THE ROYAL
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An individual-orientated model of the emergence of despotic and egalitarian societies

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Single behavioural differences between egalitarian and despotic animal societies are often assumed to reflect specific adaptations. However, in the present paper, I will show in an individual-orientated model, how many behavioural traits of egalitarian and despotic virtual societies arise as emergent characteristics. The artificial entities live in a homogeneous world and only aggregate, and upon meeting one another may perform dominance interactions in which the effects of winning and losing are self-reinforcing. The behaviour of these entities is studied in a similar way to that of real animals. It will be shown that by varying the intensity of aggression only, one may switch from egalitarian to despotic virtual societies. Differences between the two types of society appear to correspond closely to those between despotic and egalitarian macaque species in the real world. In addition, artificial despotic societies show a clearer spatial centrality of dominants and, counter-intuitively, more rank overlap between the sexes than the egalitarian ones. Because of the correspondence with patterns in real animals, the model makes it worthwhile comparing despotic and egalitarian species for socio-spatial structure and rank overlap too. Furthermore, it presents us with parsimonious hypotheses which can be tested in real animals for patterns of aggression, spatial structure and the distribution of social positive and sexual behaviour.

Keywords: despotic–egalitarian; patterns of behaviour; macaques; winner–loser effect; self-structuring; dominance

1. INTRODUCTION

Dominance is considered to be of central importance in the social behaviour of many group-living animal species because of the benefits supposedly associated with high rank (such as priority of access to mates, food and safe spatial locations). In this respect, Vehrencamp (1983) distinguished between 'despotic' and 'egalitarian' species. In the former, benefits are strongly biased towards higher-ranking individuals, while in the latter they are more equally distributed.

These terms have subsequently been used for many animal species (such as insects, birds and primates). However, due to the difficulty of estimating costs and benefits, the gradient of the hierarchy was essential in distinguishing egalitarian from despotic species. Egalitarian and despotic species vary in many behavioural characteristics, sometimes summarized as 'dominance style' (de Waal & Luttrell 1989), but comparisons between both types of species have usually been done within the framework of optimization of single traits by natural selection. However, some argue that the extent to which single, specific characteristics of social behaviour are adaptive is difficult to assess (Rowell 1979; Hinde 1982; Bernstein 1987; Hemelrijk 1996*a*) and that functional explanations alone are often insufficient. Historical and contextual approaches should be incorporated as well (Gould & Lewontin 1979; McKenna 1979; Thierry 1985, 1990; Stewart & Cohen 1997). Correspondingly, Thierry (1985, 1990) maintained that, as social dispositions evolve together, differences between despotic and egalitarian macaque species are interconnected and are just a consequence of the higher intensity of aggression and the degree of nepotism of despotic macaques.

In the present paper, I will study an even more parsimonious version of Thierry's (1985, 1990) hypothesis, i.e. whether these differences may arise in the absence of nepotism. This will be done in a model that is context orientated through its high potential of self-structuring (Hemelrijk 1996*b*). Thinking in terms of self-structuring asks for a different way of thinking about complexity. By convention it is believed that a complex system can be understood by taking it apart and studying the pieces. This analytical procedure boils down to a static description of the system. Supporters of the self-structuring view, however, advocate the opposite route: by studying interactions on a lower level, the emergence of a macrostructure on a higher level is perceived and, therefore, better understood (Hogeweg 1988). According to this view, patterns of interactions at a group level arise from local interactions between individuals and their environment. By interacting, individuals change each other and, therein, their social environment. In turn, the developing social structure feeds back to the individuals and shapes their interactions, etc. Consequently, this approach attributes the complexity of social interaction patterns to interactions between entities rather than their internal complexity. This reflects a shift of focus from objects to relationships (Cohen & Stewart 1994), whereby relationships are often considered to be self-reinforcing. Since emergent patterns cannot be traced by head alone, computer models are used. These models incorporate

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simplified versions of limited aspects of animal behaviour only and, thereby, present us with a kind of caricature. The benefit of caricatures is that by exaggerating the patterns they become better visible. In contrast to the naturally incomplete descriptions of animal behaviour, the model's complete description allows us to establish which social patterns are emergent. If these emergent patterns happen to correspond to findings on real animals, parsimonious alternative hypotheses for existing explanations may be derived from the model. Such hypotheses are often counter-intuitive and innovative. For instance, in this way it was shown that reciprocation of support in fights may not be driven by optimization of costs and benefits of these altruistic acts *per se*, as is assumed in the theory of reciprocal altruism (Trivers 1971), but may also arise as a side-effect of dominance interactions and spatial positioning of individuals (Hemelrijk 1996*b*, 1997). Furthermore, additional patterns emerging in the model, that have not yet been studied in real animals, may stimulate empirical scientists to focus on new behavioural aspects. In the present paper, all these aspects will be illustrated with an individual-orientated model on grouping and dominance interactions. In short, by showing how the intensity of aggression affects the development of the hierarchy and how the unfolding hierarchy in turn feeds back on the spatial configuration of group members, it will become clear how despotic and egalitarian virtual societies arise and why they differ in many characteristics.

With regard to the occurrence of dominance interactions, the most popular of several proposed strategies (Hemelrijk 1998*a*) is that individuals should always strive for a higher rank (Pagel & Dawkins 1997), while taking risks into account. Whether one eventually acquires a high rank has conventionally been attributed to the (possibly inherited) quality of an individual (Ellis 1994). However, results from experiments on many animal species, ranging from insects to primates (e.g. Bonabeau *et al*. 1996), have demonstrated that the effects of winning and losing competitive interactions are self-reinforcing. This so-called winner–loser effect implies that winning or losing a fight increases the probability of winning or losing again.

Concerning the perception of rank, in most species the capacity to win is directly perceived from external cues, such as pheromones and body postures (e.g. Honk & Hogeweg 1981; Copp 1986). Rank perception depends on individual recognition of others in only a few animal species (e.g. Barnard & Burk 1979; Hemelrijk 1996*b*).

The winner–loser effect and direct rank perception are incorporated in the model presented here. This model is inspired by Hogeweg's (1988) model on dominance interactions and spatial structure. It consists of a world inhabited by virtual male and female entities that only differ in their fighting capabilities and are very simple. Initially, entities are completely identical. Entities move about, have a certain angle of vision and a grouping tendency and perform self-reinforcing dominance interactions when risks are low. The development of the hierarchy and intersexual dominance relationships, frequency of aggression and social or spatial structuring are analysed for two intensities of aggression. Although the model does not aim to represent specifics of any animal species in particular, a comparison with data on macaques will be made, because in these primates special attention has been paid to despotic and egalitarian behaviour.

2. METHODS

In this section, a description of the model and behavioural measures are presented.

(a) *The model*

The model is individual orientated 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' (toroid) with its interacting agents, its visualization and special entities 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 units × 200 units. Therefore, 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. The activities of agents are regulated by a timing regime as follows. Each entity draws a random waiting time from a uniform distribution. The entity with the shortest waiting time is activated first. The decay in waiting time is usually the same for each entity, but if a dominance interaction occurs within NearView of an agent, the waiting time of this agent is reduced even more, thus increasing the probability that it will be activated. Agents group and perform dominance interactions according to the sets of rules described below (figure 1).

(i) *Grouping rules*

Usually, two opposing forces affecting group structure are postulated. On the one hand, animals are attracted to one another because participation in a group provides safety. On the other hand, aggregation implies competition for resources and this drives individuals apart (e.g. van Schaik 1983). The forces leading to aggregation and spacing are realized in the model by the following set of rules (inspired by Hogeweg (1988)).

(i) If an agent sees another nearby within its 'personal space' (parameter PerSpace), it predicts whether it will win an interaction. If it predicts victory, it performs a dominance interaction with that entity. If it predicts defeat, it remains near without interacting. In case several agents are within the PerSpace, the nearest partner is chosen. The agent that wins the actual interaction moves towards its opponent, while the loser does a full turn and moves away.

(ii) If no entity is in its PerSpace, but an agent perceives others within a larger distance of NearView, it continues moving in its original direction.

(iii) If an agent detects it nearest neighbours outside NearView, but within its maximum range of vision (MaxView), it moves towards them.

(iv) If an agent does not perceive any other agent within MaxView, it searches for group members by turning over an angle (SearchAngle) of 90° at random to right or left.

(ii) *Dominance interactions*

Dominance interactions represent competitive interactions over resources that are not specified in this model, but are presumed to include food, mates and spatial location.

Interactions between agents are modelled after Hogeweg & Hesper (1983) and Hemelrijk (1998*a*), as follows.

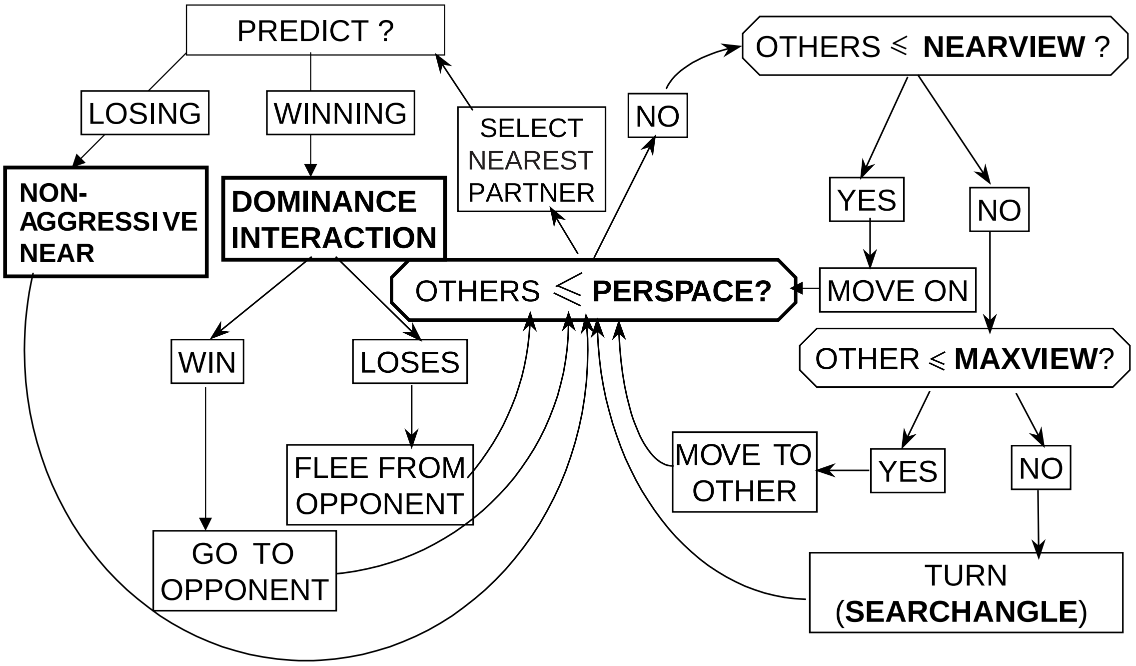

Figure 1. Flow chart for the behavioural rules of the entities.

(i) Each entity has a variable dominance value (hereafter known as Dom) which represents the capacity to win a hierarchical interaction.

(ii) After meeting one another in their PerSpace, entities 'decide' whether or not to attack following the Risk-Sensitive system (Hemelrijk 1998*a*). Here, the probability of attacking depends on the potential risk of defeat as follows. Upon meeting another and observing its Dom value, an entity may predict it will win or lose on the basis of a 'mental' battle, which follows the rules of a dominance interaction as described above. If 'ego' loses the mental interaction, it will refrain from any action (thus displaying 'non-aggressive' proximity). If it wins the mental battle, it will start a 'real' dominance interaction.

(iii) If an actual dominance interaction takes place, then entities display and observe each other's Dom. Subsequent winning and losing is determined, as follows, by chance and values of Dom

$$w_i = \left[\begin{array}{ll} 1 & \dfrac{\mathrm{DOM}_i}{\mathrm{DOM}_i + \mathrm{DOM}_j} > \mathrm{RND}(0,1). \\ 0 & \qquad\text{else} \end{array}\right. \tag{1}$$

Here, w_i is the outcome of a dominance interaction initiated by agent i (1 = winning and 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, otherwise it loses. Thus, the probability of winning is larger for the one who is higher in rank and this is proportional to the relative Dom value with its partner.

(iv) Updating of the dominance values is done by increasing the dominance value of the winner and decreasing that of the loser,

$$\begin{aligned} \mathrm{Dom}_i &:= \mathrm{Dom}_i + \left(w_i - \frac{\mathrm{Dom}_i}{\mathrm{Dom}_i + \mathrm{Dom}_j}\right) \times \mathrm{StepDom}, \\ \mathrm{Dom}_j &:= \mathrm{Dom}_j - \left(w_i - \frac{\mathrm{Dom}_i}{\mathrm{Dom}_i + \mathrm{Dom}_j}\right) \times \mathrm{StepDom}. \end{aligned} \tag{2}$$

The consequence of this system is that it behaves as a damped positive feedback: victory of the higher-ranking agent reinforces their relative Dom value only slightly, whereas success by the lower-ranking agent 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 that varies between zero and one and represents the intensity of aggression. In line with the larger rank differences in despotic rather than egalitarian societies, high values imply a large change in Dom value when updating the system and, thus, indicate that single interactions may strongly influence the future outcome of conflicts. Conversely, low StepDom values represent low impact.

(v) Winning includes chasing the opponent one unit distance and then randomly turning 45° 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.

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

(b) *Experimental set-up and data collection*

Here, the same parameter setting ($n = 8$, PerSpace = 2, NearView = 24, SearchAngle = 90° and FleeingDistance = 2 units) is used as in a former study of the Risk-Sensitive system (Hemelrijk 1999). I implement two types of entities (VirtualMales and VirtualFemales; for values of parameters and initial values see table 1). I study their behaviour for two VirtualSpecies that differ in their intensity of aggression (Mild and Fierce). In line with findings in the primate studies of Thierry (1985, 1990), variation in the intensity of aggression between VirtualSpecies is set higher than within VirtualSpecies (between the sexes) and attack by VirtualMales is more intense than by VirtualFemales (as described for primates by Bernstein & Ehardt (1985)). Moreover, to reflect the physiologically superior fighting abilities of males (e.g. muscle structure) compared to females,

Table 1. *Parameter and initial values*

	VirtualFemale	VirtualMale
StepDom of		
Fierce species	0.8	1.0
Mild species	0.1	0.2
InitDom	8.0	16.0

VirtualMales start with a higher winning tendency than VirtualFemales. Furthermore, I compare groups of both VirtualSpecies at an equal sex ratio. For each VirtualSpecies, ten runs were conducted.

During a run, every change in spatial position and heading direction of each entity was recorded. After every time-step (consisting of 160 activations), the distance between agents was calculated. Dominance interactions were continuously monitored by recording (i) the identity of the attacker and its opponent, (ii) the winner and loser and (iii) the updated Dom values of the entities.

(c) *Measurements*

At successive intervals of two time-steps (320 activations), the degree of rank differentiation and the overlap between the dominance hierarchies of VirtualMales and VirtualFemales are measured as follows.

Rank differentiation is measured by the coefficient of variation (standard deviation divided by the mean) of the Dom values (Sokal & Rohlf 1981). For each run the average value is calculated. Higher values indicate larger rank distances among entities.

At the start of each run, all VirtualMales are dominant over each VirtualFemale, but during run time some VirtualFemales may become dominant over (some or all) VirtualMales. The degree of dominance of VirtualFemales over VirtualMales is estimated by the Mann–Whitney *U* statistic (Siegel & Castellan 1988). At the beginning of the run *U* values are zero. Later on they may become positive.

The degree by which dominants occupy the centre is measured by means of the Kendall rank correlation between the dominance value and the average distance of 'ego' to others. Thus, stronger centrality of higher-ranking entities is reflected in a larger negative correlation between rank and average distance to others.

Unidirectionality of attack is calculated as a τ_{Kr} correlation between an actor and receiver matrix of attack (Hemelrijk 1990*a*,*b*). This statistic measures the correlation between the corresponding rows of two social interaction matrices. The method of calculating the probability of the observed value reckons with the statistical dependency due to recurrent observations of the same individual (Hubert 1987). A stronger negative τ_{Kr} value corresponds to a higher degree of unidirectionality of attack.

To exclude a possible bias brought about by transient values, the correlations for centrality of dominants, unidirectionality and between social behaviour and rank of the partner are calculated on data collected after time-step 200.

3. RESULTS

The coefficient of variation of Dom values among all group members, irrespective of gender, is larger in Fierce than in Mild species (table 2) and reflects a more differentiated hierarchy by its larger range of Dom values (figure 2). To explain this result, note that the higher the value of StepDom, the stronger a single event of winning (or losing) changes the former Dom values of both partners. Because the range of Dom values is larger in Fierce species, the average Dom value of the most subordinate Fierce VirtualMale is lower than that of the most subordinate mildly attacking VirtualMale (see table 2). Furthermore, counter-intuitively, ranks also overlap more between the sexes in Fierce than Mild species (figure 2), so that Fierce VirtualMales are dominant over fewer VirtualFemales when compared with Mild VirtualMales.

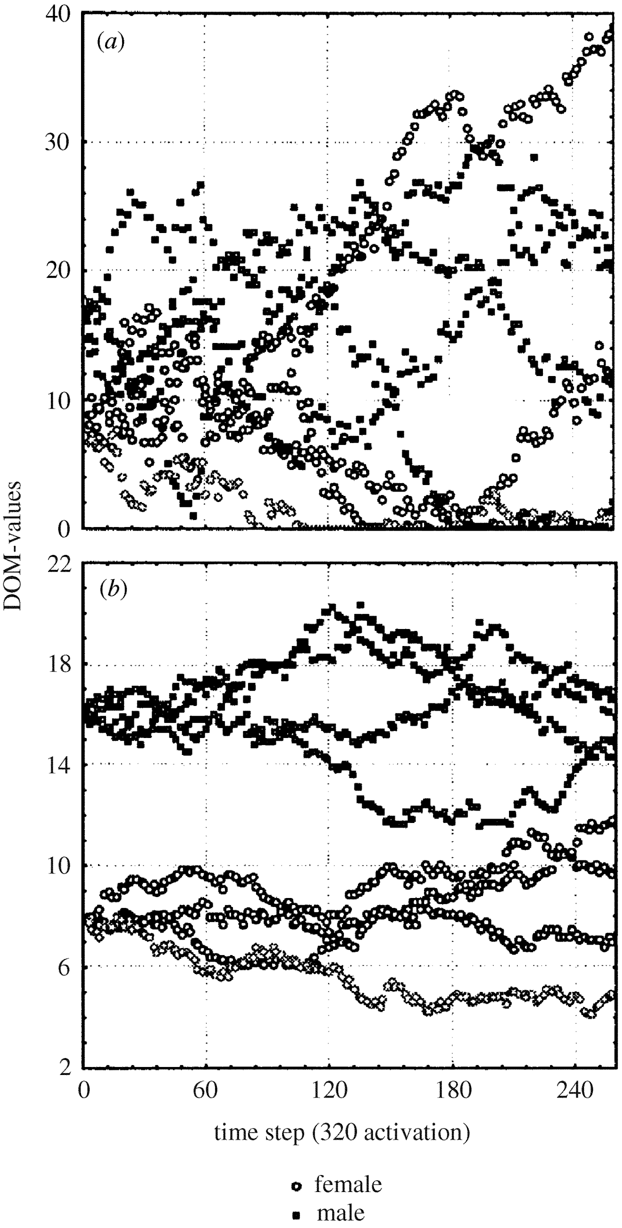

Figure 2. Differentiation of Dom values for fierce and mild entities. Typical case of rank differentiation as observed in one run of (*a*) Fierce and (*b*) Mild VirtualSpecies.

As will be shown below, the degree of rank diversification functions as a central characteristic in social behaviour.

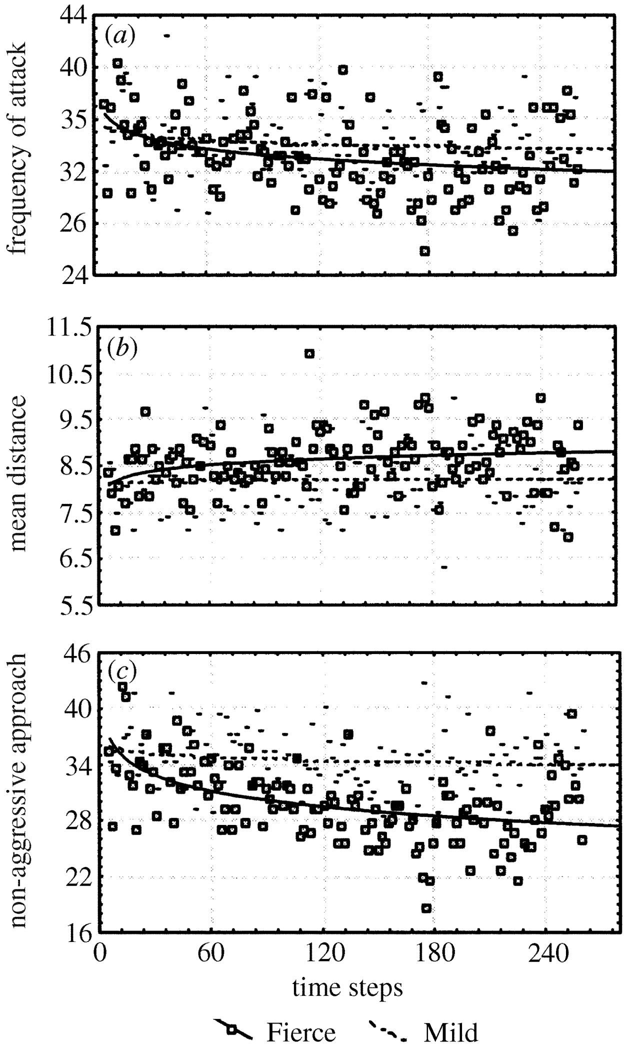

Figure 3. Development over time of (*a*) frequency of attacks, (*b*) mean distance and (*c*) non-aggressive interactions among entities of Fierce and Mild VirtualSpecies (logarithmic line fitting).

First, rank distances influence the diversity of behaviour displayed towards various interaction partners. Fierce entities attack partners of a higher rank less often (and, thus, more often non-aggressively approach higher-ranking partners), whereas such correlations are absent in Mild entities (table 2). This comes about as follows. The larger the rank distance between entities, the stronger the risk of defeat varies with the rank of the partner. Correspondingly, Fierce entities show more rank-correlated behaviour than Mild species. In addition, due to the larger asymmetry in the probabilities of winning and losing between two interaction partners, Fierce entities attack others more unidirectionally, whereas Mild entities attack each other more symmetrically.

Second, rank diversification is affected by and affects social interaction patterns via spatial structure. In Fierce, but rarely in Mild species, the increasing degree of rank diversification at the beginning of a run is accompanied by a drop in the frequency of interactions (aggressive and non-aggressive approach), due to an increase in the average distance between entities (figure 3). The increased average distance is a consequence of the increasing differentiation of ranks, which implies an enlarged diversity of winner and loser roles in Fierce species. Thus, some entities become 'habitual' losers. They are defeated again and again and, therefore, they move further and further away from others. This results in a slightly, but significantly higher, average distance and lower frequency of interaction (aggressive and non-aggressive approach) in Fierce species in general (table 2).

Furthermore, centrality of dominants, as measured by the correlation between rank and average distance to group members, is stronger in Fierce than in Mild species (table 2). This comes about as follows. Due to the larger rank distances among Fierce entities, there are fewer entities of similar rank. Only entities of similar rank have an approximately equal chance of 'getting the better of' and chasing away one another and, hence, remaining at the same location. The larger the rank distance within a pair of entities, the more asymmetrical their behaviour will be and the more frequently the dominant will chase away the subordinate. Consequently, throughout the course of time the physical distance between dominants and subordinates will reflect their rank distance. Because of the low differentiation of ranks in Mild species, the socio-spatial structure is necessarily vague too.

Spatial structure in turn affects participation in aggression: when dominants occupy the centre, they meet other group members more often than lower-ranking entities do at the periphery of the group. Consequently, the higher the rank of Fierce entities, the higher their frequency of attack. Due to their less distinct spatial structure, Mild entities of different ranks display approximately equal frequencies of attack (table 2).

The details of the parameter and initial values were chosen arbitrarily, but the results appeared robust. Similar results are obtained for doubled personal space and one type of entity only, and for half the intensity of aggression (Hemelrijk 1998*a*), for different fleeing distances (Hemelrijk 1998*b*), another initial dominance value of VirtualFemales of 14 (Hemelrijk 1999), for various differences in the intensity of aggression between both sexes and a female-biased sex ratio (six VirtualFemales and two VirtualMales). Note, however, that the effects of immigration and emigration will be studied in a future model, because they may be different from those of a skewed sex ratio as studied here. Group size was not varied, but this will also be reported in a future paper.

4. DISCUSSION

In the model proposed here, the differences in social behaviour between despotic and egalitarian societies are the consequence of changing one parameter only, representing the intensity of aggression. A higher intensity of aggression enlarges the degree of variation in dominance values, resulting in a steeper hierarchy. A steeper gradient of the hierarchy in turn leads to many emergent phenomena, affecting aspects such as cohesiveness, frequency of interaction, initial decline of aggression, rank relatedness of interaction, rank overlap between the genders and spatial centrality of dominants. This is a consequence of the feedback between the degree of differentiation of the hierarchy and the spatial position of the entities.

Table 2. *Differences between Fierce and Mild entities in the model and between despotic and egalitarian macaques as described by Caldecott (1986), de Waal & Luttrell (1989), de Waal (1991) and Thierry (1990)*

variable	Fierce versus Mild VirtualSpecies	Mann–Whitney *U*-test: U^a	despotic versus egalitarian macaque species[b]
coefficient of variation of Dom values	higher	0.0***	higher
rank overlap between genders	more	10.0**	—[c]
rank of lowest male	lower	10.0**	—
correlation between rank of partner and attack frequency	stronger	22.0*	—[d]
correlation between rank of partner and non-aggressive approach	stronger	0.0***	stronger
symmetry of attack	less	6.0***	less
initial decrease in attack	clearer	figure 2	—
initial decrease in non-aggressive approach	clearer	figure 3	—
cohesiveness	less	8.0**	less
frequency of attack	lower	14.0**	lower
frequency of non-aggressive approach	lower	0.0***	lower
spatial centrality of dominants	clearer	9.5**	—
correlation between rank and aggression	stronger	0.5***	—

[a] $n_1 = n_2 = 10$. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

[b] Despotic macaque species are typically represented by *Macaca mulatta*, *Macaca fuscata* and *Macaca fascicularis* and egalitarian macaque species by *Macaca tonkeana*, *Macaca arctoides* and *Macaca sylvanus*.

[c] Comparative data for both classes of macaques are lacking.

[d] In line with the model, significant correlations between rank and frequency of aggression in the literature were found only for despotic (e.g. *M. fascularis*; Kaplan *et al*. 1982; Shively & Kaplan 1984), but not for egalitarian macaque species.

These emergent phenomena provide us with counter-intuitive, parsimonious hypotheses for animal behaviour. First, entities start to space out gradually when their rank distances become larger due to increasing differentiation in winners and losers. By consequently encountering others less and less often, their frequency of interaction drops. This emergent phenomenon can be used as a parsimonious alternative to the functionalistic view that individuals have an internal mechanism to decrease dominance interactions once relationships are clearly established (e.g. Pagel & Dawkins 1997). It can be verified in 'real' animals by tracing interindividual distances and the frequency of interactions (both aggressive and non-aggressive) after putting new individuals together.

Second, to consider spatial structure as a side-effect of grouping and dominance interactions forms a parsimonious alternative to the conventional view on spatial location (Hemelrijk 1998*b*), such as expressed in the 'selfish herd' theory by Hamilton (1971). In this theory, the centre of the group is assumed to be the safest location for protection against predators. Therefore, individuals are supposed to have evolved to prefer this location and to compete for being in the spatial centre of a group. This model is more parsimonious, since any preference for a certain spatial location within a group is absent.

Third, spatial centrality of dominants may, of course, influence the distribution of social positive behaviour as found in mammalian species. Assume that individuals distribute their social positive behaviour in proportion to encounter frequency with partners. Then, in groups with spatial centrality of dominants they will establish mostly affiliative bonds with individuals of similar rank (Hemelrijk 1996*a*). This bears upon current functional theories on social positive behaviour in primates. Observing preferential grooming among female monkeys of similar rank, Seyfarth (1977) assumed that females were competing to groom higher-ranking partners to receive something valuable in return and, consequently, will end up grooming partners that are of near rank. Furthermore, de Waal (1991) attributed this pattern to the larger range of benefits that can be exchanged between parties that resemble each other. Note that the model serves again as a parsimonious alternative by making superfluous assumptions about exchanges for future social benefits. Another model-based inference is that social positive behaviour should be distributed according to rank-near partners in despotic species in a more outspoken way than in egalitarian ones.

(a) *Macaque social behaviour*

The outcome of the model corresponds remarkably well with the findings on real macaques (table 2), but cannot yet be brought to bear upon other despotic and egalitarian animal species, because of a lack of empirical data.

As displayed in table 2, Fierce entities show larger rank distances, less cohesiveness, lower interaction frequency, less symmetry of attack and more rank-correlated behaviour. This is in line with findings on despotic versus egalitarian macaques by Thierry (1990) and de Waal & Luttrell (1989). Furthermore, the model delivers patterns that have not yet been studied systematically in the two types of macaques, but for which incidental support is available.

For instance, first, spatial centrality of dominants is reported only for despotic macaque species, notably Japanese macaques (Itani 1954; Imanishi 1960; Yamada 1966), but never for egalitarian ones. Furthermore, from qualitative observations, the spatial structure seems clearer in rhesus than Tonkean macaques (B. Thierry, personal communication).

Second, in many primate species the lower-ranking males in particular tend to wander into other groups. Because the mean rank of the lowest VirtualMale of Fierce entities is lower than that of Mild entities, it may be inferred from the model that despotic males suffer more from within-group competition and, therefore, migration occurs more than in egalitarian species. More migration in despotic (i.e. 'group 1') species is exactly what Caldecott (1986) showed in his review.

Third, differences in rank overlap between adults of both classes of species are supported by Thierry's (1990) report that it takes adolescent males much longer to outrank adult females in despotic than egalitarian macaques. Thierry (1990) hypothesized that this is due to the higher frequency of nepotistic support received by despotic rather than egalitarian females. However, female support (recorded when an entity accidentally attacked another that was just involved in a fight with a third) is approximately as frequent in the two VirtualSpecies. Thus, the model-based view is again more parsimonious by leaving out assumptions on the degree of nepotism.

Furthermore, the unexpected stronger rank overlap between both sexes in despotic societies may have several implications for current views on primate sexual behaviour. For males, subordinance to females implies that they not only suffer from competition by males but also females (for instance, for food). Furthermore, males may be inhibited to mate with females to whom they are subordinate (Sade 1968; Rosenblum & Nadler 1971; Abernethy 1974). For instance, Rosenblum & Nadler (1971) observed that, whereas males that were dominant over females reached ejaculation after a single mount, subordinate males needed multiple mounts before ejaculation. These authors suggested that the degree of intersexual dominance may also explain species differences in male mounting behaviour. The combination of Rosenblum & Nadler's (1971) hypothesis and the model-based finding that Fierce males dominate females less than Mild males, would therefore result in the prediction that multiple mounting is typical of despotic males and single mounting of egalitarian males. In his comparative study of sexual mounting behaviour of egalitarian and despotic macaques, Caldecott (1986) described exactly this. It follows that even some specifics of male mounting behaviour may emerge as a side-effect of intensity of aggression.

Regarding females, Caldecott (1986) described despotic female macaques as having evolved stronger female choice than egalitarian ones. However, if female dominance inhibits male copulatory behaviour, it reduces the number of sexual partners available to females. Furthermore, partner choice of despotic females may be limited anyhow, since they may opt to mate with élite males simply to avoid conflicts with other males, because by mating with higher-ranking males they are less likely to be interfered with by others. In contrast, in egalitarian species aggression is redirected among all group members more equally (but causes fewer injuries; Thierry 1985). Furthermore, even if egalitarian females were choosy, their supposed complete subordinance to males (as the model predicts) may make it impossible for them to refuse mating (Smuts & Smuts 1993). The model thus provides the following parsimonious alternatives. What is called 'strong female choice' may simply reflect limited partner choice due to a high degree of female dominance over males and rank relatedness of aggression. In addition, female promiscuity may partly be due to an inability to refuse mating as a consequence of subordinance to males.

Fourth, because of these remarkable agreements, our model provides us with an explanation in which differences in social behaviour between despotic and egalitarian macaque species may stem from a genetic difference only in the intensity of aggression. The evolutionary history of this supposedly inherent difference may be related to the degree of hardship imposed by the environment, but this is not the topic of this paper.

(b) *General implications*

In conclusion, in this paper a simple model is shown to generate an astonishing amount of emergent effects. Even without including details on the distribution of food, and the degree of nepotistic behaviour (which are central variables in many socio-ecological theories) or physiological processes underlying the motivational dynamics, the behavioural patterns of the modelled entities resemble those of real animals, for instance primates in the real world. Thus, although the entities are clearly very different from real animals, the model apparently captures essential invariant characteristics of their dominance interactions and spatial structuring. Because of its simplicity, the model furnishes new insight into social or spatial patterning and the dynamics of intersexual dominance relations. This insight is subsequently used as a background from which to generate new, parsimonious, contextual hypotheses for real animals, most of which could not have been generated by thought alone.

Thus, the model contributes to the study of social behaviour in at least three ways. First, because several patterns emerge together, it provides us with an explanation for the interconnection between social variables, coined as 'dominance styles' by de Waal and Luttrell (1989), which characterize despotic and egalitarian systems. Such integration is new and is an inherent characteristic of this type of model. Second, certain emergent patterns generated by the model have not yet been studied in real animals. The model indicates that it is worthwhile looking for these patterns in real animals. Third, observing these side-effects provides us with new, parsimonious hypotheses for patterns of social interaction in real animals.

By revealing an abundance of emergent social effects, this model underscores the value of studying traits of animals within the context of other behavioural variables and of spatial configuration. By merely changing a single variable (representing the intensity of aggression) 13 behavioural differences result. This shows us the unnecessary complications we may run into if we look for separate, adaptive explanations for isolated traits and attribute them directly as (genetic or cognitive) qualities of individuals. It also makes it likely that natural selection will often operate, not on single traits, but on self-organized patterns (Boerlijst & Hogeweg 1991).

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