DESPOTIC SOCIETIES, SEXUAL ATTRACTION AND THE EMERGENCE OF MALE ‘TOLERANCE’: AN AGENT-BASED MODEL

by

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Summary

During the period when females are sexually attractive — but only then — males of certain species of primates, such as chimpanzees, allow females access to resources. Because males are usually dominant over females, such male ‘tolerance’ is explained as a special, reproductive strategy to gain access to females. In this paper a simpler hypothesis is proposed on the basis of an individual-based model (called DomWorld): male ‘tolerance’ towards females arises in ‘despotic’ artificial societies as a kind of ‘respectful timidity’, because sexual attraction automatically increases female dominance over males as a side-effect. The model consists in a homogeneous, virtual world with agents that group and perform dominance-interactions in which the effects of victory and defeat are self-reinforcing. The artificial sexes differ in that VirtualMales have a higher intensity of aggression, they start with a greater capacity to win conflicts than VirtualFemales and they are especially attracted to the opposite sex during certain periods, whereas VirtualFemales are not. I shall explain how the introduction into DomWorld of the attraction of VirtualMales by VirtualFemales leads to female dominance, why it does so only in despotic, but not in egalitarian societies, and how it leads to other phenomena that are relevant to the study of primate behaviour.

Keywords: sexual attraction, sexual exchange, male ‘tolerance’, female dominance, egalitarian and despotic society, paternity.

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Introduction

In animal species, males usually are more attracted to females than *vice versa* (Trivers, 1972). This sexual asymmetry is understandable, since males can fertilise many females, whereas females get fertilised only once per reproductive period. Also in primates, males are the ones who actively maintain proximity to females when females are in their sexually attractive (tumescent) period (*e.g.* see Hill, 1987). They are supposed to follow a special reproductive strategy to obtain access to females. For instance, chimpanzee males allow females priority of access to food during the female's sexually attractive period of tumescence (Yerkes, 1939, 1940). This is regarded as an adaptive exchange of favours, namely priority of access to food for females in exchange for copulation and offspring for males (Goodall, 1986; de Waal, 1989; Stanford, 1996). Yet, such an exchange for food is neither confirmed by our study of mating behaviour (Hemelrijk *et al.*, 1992), nor by that of fatherhood (as determined by DNA-typing methods, see Hemelrijk *et al.*, 1999; Meier *et al.*, 2000). Therefore, though male chimpanzees may be more tolerant towards any female when she is tumescent than otherwise, this behaviour does not produce a clear advantage in terms of mating and begetting offspring with her. Although the interpretation of these results is under discussion (see Hemelrijk *et al.*, 2001; Stopka *et al.*, 2001), it is of importance to offer other, simpler explanations for the way sexual attraction may influence social relationship: this is the aim of the present paper.

Using a process-oriented model, I will show that what looks like male 'tolerance' may also arise in the absence of any benefits accrued to 'tolerant' male behaviour and in the absence of any rules for exchange at the level of the individual. I will show this with the help of a model that merely consists of a number of key elements of grouping animals (it is a homogeneous world in which individuals are grouping and competing for unspecified resources). Such male 'tolerance' arises as a side-effect, because attraction to VirtualFemales produces an increase of female dominance over males as a consequence of the increased frequency of interactions between the sexes. However, this male 'tolerance' emerges only in despotic, but not in egalitarian societies. Such a model can be seen as a kind of null-model. It is important to develop such null-models because they demonstrate what patterns of behaviour result from the mutual interdependence of individuals in a group in spite of the fact that they are not coded as behavioural rules in the individual; this kind of hypotheses is difficult to generate without such models by pure reasoning.

For instance, in an earlier study (Hemelrijk, 1999b), I have described a model, called DomWorld that deals with dominance and grouping only. When in this model the value of only one variable is increased (in casu intensity of aggression) a cascade of effects follows. Higher intensity of aggression accelerates the development of the hierarchy. Consequently, individuals develop that are constant losers. They flee from everyone else and therefore, the group loosens (which in its turn reduces the frequency of aggression); as a consequence, a spatial structure develops with dominants in the centre and subordinates at the periphery; all individuals being close to those that are similar in dominance. This spatial structure in turn strengthens the hierarchy, because individuals, when mainly interacting with those that are close by, interact mostly with agents of similar dominance. Thus, if a dominance reversal takes place, it is only a minor one because the opponents were similar in dominance from the start. Therefore, the spatial structure stabilises the hierarchy and helps it to develop. In summary, at a high intensity of aggression, the gradient of the hierarchy is steeper, groups are looser, aggression is less frequent, spatial centrality is greater, etcetera. The results are biologically interesting, because they resemble in many aspects the differences between the societies of egalitarian species and of despotic ones of real animals, especially of the genus of macaques (Caldecott, 1986; de Waal & Luttrell, 1989; Thierry, 1990a, 1990b; de Waal, 1991b; Hemelrijk, 1999b).

Remarkably, in DomWorld there are several variables that unexpectedly influence female dominance over males. For instance, at a high intensity of aggression female dominance is increased compared to that at a low intensity (Hemelrijk, 1999b). This is a consequence of the stronger hierarchical development at a high intensity, which causes some females to become very high in dominance, and some males very low. Therefore, some females become dominant over some males. Similarly, in more cohesive groups the hierarchy is steeper and therefore female dominance is higher than in loose groups (Hemelrijk, 1999a). This is due to the 'spatial-social structuring' as described above and also to the higher frequency of interactions in groups that are more compact. Effects of intensity of aggression and cohesion on female dominance are both relevant to primates. As regards intensity of aggression, this resembles Thierry's impressions of differences between despotic and egalitarian societies of macaques: in despotic societies female dominance seems greater (Thierry, 1990a). As regards cohesion, this bears similarity to the greater female dominance in bonobo's than in common chimpanzees (despite their similar sexual dimorphism, see Stanford, 1998): groups of bonobo's are living in groups that are much more compact than those of common chimpanzees (fission-fusion).

In the present paper we investigate whether female dominance is also promoted by male attraction to females and whether this leads to what appears as male 'tolerance'. To study this, I vary behavioural rules (by adding and deleting sexual attraction) in DomWorld for both high and low intensity of aggression. The results can be used as testable hypotheses for real primates.

Methods

This section contains a description of the model and behavioural measures used.

The model

The model is individual-oriented and event-driven (see Judson, 1994). I have written it in object-Pascal, Borland Pascal 7.0 and it contains three basic elements: a 'world' with its interacting agents, its visualisation and its special observers that collect and analyse data of what happens in the 'world' (*cf.* the 'recorders' and 'reporters' of Hogeweg & Hesper, 1985). The 'world' is wrapped around on all sides (in the form of a three-dimensional doughnut) to avoid border effects. It consists of a space of 200 by 200 units. At the start of each run agents occupy random locations within a predefined subspace of 30 by 30 units. The space of the world is made continuous, in the sense that agents are able to move in all directions. This continuous world is used because it represents spatial patterns more precisely than a grid world, which I applied formerly (Hemelrijk, 2000a). Agents have an angle of vision of 120 degrees 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 entity receives a random waiting time from a uniform distribution. Here, I combine a random regime with a biologically plausible timing regime that is locally controlled by other artificial individuals (see also Goss & Deneubourg, 1988) in the sense that the waiting time of an agent is shortened when a dominance interaction occurs close by 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 will be activated. This agrees with observations of real animals, where dominance interactions are likely to activate individuals nearby (compare social facilitation, see Galef, 1988). Agents group and perform dominance interactions according to a set of rules described below (Fig. 1).

Grouping rules

Usually, two opposing tendencies affecting group-structure are supposed to exist: on the one hand animals are believed to be attracted to one another because living in a group provides safety; on the other, grouping implies competition for resources, and this drives individuals apart (*e.g.* van Schaik, 1983).

The tendency of individuals to aggregate and space out are represented in the model by a set of rules that are graphically displayed in Fig. 1 (see Hemelrijk, 1999b).

1. If an agent observes another within a critical distance, its ‘personal space’ (= PerSpace), it may perform a dominance interaction. If several agents are within PerSpace, the nearest interaction partner is chosen. If the agent wins the interaction, it moves one unit towards its opponent, otherwise it makes a 180° turn and flees away two units under a small random angle.
2. If nobody is observed in PerSpace, but an agent notices others at a greater distance, still within NearView (see experimental set-up and data-collection), then — in runs without ‘sexual attraction’ — it continues moving one unit in its original direction. In case of ‘attraction’, however, VirtualMales approach a VirtualFemale one unit when they observe her in nearView (see ‘attraction’ in Table 1).
3. If its nearest neighbours are outside NearView, but within its maximum range of vision (= MaxView, see experimental set-up and data-collection), the agent moves one unit towards them.

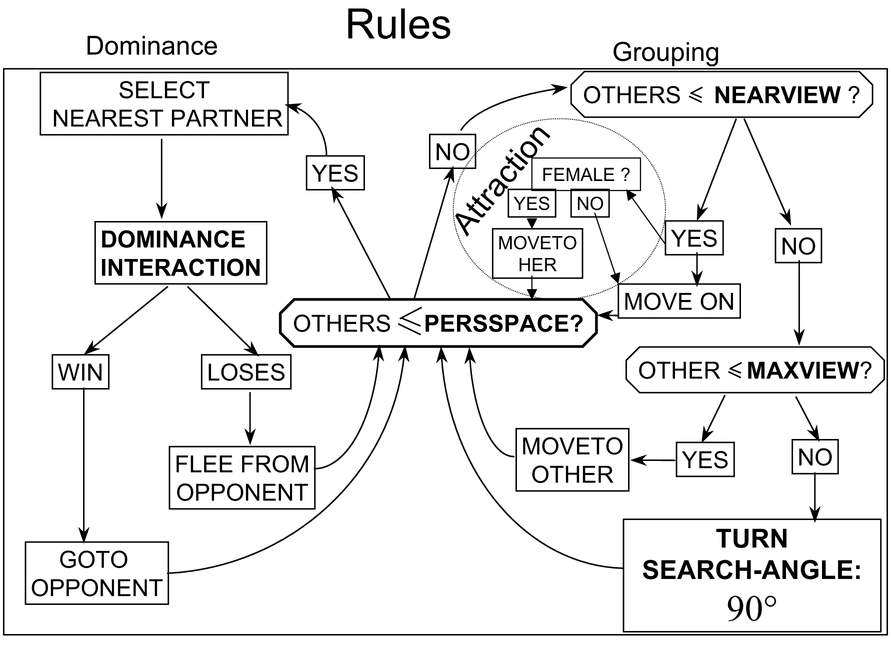

Fig. 1. Flow chart for the behavioural rules of agents. Encircled part (labelled ‘Attraction’) is the behavioural rule for attraction to females. This rule is only operative in male agents during sexual attraction.

4. If an agent does not perceive other agents within MaxView, it looks around for them by turning a Search angle of 90° at random to the right or left.

Dominance interactions

Dominance interactions in real animals consist of competitive interactions about resources (such as food, mates and spatial location), but sometimes they are considered to be part of a kind of long-term ‘power’ struggle. In the model, these two types of dominance interactions are not distinguished and resources are unspecified. Dominance interactions may be initiated when agents encounter each other nearby, but, in case of so-called risk sensitive behaviour (as used here), they happen only if the perceived risk of defeat is low (Hemelrijk, 2000b). Dominance interactions take place among initially completely identical entities and the effects of defeat and victory in competitive interactions are self-reinforcing, which implies that after winning (or losing) the chance to win (or lose) again increases (as has been empirically demonstrated in many animal species, for references see Bonabeau *et al.*, 1996; Hemelrijk, 2000b). As I have shown in former models, this suffices for a dominance hierarchy to develop.

Interactions between agents are modelled after Hogeweg (1988) and Hemelrijk (1999b), as follows:

Each agent has a variable that is called ‘Dom’ (= dominance, representing the capacity to win an interaction). After meeting one another in their PerSpace, agents ‘decide’ whether or not to attack according to the Risk-Sensitive system. Here, the probability to attack decreases according to the risk of suffering defeat, as follows. Upon meeting another agent and observing its Dom-value, an agent may foresee it will win or lose on the basis of a ‘mental’ battle, which follows the rules of a dominance interaction as described below. If ego loses the mental interaction, it will refrain from action (thus displaying ‘non-aggressive’ proximity). If it wins the mental battle, it will start an ‘actual’ dominance interaction.

If an actual dominance interaction takes place, then agents display and observe each other’s Dom. Subsequent winning and losing is determined by chance and by values of Dom as follows:

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

Here $\mathrm{w_i}$ 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 greater than a random number (drawn from a uniform distribution), then agent i wins, else it loses. Thus, the probability of winning is greater for whoever is higher in rank, and this is proportional to the Dom-value relative to that of its partner.

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

$$\mathrm{DOM_i} = \mathrm{DOM_i} + \left(\mathrm{w_i} - \frac{\mathrm{DOM_i}}{\mathrm{DOM_i} + \mathrm{DOM_j}}\right) * \mathrm{STEPDOM} \tag{2}$$

$$\mathrm{DOM_j} = \mathrm{DOM_j} - \left(\mathrm{w_i} - \frac{\mathrm{DOM_i}}{\mathrm{DOM_i} + \mathrm{DOM_j}}\right) * \mathrm{STEPDOM}$$

The consequence of this system is that it functions as a ‘damped’ positive feedback: a victory of the higher ranking agent reinforces its relative Dom-value only slightly, whereas success of the lower ranking agent causes a relatively great change in Dom. The impact thus reflects the degree to which the result is unexpected. (To keep Dom-values positive, their minimum value is, arbitrarily, put at 0.01.) The change in Dom-values is multiplied by a scaling or stepping factor, so-called StepDom, which varies between 0 and 1 and represents intensity of aggression. High values imply a great change in Dom-value when updating it, and thus indicate that single interactions may strongly influence the future outcome of conflicts. Conversely, low StepDom-values represent low impact (see experimental set-up and data-collection).

Winning includes chasing the opponent over one unit distance and then turning randomly 45 degrees to right or left in order to reduce the chance of repeated interactions between the same opponents. The loser responds by fleeing under a small random angle over a predefined FleeingDistance. In what follows, the initiation of a dominance interaction is for short referred to as ‘attack’.

The sexes and sexual attraction

In the model, the artificial ‘sexes’ differ in their competitive ability and whether or not they are attracted to the opposite sex. In line with descriptions of primates (Bernstein & Ehardt, 1985), aggression of artificial males is designed in the model to be more intense than of artificial females (implying more frequent biting as against slaps and threats, as indicated by the scaling factor of 1.0 and 0.8 for VirtualMales and Virtualfemales, respectively). Furthermore, reflecting the physiologically superior fighting ability of males, artificial males start with a higher ability to win than artificial females (*i.e.* of 16 *versus* 8), but all individuals of the same sex start with the same ability.

As regards sexual attraction, we study the case where males are more strongly attracted to females than the other way around, as is usual in the animal kingdom. Artificial males are attracted to all females independent of their identity (implemented as a preferential approach of one step by VirtualMales in the direction of females rather than males, see encircled part of Fig. 1). This attraction operates only during a certain period (as is the case when tumescence of females is synchronised, such as in species with seasonal reproduction). Females do not experience such a specific attraction to the opposite sex.

Experimental set-up and data-collection

Here, the same parameter setting ($N = 8$, persSpace = 2, nearView = 24, SearchAngle = 90, FleeingDistance = 2 units) is used as in former studies (Hemelrijk, 1999a, 2000a).

The present study is confined to a population of eight agents whereby VirtualFemales start with a lower winning tendency than VirtualMales (*i.e.* of 8 *versus* 16) and display 80% of the intensity of aggression of VirtualMales (reflected in their value of StepDom).

For two intensities of aggression, high (StepDom of VirtualMales = 1.0, of VirtualFemales = 0.8) and low (StepDom of VirtualMales = 0.1, of VirtualFemales = 0.08), the two conditions (with and without attraction towards females, see ‘Grouping Rules’) are compared. In a situation of ‘sexual attraction’ all females are supposed to be attractive, whereas in the condition without attraction none of them is. For all four situations 10 runs are conducted, resulting in a total of 40 runs.

During a run, every change in spatial position and in heading direction of each agent is recorded. After every time unit (consisting of 160 incidences of activation), the distance between agents is measured. 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

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

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

At the start of each run, all VirtualMales are dominant over all VirtualFemales, but during a run 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). Hereto, for each female the number of males ranking below her are counted. The value of the statistic is calculated as the sum of these countings. At the beginning of the run U-values are zero. Later on they may become positive.

Bidirectionality of attack is calculated as a τ_{Kr}-correlation between an actor and receiver matrix of attack (Hemelrijk, 1990). A stronger negative τ_{Kr}-value corresponds to a lower degree of bidirectionality and a higher degree of unidirectionality of attack.

The degree to which dominants occupy the centre of the group is measured by a Kendall rank-correlation between rank and the spatial directions of others around ego. For each scan the centrality of each entity is calculated by means of circular statistics (Mardia, 1972) 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 this circle. The connection of these points with the origin results in vectors. The length of the mean vector represents the degree in which the position of group members relative to ego forms a cluster; longer mean vectors reflect more clumping and indicate lower centrality (*i.e.* ‘encirclement’). Thus clearer centrality of dominants is represented by a stronger negative correlation between rank and ‘encirclement’.

Differences in behaviour between societies with and without attraction towards females are tested by means of a single data-point per run, namely the mean frequency of interaction per time-unit per sex. To exclude a possible bias brought about by transient values, the correlation for centrality of dominants is calculated on data collected after time-unit 200.

Results

Male ‘tolerance’ and female ‘assertiveness’

When we look at the effect of sexual attraction on male ‘tolerance’, the results differ markedly between a high and a low intensity of aggression: at a high intensity male ‘tolerance’ increases, but at a low one it does not.

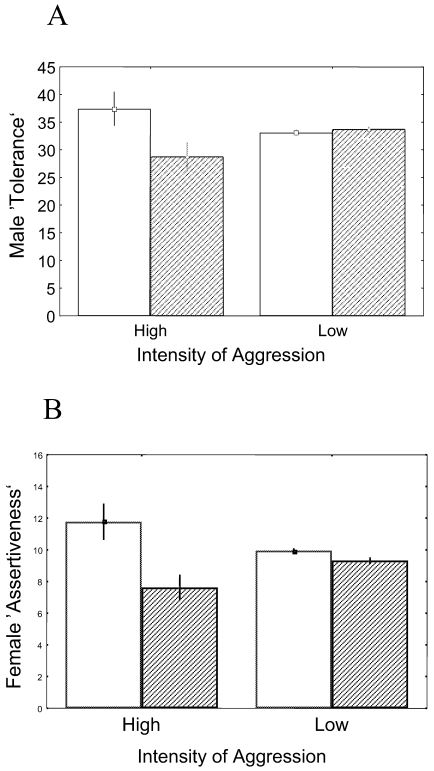

Fig. 2. Male ‘tolerance’ and female ‘assertiveness’. (A) Male ‘tolerance’ as the percentage of non-aggressive initiations of the total number of interaction-initiations by VirtualMales towards VirtualFemales, (B) Female ‘assertiveness’ as the frequency of aggression of VirtualFemales against VirtualMales, during sexual attraction (open bars) and outside these periods (filled bars), for both intensities of aggression.

At a high intensity of aggression during sexual attraction male ‘tolerance’ towards females (measured as the percentage of encounters in which they approach females non-aggressively) does clearly increase compared to periods without sexual attraction (Mann-Whitney U-test, $N_a = N_n = 10$, $U = 24$, $p = 0.05$ 2-tailed, Fig. 2A). Simultaneously, females are more ‘assertive’ to males in that they display more aggression to males (Mann-Whitney U-test, $N_a = N_n = 10$, $U = 19$, $p = 0.019$, Figure 2B). Such an increase in male ‘tolerance’ is absent, however, at a low intensity (Mann-Whitney U-test, $N_a = N_n = 10$, $U = 37$, $p = 0.353$ 2-tailed, Fig. 2A), because non-aggressive approach by VirtualMales to VirtualFemales increases (Mann Whitney U-test, $N_a = N_n = 10$, $U = 5$, $p = 0.00021$) and also

TABLE 1. *Differences during periods of sexual attraction between societies with a high and a low intensity of aggression and their resemblance to differences during periods without sexual attraction (see Hemelrijk, 1999b)*

Variable	Is greatest when StepDom is:	Mann-Whitney U-test: U-value	Without attraction results are:
Coefficient of variation of Dom-values	High	0^{***}	similar
Female dominance over males	High	0^{***}	similar
Correlation between rank of partner and attack frequency	High	8^{***}	similar
Correlation between rank of partner and non-aggressive approach	High	22^{*}	similar
Symmetry of attack	Low	0^{***}	similar
Decrease in attack over time	high	–	similar
Decrease in non-aggressive approach	high	–	similar
Decrease in cohesion over time	high		similar
Cohesion	equal	50 NS	**different**
Frequency of attack	Low	0^{***}	similar
Frequency of non-aggressive approach	Low	0^{***}	similar
Spatial centrality of dominants	equal	50NS	**different**
Correlation between rank and aggression	High	25^{*}	similar
Attack diversity[1)]	Low	0^{***}	Similar[2)]

[1)] measured by the Berger-Parker dominance index.

[2)] Similar without attraction (Mann-Whitney U-test: $U = 0$, $p < 0.000011$.

aggressive approach (Mann Whitney U-test, $N_a = N_n = 10$, $U = 0$, $p = 0.000011$). Nor is at a low intensity female 'assertiveness' affected by sexual attraction (Fig. 2B). Despite these different consequences of the introduction of sexual attraction at each level of intensity of aggression, the differences in social behaviour between both aggression intensities after introducing sexual attraction and without introducing it, are the same (Table 1). There are only two exceptions: during sexual attraction cohesion and spatial centrality are still greater at a high intensity than at a low one, but these differences are no longer significant.

Female dominance over males

At a high intensity of aggression, but not at a low one, sexual attraction increases female dominance over males (Fig. 3A).

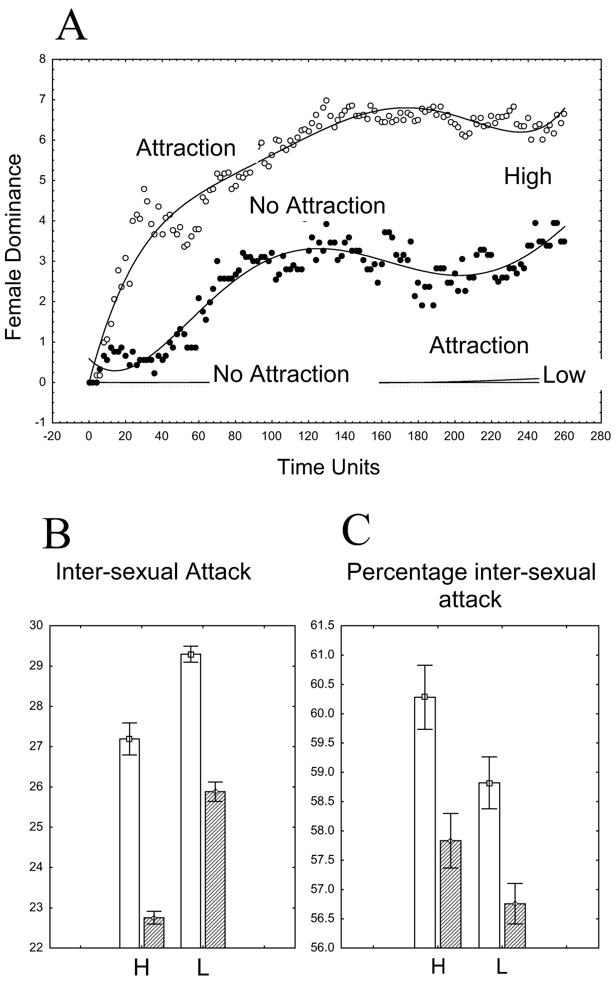

Fig. 3. Dominance and aggression between the sexes. (A) Dominance of VirtualFemales over VirtualMales as measured by the Mann-Whitney U-value as the summed countings of the number of males ranking below each female, for four conditions: with and without sexual attraction at both intensities of aggression. (B) absolute frequency of aggression between the sexes (mean and SE). (C) relative frequency of aggression between the sexes (mean and SE). Four conditions: with sexual attraction (open bars) and in other periods (shaded bars) at a high (H) and a low (L) intensity of aggression.

The question is why female dominance increases at a high intensity of aggression (see also, Hemelrijk, 2000a) but not at a low one. As mentioned in the introduction, female dominance is greater in case the hierarchy is steeper, which occurs at a higher intensity of aggression (see Hemelrijk, 1999b) and in groups that are more compact (see Hemelrijk, 1999a). However, sexual attraction does not increase the gradient of the hierarchy at either intensity of aggression (which is measured as the coefficient of variance of dominance values, at a high intensity: Mann-Whitney U-test, $N_{\mathrm{a}} = N_{\mathrm{n}} = 10$, $U = 32$, $p = 0.174$ 2-tailed; at a low intensity: Mann Whitney U-test, $N_{\mathrm{a}} = N_{\mathrm{n}} = 10$, $U = 37$, $p = 0.35$). Nor does it affect the compactness of grouping (at a high intensity: Mann-Whitney U-test, $N_{\mathrm{a}} = N_{\mathrm{n}} = 10$, $U = 46$, $p = 0.762$ 2-tailed; at a low intensity: Mann Whitney U-test, $N_{\mathrm{a}} = N_{\mathrm{n}} = 10$, $U = 48$, $p = 0.91$). This is remarkable because at both intensities, sexual attraction increases the aggression between the sexes (at a high intensity: Mann-Whitney U-test, absolute frequency, $N_{\mathrm{a}} = N_{\mathrm{n}} = 10$, $U = 0$, $p = 0.00016$; relative frequency $U = 21$, $p = 0.029$; at a low intensity: Mann Whitney U-test, absolute frequency: $N_{\mathrm{a}} = N_{\mathrm{n}} = 10$, $U = 0$, $p = 0.000011$; relative frequency: $N_{\mathrm{a}} = N_{\mathrm{n}} = 10$, $U = 13$, $p = 0.0039$, Fig. 3BC). Apparently, for the present parameters, attraction between the sexes brings them together more frequently, but just as often drives them apart, and therefore, attraction does not change the cohesion of grouping.

High intensity of aggression, however, increases the development of the hierarchy compared to that at a low intensity, both during sexual attraction and otherwise (Fig. 4A). Consequently, whether or not sexual attraction is added to DomWorld, female dominance is higher at a high intensity of aggression than at a low one (Table 1, Fig. 4B, C and see Hemelrijk, 1999b). The consequence of this is that at a high intensity (lower-ranking) females may once in a while be (unexpectedly) victorious over (higher-ranking) males (Fig. 4B). Because of the (absolutely and relatively) increased frequency of interaction between the sexes, the females will be victorious over males more often during sexual attraction than at other times. As a consequence of the rule inbuilt in the model, that the dominance values of both partners undergo a greater change if, unexpectedly, a lower-ranking agent defeats a higher-ranking one than if, as may be expected, a subordinate is beaten by a dominant agent, a higher percentage of interactions between the sexes will lead to a relatively increased number of victories of females over males. This will accelerate female dominance.

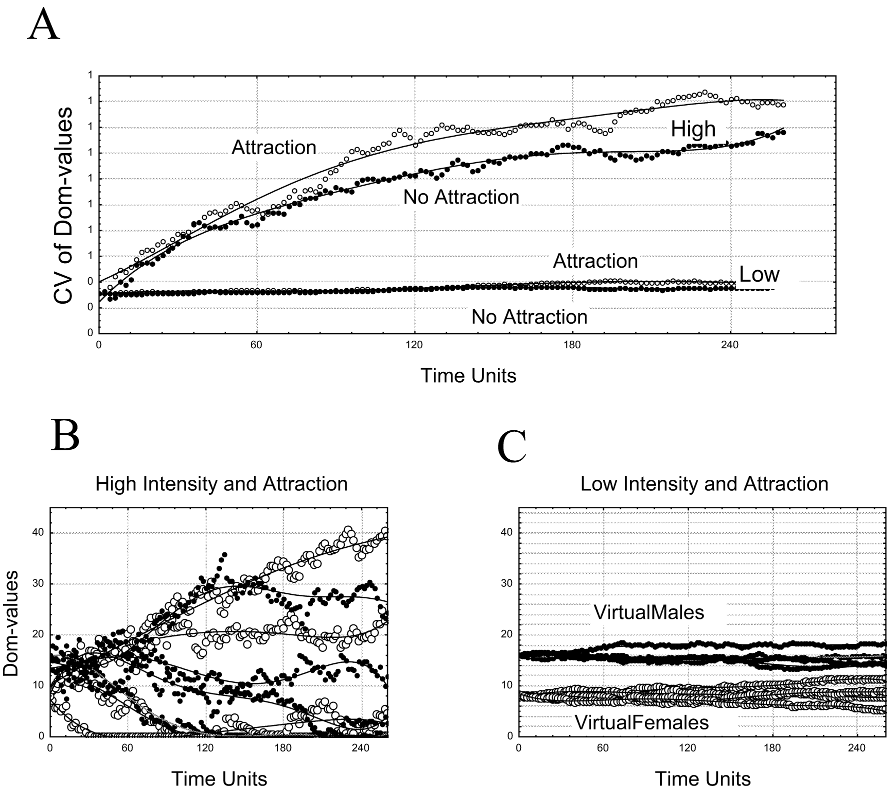

Fig. 4. Differentiation of the dominance- hierarchy. (A) Measured by the coefficient of variation of dominance values with and without sexual attraction at a high and a low intensity of aggression (SD). Open circles: Attraction. Closed: no attraction. Typical examples of dominance differentiation of both sexes during sexual attraction at high (B) and low (C) intensity of aggression (SD). Closed circles: VirtualMales, open: VirtualFemales.

Female dominance does not increase at a low intensity, because the weaker female dominance over males (due to the weaker hierarchical differentiation, see Fig. 4A, C), makes the chance of defeating VirtualMales almost negligible for VirtualFemales. Therefore, despite the more frequent inter-sexual dominance-interactions during sexual attraction, female dominance does not increase. Besides, even if so rare an event occurs, its effect is smaller than at a high intensity of aggression.

Discussion

What looks like 'male tolerance' towards females at a high intensity of aggression in DomWorld is nothing but a kind of increased 'respectful timidity' towards females, which withholds males from attacking females, because some females have become dominant over males. Simultaneously, female 'assertiveness' increases because it is less risky for VirtualFemales to attack VirtualMales because of their increased dominance during periods of sexual attraction. None of these effects (neither male 'tolerance' nor female 'assertiveness' nor increased female dominance) is found at a low intensity of aggression. This is due to the difference in hierarchical differentiation at a low and at a high intensity of aggression which influences the chance of VirtualFemales to be victorious over males, as explained above.

Thus, DomWorld shows that there is a complex interdependence between intensity of aggression, sexual attraction, female dominance over males, male 'tolerance' and female 'assertiveness'. Such a complex interdependence in social organisation has already been mentioned by Hinde & Stevenson-Hinde (1976). They distinguishe several levels of a society (such as the individual, the relationships between individuals, the group and the species) and argue that all these may influence each other mutually.

Clearly in DomWorld, these interdependencies lead to phenomena that are observed in real animals, but are explained in a different way. For instance, increased male 'tolerance' to females is observed at food sources during female tumescence in chimpanzees (Tutin, 1980; Goodall, 1986; Stanford, 1996). The traditional adaptive explanation for this is, that males hope to increase their number of offspring by exchanging food for sex, but the model shows that even in the absence of any benefits accrued to 'tolerant' male behaviour, attraction to VirtualFemales may produce male 'tolerance' (or rather timidity) via the increase of female dominance over males. Similarly, primate females are described as being more aggressive when in oestrus (*e.g.* see Michael & Zumpe, 1970; Goodall, 1986). Though this may be due to their special hormonal state (as is traditionally supposed), the model suggests two simpler mechanisms that may be operative: an increase in the frequency of encounters with males and, consequently, an increased female dominance over males.

Note that in the present model all females are simultaneously sexually attractive and sexually not attractive, as in real animals where all of females are synchronously tumescent. Although this is true for some primate species, in others, female menstrual cycles are not synchronised. The effects of such asynchrony will be studied in a future model. To test the relevance of the suggested interconnections empirically, we must study them in real primates, such as macaques and chimpanzees.

Further, the explanation, that more frequent interaction between individuals of two dominance classes makes them more alike, may hold for many other species. For instance, it is also observed in the behavioural studies of dominance interactions among bumblebees (Honk & Hogeweg, 1981): At the start of the colony there are two dominance classes of Bumblebees, the high-ranking queen and the low-ranking ‘common’-workers. In due time, a third dominance class of high-ranking ‘elite’-workers develops. These elite-workers interact more often with the queen than the common ones do. Consequently, they come to resemble her. Note that this process of becoming more and more similar, will also contribute to greater female dominance the more compact their groups are (Hemelrijk, 1999a), because compared to loose groups, the frequency of interaction between the sexes is higher, and therefore, the opportunities for incidental victories of the weaker sex increase; thus the sexes become more and more similar in dominance.

Obviously, the model does not mirror the complexity of real animals. It does not even incorporate social positive and sexual behaviour, but it simply incorporates the self-reinforcing effects of dominance-interactions among agents that are grouping indiscriminately, and among agents among which the males preferentially move towards females. This simplification is useful, because it makes the implications of these features detectable, which is impossible in studies of real animals (due to the many unknown variables).

Knowledge of emergent phenomena influences theories about the relation between genotype and phenotype. It presents an alternative for the one-to-one relationship between a phenotypic trait and a gene, because if behavioural phenomena arise as side-effects, much less needs to be encoded in our genes. This view about the relation between genotype and phenotype implies that natural selection does not only operate on the genotype, but simultaneously on the accompanying emergent phenotypic properties, in line with selection theories in which selection acts on more than one level (Lewontin, 1970; Hogeweg, 1994; Hemelrijk, in press). In our case, increased male ‘tolerance’ (lowered aggressiveness) to females is a side-effect and this side-effect will probably be advantageous in the real world and therefore, will not counter the evolution of intense aggression.

Note further, that if we would observe in real animals that such male 'tolerance' to females occurred only in despotic societies but not in egalitarian ones, we would tend to argue that this 'tolerance' is clearly adaptive, because particularly in fierce species with a high intensity of aggression, 'friendliness' by males to females is needed to suppress fear in females to males during mating. Thus, male 'tolerance' would probably be considered as a separate adaptation. However, DomWorld shows that such a distribution of male 'tolerance' over both types of societies can arise as a side-effect. Thus, results of DomWorld change our views on the number of adaptations. Not every trait necessarily corresponds to a separate adaptation; instead, DomWorld shows that complex behaviour may arise in the absence of a correspondingly complex form of cognition (this in contrast to the assumptions of the social intelligence hypothesis, Byrne & Whiten, 1988) and, besides, that one adaptation may have many effects. For instance, by changing a single value in DomWorld (that of intensity of aggression) the artificial society transforms from a characteristically egalitarian into a despotic society and the differences between the two societies (see Hemelrijk, 1999b) resemble those described for egalitarian and despotic primates, particularly of the genus Macaca (see Caldecott, 1986; de Waal & Luttrell, 1989; Thierry, 1990a; de Waal, 1991a). To this we may add the present findings: the introduction of sexual attraction leads to male 'tolerance', female 'assertiveness' and increased female dominance in a despotic society, but not in an egalitarian one. Thus, all these differences may result from one single adaptation (an increase in intensity of aggression). Besides, we may imagine that a difference in intensity of aggression evolved because in the long distant past a population of an egalitarian group-living species (living in an environment with abundant food in clumped patches) was forced to enter a new area where food was limited. In the groups of such a population, a so-called contest competition (Nicholson, 1967) arises in which individuals limit the access to food for others. Obviously, individuals with the strongest aggression may benefit from this feature, because they get hold of more food than others: And so we may imagine that a population with on average fiercer aggression than the original population evolved with all the consequences on patterns of social interactions as described above.

In summary, this and earlier models (Hemelrijk, 1999b, 2000b) have shown that intensity of aggression (and also increased cohesion, see Hemelrijk, 1999a), via socio-spatial structuring and the gradient of the hierarchy, may affect many aspects of social behaviour. In the present study we add to this that aggression intensity may result in what seems to be male 'tolerant' behaviour towards females during sexual attraction and also in female 'assertiveness' to, and dominance over, males. At first sight such a connection between aggression-intensity, the type of society and what looks like 'sexual exchange' is far from obvious. It is hardly possible to arrive at this kind of explanations by the usual method of partitioning or decomposing behaviour into independent components. This shows that individual-based models are indispensable for generating hypotheses how and when social behaviour, whether in animals or in humans, may emerge as side-effects.

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