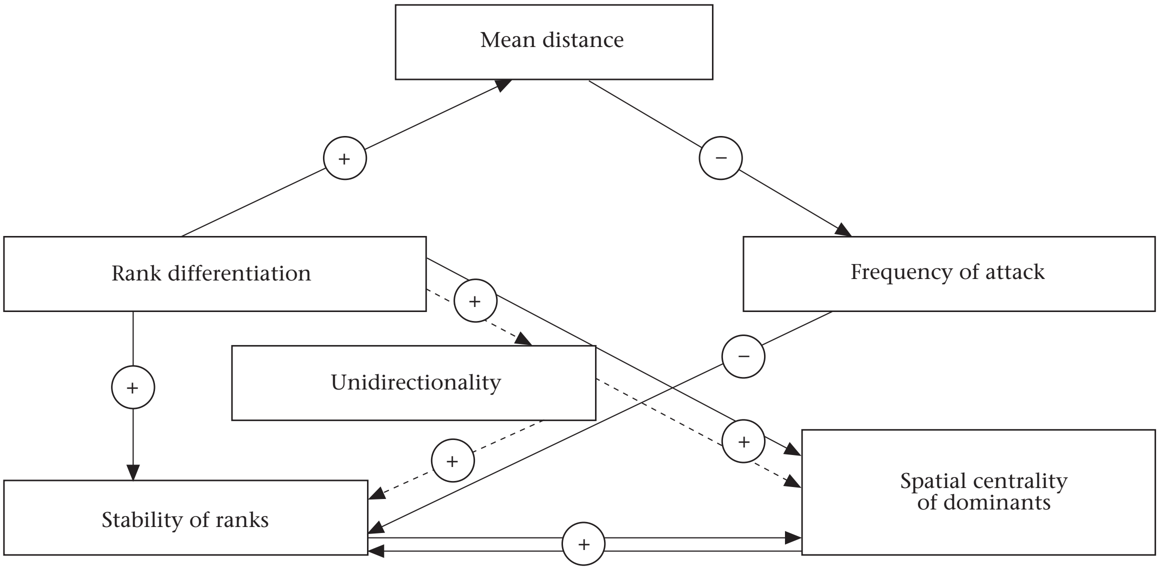

Figure 5. Summary of the associations underlying social-spatial structuring for the Risk-sensitive and Obligate-attacking agents at high intensity of aggression (*StepDom*; continuous lines). Note that the dotted lines apply only to the Risk-sensitive, not the Obligate strategy. Spatial centrality is inversely proportional to the correlation between rank and the length of the mean vector of the mean direction of others.

opportunities to attack others and this reduces the degree of symmetry of attack.

Indirect Rank Perception (i.e. Estimators)

So far, we have seen what happens if rank perception depends on direct rank perception in agents named Perceivers. I now compare this to outcomes based entirely on individual recognition in agents called Estimators.

The hierarchy of Estimators appears to be underdeveloped compared with that of Perceivers (for every attack strategy and independent of the value of *StepDom*; Fig. 8). This is due to the variation in experience that Estimators have with each group member and the ensuing difference of opinions they develop about each other. For instance, Estimators can have long-term intransitive relationships (in which A dominates B, B dominates C, but C defies A) whereas Perceivers are unlikely to. Among Perceivers, circular relationships may arise temporarily because of the sequential and stochastic nature of interactions, or occur only in the eye of the observer who does not yet record concomitant reversals. Therefore, intransitive relationships among Perceivers may arise after a rank reversal between two individuals A and C (whereby initially A was dominant to C and to B and B was dominant to C). Once C dominates A, there is intransitivity until each of them meets B again (and these interactions are observed).

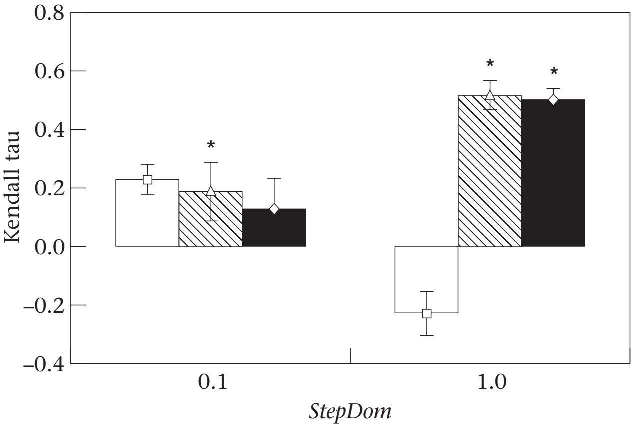

Figure 6. Correlation between rank and attack frequency of Perceivers for all strategies and two values of intensity of aggression (*Stepdom*; mean Kendall τ±SE). □: Ambiguity-reducing strategy; ▨: Risk-sensitive strategy; ■: Obligate attack strategy. *Improved Bonferroni method $P<0.05$.

Owing to the Estimators' weak hierarchy, their patterns of social interactions are unclear. This is because strong hierarchical differentiation is a central feature from which many social–spatial interaction patterns emerge.

The less pronounced patterns of interactions among Estimators than Perceivers in the present study correspond to those of a former study (Hemelrijk 1996a, 1997) in which Estimators were less mutually cooperative and spiteful in fights than Perceivers. Remarkably, it thus seems as if patterns of social interaction more clearly originate from lower than higher cognition.

Robustness of the Model

Although the details of parameter and initial values were chosen arbitrarily, the results appear robust against these variations. Similar results are obtained for a group size of eight Perceivers with initial *Dom* value of 8 and a *PerSpace* of 2, for different fleeing distances, for the same and for half the intensity of aggression (Hemelrijk 1998a, b). The same holds for populations composed of different proportions of two types of Perceivers that differ

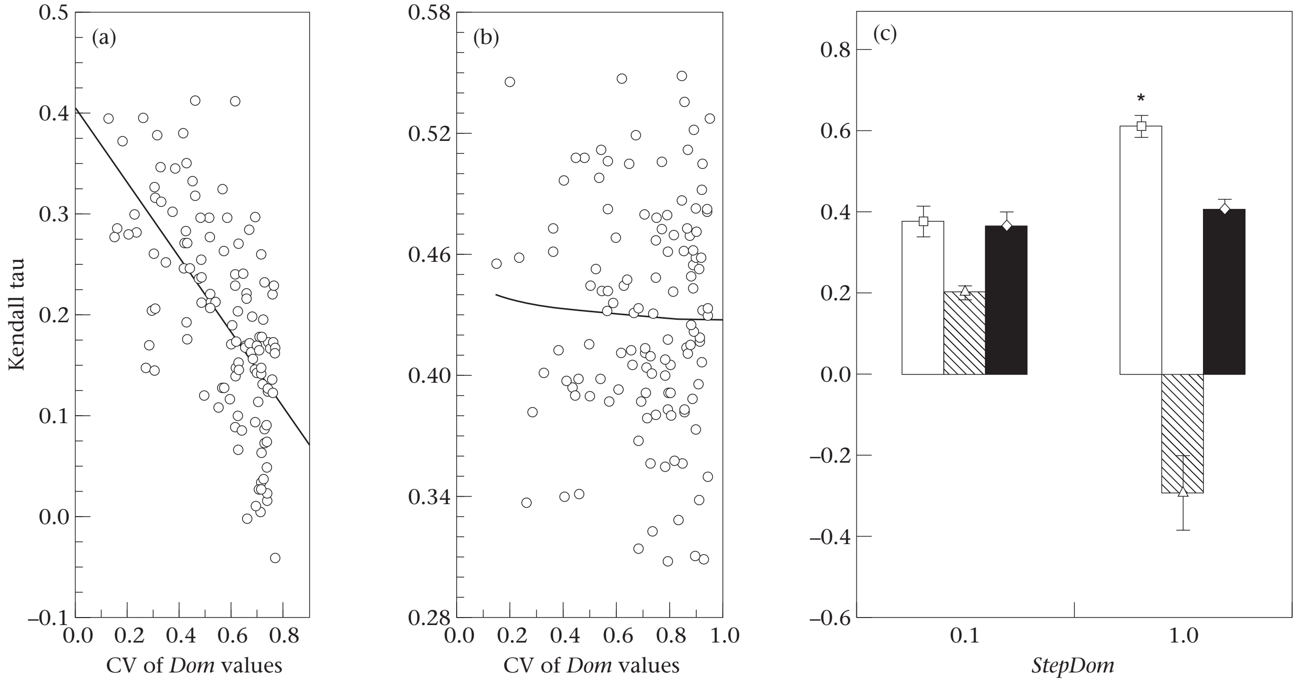

Figure 7. Unidirectionality of attack for different strategies (measured by the τ_{Kr} correlation between the matrix of attack and its transposed form, i.e. of received attack). Degree of unidirectionality (*Y* axis) and differentiation of the hierarchy (i.e. the coefficient of variation of dominance values) over time (*X* axis) for (a) Risk-sensitive and (b) Obligate-attacking Perceivers at high intensity of aggression (*StepDom*). (c) Unidirectionality of aggression of Perceivers for three attack strategies and two intensities of aggression (mean $\tau_{Kr}\pm$SE excluding transient data before time unit 200). Note that a lower, or more negative, correlation indicates more unidirectionality. Conversely, the higher the correlation values, the stronger the degree of symmetry of attack. *Improved Bonferroni method $P<0.05$. □: Ambiguity-reducing strategy; ▨: Risk-sensitive strategy; ■: Obligate attack strategy.

in their fighting capacity (initial *Dom* value and intensity of aggression; Hemelrijk 1999b, in press).

DISCUSSION

In this paper, I have studied in a model the consequences of two different assumptions about the function of dominance interactions, namely, aiming for high rank (implemented as the Obligate and Risk-sensitive strategies) and, second, reduction in aggression (the Ambiguity-reducing strategy). It appears that even in the absence of explicitly implemented resources (agents compete only for unspecified resources), complex patterns of behaviour arise.

The most remarkable aspects of this model are that societies of artificial agents that differ only in the implemented function of dominance interactions appear to be similar in that aspect in which the internal rules of agents of both societies differ and appear to differ in a multitude of additional social interaction patterns that are seemingly unrelated to the different functions! More specifically, only in the Ambiguity-reducing strategy, and not in the Obligate strategy, is there a mechanism that reduces the frequency of aggression during differentiation of the hierarchy, yet aggression declines in both strategies. Obviously, there is no simple connection between mechanism and resulting behaviour. In the absence of specific rules for it, the decline in aggression in the Obligate strategy is caused by social-spatial structuring. The decrease in attack is due to the consistent tendency of lower-ranking individuals to flee from others. Interindividual distances thus increase. This diminishes encounter frequency and thus causes aggression to abate. The decline in aggression occurs in a similar way among Risk-sensitive agents (Hemelrijk 1999b). Although the Risk-sensitive strategy implies an aggression-inhibiting mechanism, this cannot explain the overall aggression reduction, because, whereas losers are inhibited from attacking, winners are equally instigated to do so.

Furthermore, implementation of both functions appears to differ unexpectedly in many other social interaction patterns, for instance, spatial configuration. If agents follow rules to improve rank (Obligate and Risk-sensitive strategies), spatial centrality develops at high *StepDom*, but not if they execute rules to diminish aggression once relationships are clear (Ambiguity-reducing strategy). Under the Ambiguity-reducing strategy, agents end up close to partners distant in rank, because with these their fighting tendency is lowest. In the other strategies, however, subordinates, by fleeing from everyone else, while at the same time all agents aggregate, cause dominants to end up in the centre. In this way, spatial centrality of dominants occurs, although agents do not prefer any special location within the group. In turn, such spatial structure enhances correlations between dominance and attack frequency for the simple reason that dominants encounter others more often than subordinates do (Hemelrijk 1999b).

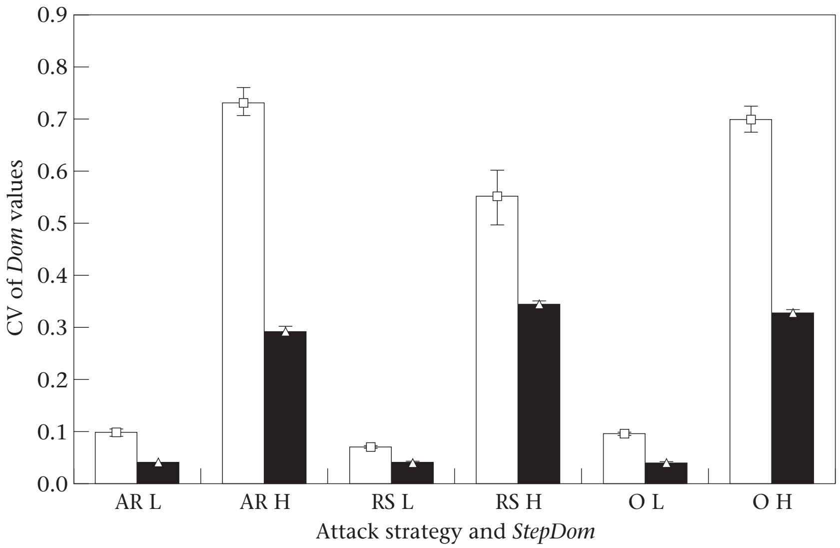

Figure 8. Dominance differentiation for Estimators (with memorized-experience-based rank perception) and Perceivers (with direct rank perception), measured by $\bar{X}$±SE of the coefficient of variation of dominance values. □: Perceivers; ■: Estimators. AR: Ambiguity-reducing strategy; RS: Risk-sensitive strategy; O: Obligate attack strategy; L: low aggression intensity (*StepDom*); H: high *StepDom*.

Thus, if these results are biologically relevant, it follows that we need to study animal behaviour not as isolated strategies, but in terms of clusters of interconnected variables and in terms of feedback between social behaviour and spatial structure. What does the present model imply for our studies of animal behaviour?

First, reduction in aggression is obvious in real animals particularly when unacquainted individuals are brought together (e.g. chickens: Guhl 1968; primates: Kummer 1974). Usually, this decline is assumed to be due to an internal mechanism (e.g. see Pagel & Dawkins 1997), but following the model, it may (at least partly) be due to expanding distance among individuals. This can be tested by tracing whether, indeed, simultaneously with the differentiation of the hierarchy, interindividual distances also increase when unfamiliar individuals are put together.

Second, spatial centrality of dominants has been described for many species (such as primates: Janson 1990; spiders, fish, birds: Krause 1994a). According to the 'selfish herd theory' (Hamilton 1971) it arises because individuals have evolved a centripetal instinct for safety reasons, that is, individuals try to position others between themselves and the predator. However, in the model, spatial centrality arises as a side-effect in spite of the absence of any spatial preference within the group (as I have noted for the Risk-sensitive strategy before; Hemelrijk 1999b). Note that spatial centrality is not covertly implemented. Although the model contains rules for aggregation, these rules do not specify spatial centrality. Despite the clustering of the agents, spatial centrality is even absent under most conditions: in all three strategies at low intensity of aggression, and under the Ambiguity-reducing attack strategy also at high intensity of aggression. Spatial centrality arises only with the Risk-sensitive and the Obligate attack strategies and only if intensity of aggression is high. Thus rules for aggression function like ink in writing (Rose 1995, page 349): one needs ink for writing, but ink does not determine what kind of text one produces. Similarly here, clustering is needed, but it does not dictate the spatial structure.

To have a parsimonious alternative for a centripetal instinct, as assumed by Hamilton's (1971) theory, is important, because no centripetal instinct has yet been demonstrated in living animals. Remarkable in this respect are the very elegant experiments with fish by Krause (1993, 1994b), in which it proved to be impossible to verify a centripetal instinct, although spatial centrality was clearly established. Also pertinent is the clear demonstration of centrality of dominants in animals that do not suffer from predation such as in scalloped hammerheads, *Sphyrna lewini*, by Klimley (1985).

Third, this way of thinking affects our evolutionary reasoning. The clearest example of this comes from the resemblance between results of the Risk-sensitive strategy and behavioural studies of species of macaques (Hemelrijk 1999b). Thierry (1990) showed that aggression of despotic macaques (such as *Macaca fuscata* and *M. mulatta*) is more intense and unidirectional than that of egalitarian species (such as *M. tonkeana*). Furthermore, correlations between rank and attack frequency (Kaplan & Zucker 1980; Kaplan et al. 1982), as well as evidence for spatial structure, have been established in the fiercer, despotic, but not in the milder, egalitarian species. This resemblance between reality and my model leads to an unexpected evolutionary explanation for an actual difference between species in the degree of spatial centrality of dominants: this may well be a side-effect of the variation in intensity of aggression. Such variation, in turn, may have evolved from differences in feeding competition (McKenna 1979; Hemelrijk 1999b).

Note that a spatial configuration may also structure sociopositive behaviour (Hemelrijk 1996b). Again, this is in line with observations on macaques (Thierry et al. 1990). Whereas in egalitarian macaque species individuals freely groom with everybody, grooming relations in despotic species are more often ruled by rank. Such differences, therefore, do not require separate adaptive explanations. Furthermore, to test whether spatial centrality, the gradient of the hierarchy, unidirectionality of attack and sociopositive behaviour are interrelated in real animals in the same way as in the model, all these aspects have to be studied simultaneously in one and the same group of animals.

I now compare this model to two other, related models on dominance interactions. First, Dugatkin (1997) studied the characteristics of hierarchies that develop in the presence of either the winner or the loser effect, but not both simultaneously. He concluded that loser effects induce weaker hierarchies than winner effects. However, this outcome arose because Dugatkin added certain assumptions about the tendency to attack in his operationalization of the winner/loser effect: his definition of the loser effect implies that individuals are less likely to attack again after losing and the definition of the winner effect implies the reverse. Consequently, if only such a loaded loser effect is important, the hierarchy remains weaker because interactions are fewer. That fewer interactions result in a weaker hierarchy corresponds to what happens in the present model during my experiments with loser groupings. In loose groups compared to dense groups, fewer interactions result in a weaker hierarchy (Hemelrijk 1999a). Note, however, that in my model this result arises despite both winner and loser effects operating together. Dugatkin's result may thus point to the effects of low frequencies of interactions rather than to the separation of winner and loser effects.

The second example is the mathematical model on self-organizing dominance hierarchies by Bonabeau et al. (1996). In both Bonabeau et al.'s and Dugatkin's models, interaction partners are chosen at random and the change in dominance value is linear. In my model, however, interaction partners are determined by proximity and the more unexpected the result of a dominance interaction is, the greater is the subsequent change in dominance value (based on observations on bumblebees by van Honk & Hogeweg 1981).

In the growing literature on aggression and dominance hierarchy, the model presented here differs in focus and methods. The most important modelling approach towards aggression and dominance is game-theoretical modelling, which is based on payoff rationalizations (e.g. Parker 1974; Maynard Smith 1983; Pagel & Dawkins 1997; Matsumura & Kobashi 1998; Riechert 1998), whereby natural selection is treated as a statistical process on an aggregate of quantities. Behaviour is decomposed in independent components (Frank 1998). Each trait is thought to have certain costs and benefits, which are defined independently of other aspects of behaviour (such as grouping tendency, spatial positioning) and contribute a certain value to the fitness of the bearer. Each trait is typically given a separate evolutionary explanation. For instance, escalation of aggression is regarded as a, genetically encoded, quality of the individuals, and represented by such metaphors as 'hawks' (always escalating fights) or 'doves' (never doing so). To study its evolution, both strategies (hawks and doves) are pitted against each other. The strategies that survive at equilibrium are so-called evolutionarily stable strategies (ESS; Maynard Smith 1983).

In contrast to game theory, individual-oriented modelling is not about pay-off rationalization. The emphasis of this approach is on the macropatterns that arise by self-organization from the interaction between agents and their social organization. Like related studies in theoretical biology (Deneubourg & Goss 1989) and in new artificial intelligence (Pfeifer & Scheier 1999), individual-oriented modelling is context oriented and value free instead of normative. Almost without considering fitness benefits, it only traces the direct consequences of well-known behavioural assumptions in their spatial context for different levels of social complexity (i.e. individuals, interactions, relationships, group, see Hinde 1982). It tends to ignore exceptional internal complexities, such as deceit and it even neglects genetic differences, because in this way other effects arising from the interactions between agents (or with their environment) become more visible. Phenotypic polymorphic populations arise, but this variation is due only slightly to genetic differences, originating mainly from different experiences of agents and their interaction with their environment. For instance, I have shown how reciprocation of support in fights may not be the effect of optimization of costs and benefits of these 'altruistic' acts per se (as in the theory of reciprocal altruism by Trivers 1971), nor of complex record-keeping mechanisms, but they may arise as a side-effect of dominance interactions and spatial positioning of individuals (Hemelrijk 1996a, b, 1997). In other words, instead of predicting what can evolve by natural selection, the approach presented here serves a very different aim.

Finally, it may be said that the main value of a model is that it generates hypotheses that can be tested successfully (Levins 1966). This is what the present model does. It demonstrates how patterns may emerge from the dynamics of interactions between agents. In this way, it provides a new starting point (a null model) for generating parsimonious, integrative hypotheses for the occurrence and evolution of social behaviour in any group-living species that has dominance interactions.

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