

Spatial Centrality of Dominants Without Positional Preference.

Charlotte K. Hemelrijk

AI Lab, Department of Computer Science, University of Zürich,
Switzerland, Fax 0041-1-363 00 35, Email: hemelrij@ifi.unizh.ch.

Abstract

In many group-living animals dominant individuals occupy the center of a group. This is generally thought to reflect a preference for locations, that provide optimal protection against predators. However, in this paper I will show that such spatial-structure also emerges among artificial entities that lack preference for any spatial location.

The artificial entities dwell in a homogeneous world and are completely identical at the start of the simulation. They are gregarious and perform dominance interactions in which the effects of winning and losing are self-reinforcing. Varying essential parameters of the model revealed that: 1) Social-spatial patterns are stronger among entities that perceive each others rank directly compared to those that estimate rank of others based on personal experiences. 2) Stronger social-spatial patterns result when entities obligatory attack others than when attack-rate was negatively dependent on rank-distance. 3) Raising the intensity of attack increased the centrality of dominants for the Obligatory attack system, but weakened it for the Rank-Distance Decreasing attack system. Also, other social interaction patterns emerged, such as bidirectionality of aggression and a correlation between rank and frequency of attack. Such epiphenomena may underlie the variation of social-spatial patterns found in real animals.

1 Introduction

Following Hamilton's (1971) influential model of the 'selfish herd', a spatial position in the center of a group is functionally attributed to optimal protection against predators. To test the hypothesis that animals compete for this safe location, much research has been devoted to studying nonrandom positioning of individuals and position-related fitness differences (for a review see Krause 1994). Observations on natural groupings (e.g. fish: Krause 1994), results of experiments (e.g. spiders: Rayor and Uetz 1990) and models on benefits of position preferences (e.g. Bumann, Krause, Rubenstein 1997) have been interpreted as support for Hamilton's ideas. However, conflicting observations on spatial structure (primates: Altmann 1979; Janson 1990ab; Rhine and Westland 1981)

and its fitness consequences (e.g. highest mortality in the center in groups of certain species of fishes: Parish 1989) were reported as well. These contradictory results have been suggested to be a consequence of differences in measurement methods (Collins 1984; Krause 1994) and neglect of essential variables in the optimization models.

Note that these amendments function as excuses to leave the soundness of the theoretical principles undisputed. It should be recognized, however, that the optimization approach is not without problems. Optimization models treat features as independent properties of individuals and therefore come up with a separate explanation for each trait. However, there is a growing awareness, fostered by 'Artificial Life' studies, that what are supposed to be traits actually are emergent properties from interactions between agents and their local environment (including other agents) (e.g. Pfeifer and Verschure 1995) and that such interactions may bring about more than one pattern. An example is the study on the formation of diverse spatial structure of groups of ants by Deneubourg et al. (1989). Using Monte Carlo simulations, they showed that one simple rule set of trail laying/following behavior can generate different characteristic swarm patterns of ants depending on density and distribution of food.

Similar considerations may hold for spatial-social structures with dominants in the center and subordinates at the periphery, that conventionally would be associated with Hamilton's notion of the 'selfish herd'. Such a configuration was indeed found as a side-effect in an artificial world in which group-living entities perform self-reinforcing dominance interactions but lack spatial preference (Hogeweg 1988). The aim of this paper is to understand the dynamics of such spatial structuring in detail in order to bring it up as an alternative to the selfish herd theory. Hereto, I have set up an artificial world comparable to that of Hogeweg, but in addition I varied the cognitive sophistication involved in dominance interactions, the tendency of entities to attack others and the impact of these interactions on their subsequent dominance position.

To examine the influence of mental sophistication on spatial patterning, I created two types of entities that differ in their way to perceive dominance of others. The simplest agents are called Perceivers, because they observe the rank of others directly and do not

recognize others individually. The more sophisticated entities, the Estimators, assess a partner's dominance by recalling their last experience with them and are similar to those used by Hogeweg. Two attack systems are devised. In the simplest one, Perceivers always attack others upon encountering them. In the other, in line with a model of Bonabeau et al. (1996), I implemented the probability to attack a partner as a decreasing function of rank distance. To mirror differences in intensity of aggression (as described for primates by Thierry 1985,1990), the impact of single acts of attack on future probabilities of winning/losing was varied. Apart from analyzing the effects of probability of attack and its impact on social-spatial structure, I will also report on other emergent social interaction patterns, such as bidirectionality of aggression and correlation between rank and frequency of attack.

2 Methods

In this Section I will present a description of the model and outline how spatial structure and stability of the hierarchy is measured.

2.1 The Model

The model is individual-oriented and event-driven (see Hogeweg & Hesper 1979; Hogeweg 1988; Villa 1992; Judson 1994). The modeling environment (written in object-Pascal, Borland Pascal 7.0) consists of three parts:

- * the 'world' (toroid) with its interacting agents,
- * its visualization,
- * special entities that collect and analyze data on what happens in the 'world' (cf. the 'recorders' and 'reporters' of Hogeweg 1988).

Unlike in former lattice-based models (Hemelrijk 1996,1997), the 'world' presented here consists of a continuous space of 200 by 200 units. Therefore, agents are able to move in any direction. They have an angle of vision of 120 degrees and their maximum perception distance (MaxView) is 50 units. I will confine myself to a small ensemble of 8 entities. Agents group and perform dominance interactions according to the sets of rules described below (Figure 1).

2.1.1 Grouping rules

In the literature, two opposing forces affecting group structure are often postulated: on the one hand animals are attracted to one another, because being in a group provides safety. On the other hand, aggregation implies competition for resources and this drives individuals apart.

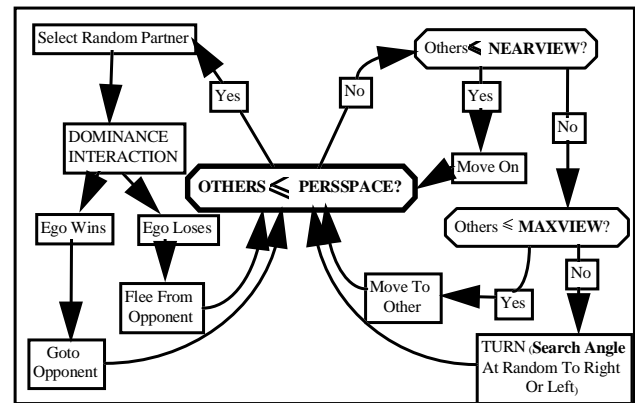


Figure 1. Flow chart for the behavioral rules of the entities

The forces leading to aggregation and spacing are realized in the model by the following set of rules (cf. Hogeweg 1988):

- If an agent sees another within a critical distance (parameter PerSpace), it performs a dominance interaction with that entity. In case several agents are within PerSpace, the interaction partner is chosen at random. If the agent wins the interaction, it moves towards its opponent, otherwise it makes a full turn and moves away from its rival.
- If nobody is in its PerSpace, but an agent perceives others within a distance of NearView, it continues moving in its original direction.
- If an agent detects its nearest neighbors outside NearView, but within its maximum range of vision (= MaxView), it moves towards them.
- If an agent does not perceive any other agent within maxView, it searches for group members by making a turn over an angle (= SearchAngle) of 90 degrees at random to the right or left.

2.1.2 Dominance types

Conventionally, rank-acquisition is attributed to a (possibly inherited) quality of an individual (Ellis 1994). However, experimental results from various animal species (for a listing see Bonabeau et al 1996) have shown that winning is determined by chance and self-reinforcement: once an animal has won, it has a larger chance of winning again in a subsequent fight (the so-called 'winner-effect', see Chase et al 1994). Because this study emphasizes the self-organizing properties of interactions, I confine myself to the self-enhancing effects

of winning/losing by starting with completely identical entities.

About the perception of rank by others, a number of hypotheses are entertained by various authors (e.g. Barnard and Burk 1979; Hemelrijk 1996,1997). The most simple one is that the capacity to win is directly perceived from external cues, such as pheromones in social insects (e.g. van Honk and Hogeweg 1981) and body postures in crustaceans (e.g. Copp 1986). In many species, however, dominance may not be recognized externally, but may be estimated on the basis of an individuals' former encounters with a partner. Such a representation asks for more 'cognition' and was used in Hogeweg's (1988) model. Agents endowed with direct and estimated rank perception will be called Perceivers and Estimators respectively. The effects of both types of dominance perception will be compared in this paper.

2.1.3 Dominance interactions.

Interactions between agents with direct perception of dominance ranks (i.e. Perceivers) are modeled after Hogeweg & Hesper (1983) as follows:

1. Each entity has a variable DOM (representing the capacity to win a hierarchical interaction).
2. After meeting one another in their PerSpace, entities display and observe each others DOM. This represents an active display and only through such a display the partner obtains information about the DOM value of its opponent. Subsequent winning and losing is determined as follows by chance and values of DOM:

$$w_i = \begin{cases} 1 & \frac{DOM_i}{DOM_i + DOM_j} > RND(0,1) \\ 0 & \text{else} \end{cases} \quad (1)$$

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, else it loses.

3. Updating of the dominance values is done by increasing the dominance value of the winner and decreasing that of the loser:

$$\begin{aligned} DOM_i &:= DOM_i + \left(w_i - \frac{DOM_i}{DOM_i + DOM_j} \right) * STEPDOM \\ DOM_j &:= DOM_j - \left(w_i - \frac{DOM_i}{DOM_i + DOM_j} \right) * STEPDOM \end{aligned} \quad (2)$$

The consequence of this system is that it behaves as a damped positive feedback: winning by the higher ranking agent reinforces their relative DOM-values only

slightly, whereas winning by the lower ranking gives rise to a relatively large change in DOM. To keep DOM values positive, their minimum value was arbitrarily put at 0.01. STEPDOM is a scaling factor which varies between 0 and 1 and is analogous to intensity of aggression. High values imply a large change in DOM-value when updating it, and thus indicate that single interactions may strongly influence future outcomes of conflicts. Conversely, low STEPDOM-values represent low impact. Unless stated otherwise, STEPDOM is set at 0.5.

4. Winning includes chasing the opponent one unit distance and then turning randomly 45 degrees to the right or left in order to reduce the chance of repeated interactions between the same partners. The loser responds by fleeing under a small random angle over a predefined FleeingDistance.

In the case of indirect rank perception, the agents (i.e. Estimators) recognize each other individually and remember their personal experience with each partner. Dominance interactions are defined similarly as in the SKINNIES of Hogeweg (1988):

1. If an entity meets another in its PerSpace, it first consults its memory to establish whether it might win or loose a potential dominance interaction with that partner. Hereto, it performs the same dominance interaction as described in (1) and (2), but now based on the mental impressions it has of its own dominance rank and that of the other. If it loses this 'mental battle', it moves away while updating the impression of its own rank and that of the partner. If it wins, it updates and initiates a 'real' fight. Thus, unlike the Perceivers, the Estimators 'decide' whether or not to attack.
2. If it wins, a 'real' fight is initiated by displaying its expectancy to win as its updated relative dominance rank ($=D_i$) and the partner displays in return ($=D_j$). That is:

$$\begin{aligned} D_i &= \frac{DOM_{i,i}}{DOM_{i,i} + DOM_{i,j}} \\ D_j &= \frac{DOM_{j,j}}{DOM_{j,j} + DOM_{j,i}} \end{aligned}$$

Thus entities display their 'self-confidence'. Note that this self-confidence varies depending on the experience ego has with a particular partner. The variability of the display is not a strategic option (such as dishonest signalling in a typical game-theoretic

setting), but a direct consequence of behavioral constraints.

3. Winning is decided as in (1), using D_i and D_j instead of DOM_i and DOM_j .

4. Updating of the experiences of each of both entities is done similar to (2), but involves two representations for agent i :

$$DOM_{i,i} := DOM_{i,i} + \left(w_i - \frac{DOM_{i,i}}{DOM_{i,i} + DOM_{i,j}} \right) * STEPDOM$$

$$DOM_{i,j} := DOM_{i,j} - \left(w_i - \frac{DOM_{i,i}}{DOM_{i,i} + DOM_{i,j}} \right) * STEPDOM$$

Updating for agent j is obtained by replacing $DOM_{i,i}$ by $DOM_{j,j}$.

From now on, the initiation of a dominance interaction will also be referred to as ‘attack’ for short.

2.1.4. Probability of attack.

In former versions of the model (Hemelrijk 1996,1997) entities always engaged in dominance interactions when encountering others nearby. However, the ‘Obligate attack system’ may not meet certain observations on real animals. In a variety of species (e.g. chickens: Guhl 1968; primates: Kummer 1974), it has been found that some time-period after putting unacquainted individuals together, hierarchical activity subsides and non-aggressive proximity prevails. This suggests that eventually animals acknowledge the rank of others. To reflect this directly, I also implemented a version of the model in which the probability of attacking a partner decreases linearly with the rank-distance to that partner (for a comparable implementation see Bonabeau et al. 1996). This will hereafter be referred to as the Rank-Distance-Decreasing attack system. In this paper, I will compare spatial structuring and several other characteristics in the two systems.

2.1.5. Timing regime

Since parallel simulations cannot be run on most computers, a timing regime regulating the sequence of the activation, has to be included. The type of timing regime influences the results of a simulation. A biologically plausible timing regime must be locally controlled, i.e. by other entities and not by a monitor (e.g. Goss & Deneubourg 1988). In the timing regime used here, each entity draws a random waiting time from a uniform distribution. The entity with the shortest waiting time is activated first. The decay of waiting time is the same for each entity. However, if a dominance interaction occurs

within NearView of an agent, the waiting time of this agent is reduced stronger.

2.2 Experimental setup and Data collection

Because animal groupings vary in their cohesiveness, also a comparison between spacious and cohesive groups is included. Cohesive groups (Hemelrijk 1996, 1997) result from a small personal space of two units (this makes entities tolerate others very nearby before chasing them away), a small nearView (which causes entities to turn towards others soon) and a large searchAngle of 90 degrees (by which lost entities quickly find the group back). Starting from cohesive groups, I created spacious groups by enlarging personal space to 4 units and nearView from 8 to 24. Five runs were done per type of entity (Perceiver, Estimator), grouping (Cohesive, Spacious) and FleeingDistance (from one to four units), resulting in a total of 80 experiments.

The effects of attack-probability and STEPDOM were studied for Perceivers only and were evaluated on the basis of sixty runs, consisting of ten runs of each system of attack and for three values of STEPDOM (0.1, 0.5 and 1.0).

During a run, every change in spatial position and heading direction of each entity was recorded. Every time step (consisting of 160 activation) the distance between agents was calculated. Dominance interactions were continuously monitored by recording: 1) the identity of the attacker and its opponent; 2) the winner/loser; 3) the updated DOM-values of these entities.

2.3 Measures of spatial centrality of dominants and hierarchical stability

The degree with which dominants occupied the center was measured in two ways, by the spatial directions of others around ego and by the average distances of partners towards ego. Using circular statistics (Mardia 1972), for each scan the centrality of each individual was calculated by drawing a unit circle around it and projecting the direction of other group members (as seen by ego) as points on the circumference of that circle. Connecting these points with the origin gives vectors. The length of the mean vector represents the degree in which the position of group members relative to ego is clumped; longer mean vectors reflect more directedness and indicate lower centrality (i.e. ‘encirclement’). Thus stronger centrality of higher ranking entities is reflected in a larger negative correlation between rank and encirclement.

The second measure is the Kendall rank correlation between dominance value and the average distance of Ego to others. Again, centrality of dominants is represented by a negative correlation. Both measures appeared to be strongly correlated and only the rank-encirclement correlation will be mentioned in the analysis.

The stability of the dominance hierarchy was expressed as the relative number of rank reversals. This

was established by calculating the Kendall rank correlation between the dominance ranks of entities at successive intervals of two time steps (320 activation).

3 Results

3.1 Parameters for strong social-spatial structure.

As in the previous lattice-based world, a dominance hierarchy developed among initially completely identical entities (see Figure 4 of Hemelrijk 1996). Furthermore, due to the continuous version of the world used here, a much clearer social-spatial structure (with dominants in the center and subordinates at the periphery) originated.

Rank-correlated encirclement appeared stronger among Perceivers than Estimators (Figure 2). Assuming that this type of social-spatial structure emerged because dominants chased away subordinates to the periphery, this is probably due to the Perceivers' higher frequency of aggression and clearer rank-differentiation. In the remainder, only the behavior of Perceivers will be considered; for a detailed discussion about differences between Perceivers and Estimators see Hemelrijk (1996,1997).

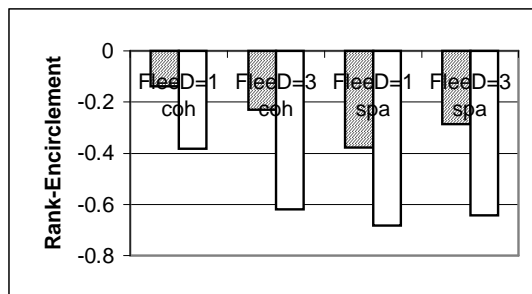


Figure 2. Kendall rank correlation between rank and encirclement for various parameter settings of groups of 8 entities. Shaded bars: Estimators, white bars: Perceivers; FleeD: FleeingDistance; coh: cohesive, spa: spacious groups.

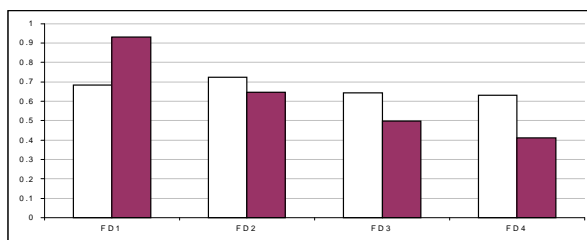


Figure 3. Frequencies of aggression and centrality of dominants for 4 FleeingDistances (FD) in spacious groups of 8 Perceivers. Shaded bars: frequency of aggression * 2000. White bars: absolute value of rank-encirclement correlation.

Social-spatial structuring appeared somewhat weaker in cohesive than in spacious groups (Figure 2). Cohesive groups have a small diameter and this implies that minor displacements suffice too bring an entity to the periphery. Thus, incidental fleeing by dominants disturbs spatial structure more in cohesive than spacious groups.

In spacious groups, the strongest social-spatial structure showed up at an intermediate FleeingDistance of two units (white bars in Figure 3). This may indicate the existence of two conflicting constraints: on the one hand, larger FleeingDistance brings subordinates quicker towards the periphery, thus enhancing spatial structure. On the other hand, larger FleeingDistances increase the average distance among entities thus reducing the frequency of interaction (shaded bars in Figure 3) and hence the ordering force responsible spatial structure.

From now on, the analysis will be restricted to data from runs that yielded the strongest spatial structure (i.e. from Perceivers with PersSpace=4, NearView=24 and FleeingDistance=2) (Figure 4).

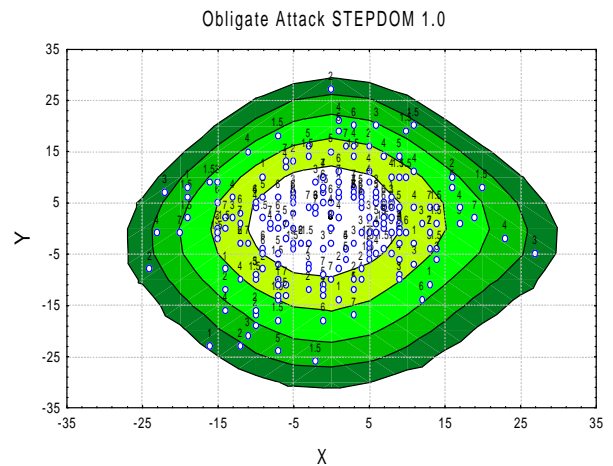


Figure 4. Visualization of social-spatial structure during the last 60 time-steps of a run. The correlation between rank-encirclement was -0.724 for this sub-period. Shown are the position of 8 entities every other time-step. Numbers indicate relative rank (from 1 to 8). Surface contours are isoclines of identical mean rank and were obtained by using a cubic spline smoothing procedure. Darker shading indicates lower mean rank.

3.2 Impact of single acts and probability of attack.

Unexpectedly, a higher STEPDOM-value led to reduced levels of aggression in both systems. In turn, this enforced the stability of the hierarchy (Figure 5).

Furthermore, a higher STEPDOM had - depending on the type of attack- opposite consequences for spatial structuring (Figure 6). For Obligatory attack, it strengthened social-spatial structure, whereas for Rank-Distance-Decreasing Attack-rates the opposite was found.

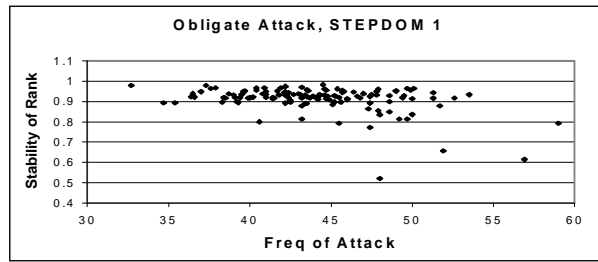


Figure 5. Relationship between frequency of aggression and stability of dominance ranks in successive periods for the Obligate Attack System and STEPDOM 1. For various parameter settings, the product-moment correlation between aggression and rank-stability was as follows: Obligate attack: at StepDom0.5, $r=-0.545$, at StepDom1.0, $r=-0.827$, $N=128$. Rank-Distance-decreasing Attack: $N=128$, StepDom0.5, $r=-0.777$; StepDom1.0, $r=-0.829$

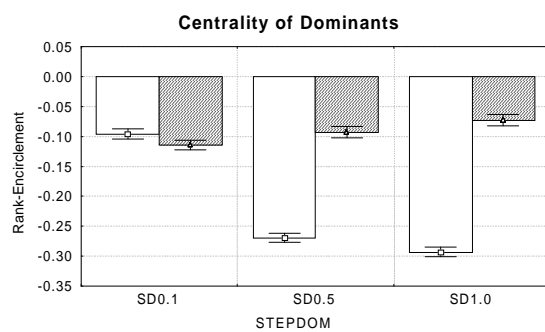


Figure 6. Intensity of aggression (STEPDOM) and centrality of dominants as measured by the rank-encirclement correlation (mean and S.E.). White bars: Obligate attack system, shaded bars: Rank-Distance Decreasing attack system. Note that the degree of rank-related encirclement is similar for both systems at STEPDOM 0.1, because under this condition no clear hierarchy forms.

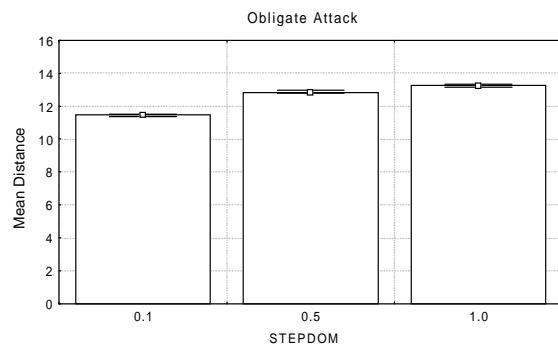


Figure 7. Average inter-individual distances and intensity of aggression (STEPDOM) of the Obligate Attack System

To explain these results, note that the higher the value of STEPDOM the stronger a single event of winning and losing influences the outcome of future interactions. Thus, starting from completely identical entities, ranks differentiate faster at higher STEPDOM. In the system with Obligatory attack, this resulted in larger average distances among entities (Figure 7): By being defeated

again and again, losers moved away further and further from others. Consequently, the frequency of aggression dropped (Correlation between distance and aggression at StepDom0.5: $r=-0.351$, at StepDom1.0: $r=-0.461$, $N=130$) and this lowered the probability of rank-reversals (Figure 5). The thus induced higher stability and larger differentiation of ranks enhance social-spatial structure as follows. If entities are similar in rank, both partners are about as likely to chase away the other and are treated by other group-members similarly. As a consequence they remain near one another. The larger the rank-distance between two entities, however, the more subordinates will flee from dominants and in time a correspondence between rank and physical distance will develop. Obviously, when rank is not stable, the frequent rank-reversals hamper the development of a clear spatial structure.

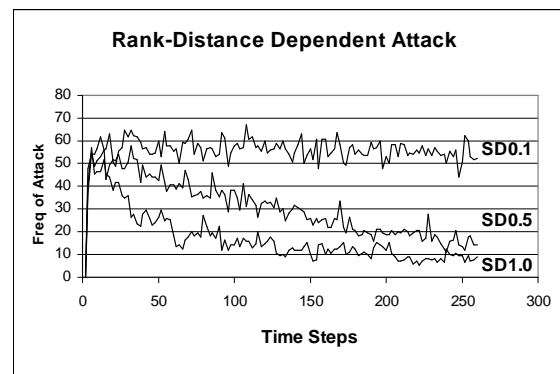


Figure 8. Intensities of aggression (STEPDOM) and decrease of frequency of attack over time in the Rank-Distance Decreasing Attack System.

The situation is different for the Rank-Distance-Decreasing Attack System. In this case, entities also reduce their attack-rate as their ranks differentiate (Figure 8). However, in contrast to the Obligate attack system, they particularly refrain from attacking partners more distant in rank. In other words, they increasingly tolerate nearby partners of more distant rank and this impairs spatial structure. However, it does not reverse the spatial configuration into one with dominants at the periphery and subordinates in the center. This is due to two forces. First, if a fight takes place, then in both systems, dominants win more often from subordinates the larger their rank-distance with these partners and second, aggressive interactions especially occur among rank-near entities. Note that in the Rank-Distance Decreasing attack system the latter is implemented a priori as a behavioral rule, whereas in the Obligate system it is due to the emergent proximity of rank-near entities.

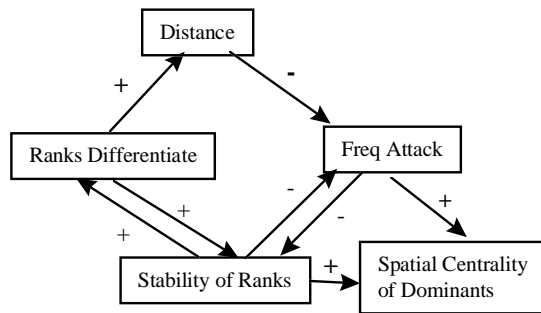


Figure 9. Summary of results for the Obligate Attack System. Arrows indicate direction of the effect.

3.4 Some other effects of spatial structure

An important property of a self-organizing system is the feedback between macro-patterns and the rules operating at the micro-level. In the Obligate attack system, this is illustrated by the reduced aggression that ensues with the growing spatial structure (which in itself arises as a consequence of dominance interactions). Lowered aggression in turn, strengthens spatial structure by decreasing the probability of rank-reversals (Figure 9).

Another example is the spontaneous development of a positive correlation between rank and aggression, as I reported before for a lattice-based artificial world (Hemelrijk 1996). In the continuous version, this correlation was found more profoundly for higher STEPDOM-values in the Obligate Attack System (being significant in respectively 0%, 30% and 60 % of the runs for STEPDOM of 0.1, 0.5 and 1.0), but was never significant for the Rank-Distance-Decreasing Attack System. This supports my previous suggestion that rank correlated aggression arises as a consequence of a spatial structure with dominants in the center. In such a configuration, dominants are surrounded at all sides by others, whereas subordinates at the periphery experience fewer encounter frequencies and therefore their opportunities to attack others are reduced.

Compared to the Obligatory Attack System, in the Rank-Distance Decreased Attack System, bidirectionality of attack was stronger, particularly so at higher STEPDOMs (Figure 10). This is understandable, because if attack rate decreases proportional to rank-distance, this means that entities more often attack partners the nearer the rank of the partners. Since all individuals do so and rank-distance is a symmetrical characteristic, rank-nearer entities will mutually attack each other more often.

For the same reason higher STEPDOMS were associated with stronger reciprocity of non-aggressive proximity as well.

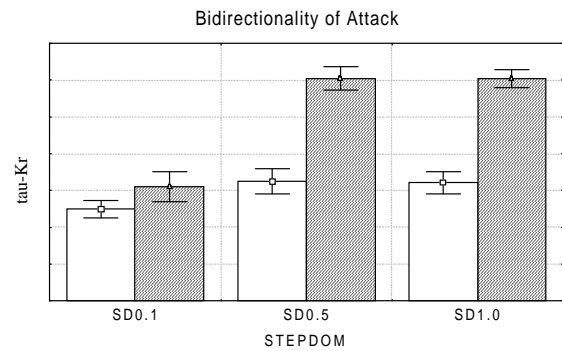


Figure 10. Bidirectionality of aggression for both systems of attack and increasing STEPDOM (mean τ_{Kr} plus/minus S. E.) Bidirectionality of attack is measured as a τ_{Kr} -correlation between an actor and receiver matrix (Hemelrijk 1990). White bars: Obligate attack system; Shaded bars: Rank-Distance decreased attack system.

4 Discussion

In line with Hogeweg's (1988) observations, this model clearly shows that a spatial structure with dominants in the center and subordinates located at increasingly larger distances from the core, may emerge as a side-effect from self-reinforcing dominance interactions and a tendency to aggregate. Moreover, such a structure arises in the absence of any positional preference of the entities.

This implies an alternative explanation to the commonly held view that centrality of dominants reflects their positional predisposition for a safer location in the group, which in turn is assumed to be optimized by natural selection. In the model, centrality of dominants arises because dominants have a larger chance to win from (and chase away), subordinates that are more distant in rank. Provided the level of aggression is sufficiently high, this process is strengthened when dominance hierarchies are less ambiguous (because of more outspoken rank-differentiation) and more stable. Although the process is weaker in the Rank-Distance Decreasing Attack System, the pattern is generally robust; the correlation between rank and encirclement was negative for every parameter setting. Robustness was further supported by results from an extended model, in which I made FleeingDistance and SearchAngle rank dependent. As a consequence, low-ranking entities flew further (FleeingDistance of 5 versus 1 units) and returned to the group slower when lost (searchAngle of 60 instead of 90 degrees) than high-ranking ones. The resulting social-spatial structure for both attack systems and increasing STEPDOM appeared similar to vary that reported here.

The model yielded a host of other emergent effects. For instance, under the Obligate attack system, higher ranking entities aggressed others more frequently than lower-ranking ones did. This came about as a consequence of spatial structure: dominants simply have more interaction opportunities because of their central location (which itself is a result of dominance interactions). Note that this

perspective is very different from the conventional one, which assumes that a rank-correlated rate of aggression is an internal characteristic of dominants. Another example is the decline of aggression due to rank-differentiation and the higher attack-rate towards rank-nearer entities. This is not only a feature of the Rank-Distance Decreasing attack system (in which it was explicitly implemented), it also originated as a self-organized feature in the Obligate attack system. In the latter, reduced aggression resulted from larger individual distances, which in turn was a consequence of dominance differentiation. Note that this feature of the Obligate attack system fulfills the original motivation for implementing the Rank-Distance Decreasing attack system, and makes them appear equally 'natural'. Furthermore, rank-near entities were more often attacked, because they were closer than rank-distant ones.

It is especially this abundance of emergent effects, that highlights the complex intertwining of behavioral variables. This complexity hampers predictability. What, for instance, will happen when entities belong to different STEPDOM classes (compare sex-age categories in primates, Bernstein and Ehardt 1985) ? Although we could expect entities of the same STEPDOM to cluster (because they react similarly to their social environment, cf. Hogeweg 1988) and within such clusters, dominants to occupy the center, it is very hard to foresee how clusters of different STEPDOM types will arrange themselves spatially relative to one another. Insight in these matters may shed light on an ongoing polemic about the spatial positioning of sex-age categories in primate groups (Altmann 1979; Rhine and Westland 1981) and is the topic of my current research. In such indecisive disputes, individual-oriented models are particularly useful, because the consequences of biologically plausible extensions can be studied directly in silica. In this context, artificial worlds may function as a kind of virtual laboratories that allow for 'social experiments' that are impossible in the real world (Epstein and Axtel 1996), but provide behavioral scientists with 'tools for thought'.

Acknowledgments

I am grateful to and Rolf Pfeifer and Bob Martin for continuous support. I like to thank René te Boekhorst for improving former versions of this paper. This work is supported by the Swiss National Science Foundation by a grant from the Marie Heim-Voegtlin Foundation.

References

- Altmann, S. A. 1979. Baboon progressions. Order or chaos ? A study of one-dimensional group geometry. *Animal Behaviour* 27: 46-80.
- Barnard, C. J., and Burk, T. E. 1979. Dominance hierarchies and the evolution of 'individual recognition'. *Journal of theoretical Biology* 81: 65-73.
- Bernstein, I. S., and Ehardt, C. L. 1985. Intragroup agonistic behavior in Rhesus monkeys (*Macaca mulatta*). *International journal of Primatology*, 6(3): 209-226.
- Bonabeau, E., Theraulaz, G., and Deneubourg, J.-L. 1996. Mathematical models of self-organizing hierarchies in animal societies. *Bulletin of mathematical biology* 58(4): 661-717.
- Bumann, D., Krause, J., and Rubenstein, D. 1997. Mortality risk of spatial positions in animal groups: the danger of being in the front. *Behaviour* 134: 1063-1076.
- Chase, I. D., Bartelomeo, C., and Dugatkin, L. A. 1994. Aggressive interactions and inter-contest interval: how long do winners keep winning ? *Animal Behaviour* 48: 393-400.
- Collins, D. A. 1984. Spatial pattern in a troop of yellow baboons (*Papio cynocephalus*). *Animal Behaviour* 32: 536-553.
- Copp, N. H. 1986. Dominance hierarchies in the crayfish *Procambarus clarkii* (Girard, 1852) and the question of learned individual recognition (Decapoda, Astacidea). *Crustaceana* 51(1): 9-24.
- Deneubourg, J. L., and Goss, S. 1989. Collective patterns and decision-making. *Ethology, ecology and evolution* 1: 295-311.
- Depew, D. J., Weber, B. H. 1995. Darwinism evolving. Systems dynamics and the genealogy of natural selection. The MIT Press.
- Ellis, L. (Ed.). 1994. Reproductive and interpersonal aspects of dominance and status. Westport: Greenwood publishing group.
- Epstein, J. M., Axtell, R. 1996. Growing artificial societies. Social science from bottom up. Cambridge: The MIT Press.
- Goss, S., and Deneubourg, J. L. 1988. Autocatalysis as a source of synchronised rhythmic activity in social insects. *Insectes Sociaux* 35(3): 310-315.
- Guhl, A. M. 1968. Social inertia and social stability in chickens. *Animal Behaviour* 16: 219-232.
- Hamilton, W. D. 1971. Geometry for the Selfish Herd. *Journal of theoretical Biology*, 31: 295-311.
- Hemelrijk, C. K. 1990. Models of, tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. *Animal Behaviour* 39: 1013-1029.
- Hemelrijk, C. K. 1996. Dominance interactions, spatial dynamics and emergent reciprocity in a virtual world. In P. Maes, M. J. Mataric, J-A Meyer, J Pollack, and S. W. Wilson (Eds.), *From Animals to Animats 4: Proceedings of the fourth international conference on simulation of adaptive behavior*, 545-552. Cambridge, MA: The MIT Press/Bradford Books.
- Hemelrijk, C. K. (1997). Cooperation without genes, games or cognition. In P. Husbands, I. Harvey (Eds), 4th European conference on artificial life, 511-520. Brighton, UK: MIT-Press.

- Hogeweg, P. 1988. MIRROR beyond MIRROR, Puddles of LIFE. Artificial life, SFI studies in the sciences of complexity. Redwood City, California, Addison-Wesley Publishing Company, 297-316.
- Hogeweg, P. and B. Hesper 1979. Heterarchical, selfstructuring simulation systems: concepts and applications in biology. Methodologies in systems modelling and simulation. Amsterdam, North-Holland Publ. Co., 221-231.
- Hogeweg, P. and B. Hesper 1983. The ontogeny of interaction structure in bumble bee colonies: a MIRROR model. Behavior al Ecology and Sociobiology 12: 271-283.
- Janson, C. H. 1990a. Ecological consequences of individual spatial choice in foraging groups of brown caopuchin monkeys, *Cebus apella*. Animal Behaviour 40: 922-934.
- Janson, C. H. 1990b. Social correlates of individual spatial choice in foraging groups of brown capucin monkeys, *Cebus apella*. Animal Behaviour 40: 910-921.
- Judson, O. P. 1994. The rise of the individual-based model in ecology. Trends in ecology and evolution 9: 9-14
- Krause, J. 1994. Differential fitness returns in relation to spatial position in groups. Biological Reviews 69: 187-206.
- Kummer, H. 1974. Rules of dyad and group formation among captive baboons (*Theropithecus gelada*). In Symposium 5th Congress Int'l. Primat. Soc., 129-160. S. Karger, Basel.
- Mardia, K. V. 1972. Statistics of directional data. London and New York: Academic Press.
- Parish, J. K. 1989. Re-examining the selfish herd: are central fish safer ? Animal Behaviour 38: 1048-1053.
- Pfeifer, R., and Verschure, P. 1995. The challenge of autonomous agents: Pitfalls and how to avoid them. In L. Steels and R. Brooks (Eds.), The artificial life route to artificial intelligence: building embodied, situated agents, 237-263. Hillsdale, New Jersey: Lawrence Erlbaum associates.
- Rayor, S. R., Uetz, G. W. 1990. Trade-offs in foraging success and predation risk with spatial position in colonial spiders. Behavioural Ecology and Sociobiology 27: 77-85.
- Rhine, R. J., and Westland, B. J. 1981. Adult male positioning in baboon progressions: order and chaos revisited. Folia Primatologica 35: 77-116.
- Thierry, B. 1985. Patterns of agonistic interactions in three species of macaque (*Macaca mulatta*, *M. fascicularis*, *M. tonkeana*). Aggressive Behavior 11: 223-233.
- Thierry, B. 1990. The state of equilibrium among agonistic behavior patterns in a group of Japanese macaques (*Macaca fuscata*). C. R. Acad. Sci. Paris 310(3): 35-40.
- van Honk, C., and Hogeweg, P. 1981. The ontogeny of the social structure in a captive *Bombus terrestris* colony. Behavior al Ecology and Sociobiology 9: 111-119.
- Villa, F. 1992. New computer architectures as tools for ecological thought. Trends in ecology and evolution 7: 179-183.