

# Sexual Attraction And Inter-Sexual Dominance Among Virtual Agents

Charlotte K. Hemelrijk,

Department of Information Technology and Anthropological Institute and Museum,  
University of Zürich, Switzerland, Email: hemelrijk@ifi.unizh.ch

**Abstract.** In many group-living primates, males are dominant over females, but despite this dominance, they allow females access to resources during the period when females are sexually attractive - but only then and not otherwise. Conventionally, such male 'courtesy' is explained as a special strategy to gain mating access to females. In the present paper I propose a simpler hypothesis that is based on an agent-centered model, namely that male 'courtesy' to females is in fact a kind of 'timidity' that arises because sexual attraction automatically increases female dominance. The model consists in a homogeneous, virtual world with agents that group and perform dominance interactions. VirtualMales have a higher intensity of aggression and start with a greater capacity to win conflicts than VirtualFemales. I shall explain how the addition of attraction of VirtualMales by VirtualFemales leads to female dominance, and other phenomena that are relevant to the study of animal behaviour.

## 1 INTRODUCTION

In many animal species, males are extremely attracted to females, whereas females are relatively uninterested in males [1]. Male guppies are a good example [2]. They spend almost all their time courting and only if there is direct danger of a predator, they may pause. Although primate males are less ardent, males are the ones who actively maintain proximity to females when females are in their sexually attractive, oestrus period [e.g. see 3]. This sexual asymmetry is understandable, because males can fertilise many females, whereas females get fertilised only once per reproductive period. To obtain access to females, males have been supposed to develop many strategies. For instance, primate males are observed to allow oestrus (but not anoestrus) females priority of access to food sources [4-6]. This is regarded as an intentional manipulation by the male [7] and as an adaptive exchange of favours, namely priority of access to food for females in exchange for copulation for males. Evidence for such exchange is, however, very limited, if existing at all [8] and probably not every behavioural act should be interpreted separately in terms of costs and benefits to the number of offspring [9]; Surely, simpler alternative explanations are badly needed [10].

Here, artificial life models come in as a useful tool, because they show that animal behaviour is determined not only by specific inherited properties and individual

intentions, but also emerges by self-organisation from simple behavioural rules that lead to very complex behaviour in unexpected ways from the feedback between qualities of individuals and their changing environment. Whereas in the behaviour of real organisms, the effects of different contributing factors cannot be distinguished, they can be more easily traced in an Artificial World, for several reasons. An Artificial World can be used as a kind of Virtual Laboratory in which behavioural rules and parameters can be changed at will and the consequences analysed. Further, the behavioural rules of the artificial agents and the changes in their variable features are fully known. This makes such a model a suitable tool for developing our knowledge of the rules that may underlie observed behavioural patterns.

The aim of the present paper is to study whether in the absence of benefits and of calculative intentions, female dominance and, consequently, male 'tolerance', increases by self-organisation more strongly when males are attracted to females than when they are not. Besides, I investigate some other patterns of social behaviour usually studied by ethologists.

This paper is one of a series of papers [e.g. 11, 12, 13], in which I have shown that unexpected behavioural patterns, such as cooperation and exchange [14, 15] emerge by self-organisation in a model of competing, group-living artificial agents. Such a model represents only a few important features of an animal society [and is originally inspired by 16]. It consists of a homogeneous artificial world inhabited by agents that are equipped merely with a tendency to group and to perform competitive interactions. The effects of winning and losing such interactions are self-reinforcing [as has also been empirically observed in many animals species, for references see 10, 17]. To make the effects of experienced winning and losing of the agents and of pure chance as clear as possible, all agents are at the start completely identical. Yet, a dominance hierarchy develops over time. This development appears to depend on the intensity of aggression and the cohesion of grouping. For medium and higher values for both [18], a steep hierarchy develops in mutual reinforcement with a spatial structure with dominants in the centre and subordinates at the periphery [12]. This feedback has many unexpected consequences that all resemble observed behaviour of despotic species of primates, e. g. macaques. However, when the hierarchy is weak, the society resembles that of egalitarian macaques [19]. This correspondence makes the model a suitable tool for generating hypotheses for real primates.

In my model, I have introduced artificial 'sexes', by creating two types of agents that differ exclusively in their competitive ability [20]. In line with descriptions of primates [21], aggression by artificial males is made more intense than that by artificial females (implying more frequent biting compared to slaps and threats). Furthermore, reflecting the physiologically superior fighting ability of males (e.g. muscle structure), artificial males start with a higher tendency to win than artificial females. Unexpectedly, in a society with a steep hierarchy artificial females appear to dominate more males than in a society with a weak hierarchy. This arises as a side-effect of the stronger differentiation of dominance values for each sex separately [19]. Up till now, however, my models have ignored, the fact that in real animals, during certain periods of the year females are sexually attractive and males are highly interested in them.

In the present model, I study the consequences of this attraction. Hereto, I introduce attraction of VirtualMales to VirtualFemales and examine its effect on inter-

sexual dominance relations and other variables studied previously [such as cohesion, spatial centrality of dominants, hierarchical differentiation and frequency of aggression e.g. see Hemelrijk 14, 18, 20]. I shall show how indeed dominance of artificial females inevitably increases and how this can be used as a parsimonious alternative for the evolutionary hypothesis of sexual exchange. At the same time, females become more aggressive and, as another side effect, artificial males appear to develop more aggression among themselves.

## **2 METHODS**

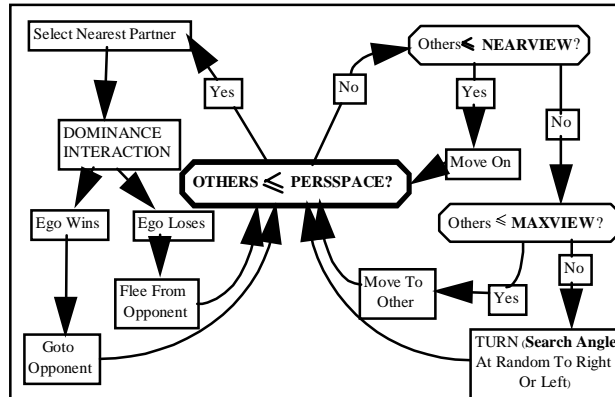
In this section, a description of the model and behavioural measures is given.

### **2.1 THE MODEL**

The model is individual-oriented and event-driven [see 22]. I have written it in object-Pascal, Borland Pascal 7.0 and it consists of three parts: a 'world' with its interacting agents, its visualisation and special observers that collect and analyse data on what happens in the 'world' (cf. the 'recorders' and 'reporters' of Hogeweg, 1988). The 'world' has the form of a torus (a seemingly three-dimensional donut) to avoid border effects and 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 [32]. 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 [33]. Often a random regime is applied in which each entity receives a random waiting time from a uniform distribution and the one with the shortest waiting time is activated first. Here, I combine a random regime with a biologically plausible timing regime that is locally controlled by other entities [see also, 34,35]. The locally controlled timing regime reduces the waiting time of an agent if a dominance interaction occurs within the agent's NearView (24 units). A nearby dominance interaction is thus considered as a kind of 'disturbance' that increases the chance that the agent is activated. This reflects observations on real animals, whereby dominance interactions are likely to activate individuals nearby [compare social facilitation, see 36]. Agents group and perform dominance interactions according to a set of rules described below (Figure 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 participation in a group provides safety; on the other, aggregation implies competition for resources, and this drives individuals apart [e.g., 23].



**Fig. 1.** Flow chart for the behavioural rules of agents that are not attracted to another type (sex)

The tendency of individuals to aggregate and space out are represented in the model by a set of rules that are graphically displayed in Figure 1 [see 19].

1. If an agent observes another within a critical distance, its 'personal space' (= PerSpace, see 2.2), 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, but still within NearView (see 2.2), then it 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.
3. If its nearest neighbours are outside NearView, but within its maximum range of vision (= MaxView, see 2.2), the agent moves towards one unit them.
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 nearby resources (such as food, mates and spatial location), but seem not always motivated by competition for immediate resources and some interactions are considered 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 happen only if the perceived risk of defeat is low [in the so-called risk sensitive behaviour, 19]. Interactions between agents are modelled after Hogeweg [24] and Hemelrijk [19], 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 following the Risk-Sensitive system. Here, the probability to attack decreases according to the risk of 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 a ‘real’ 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 values of Dom as follows :

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

Here  $w_i$  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.

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 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 gives rise to 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. This study is confined to high values near 1.

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’.

## 2.2 EXPERIMENTAL SET-UP AND DATA COLLECTION

Here, the same parameter setting ( $n=8$ ,  $\text{persSpace}=2$ ,  $\text{nearView}=24$ ,  $\text{SearchAngle}=90$ ,  $\text{FleeingDistance}=2$  units) is used as in a former study [18].

The present study is confined to a population size of eight agents consisting of two types that differ in fighting capacity. VirtualMales start with a higher winning tendency than VirtualFemales (i.e. of 16 versus 8) and display a higher intensity of aggression (i.e.  $\text{StepDom}$  value of 1.0 versus 0.8).

Two conditions (with and without attraction to females, see 2.1.1. ‘Grouping Rules’) are compared. In the condition of ‘sexual attraction’ all females are supposed to be attractive, whereas in the condition without attraction none of them is. For both conditions 10 runs are conducted, resulting in a total of 20 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  $\text{Dom}$ -values of the agents.

## 2.3 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  $\text{Dom}$ -values [25]. For each run the average value is calculated. Higher values indicate larger rank distances among agents.

At the start of each run, all VirtualMales are dominant over all VirtualFemales, 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 [26]. 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.

The clustering together of agents of the same sex is measured as a  $\tau_{K_r}$ -correlation between a matrix of mean distance among agents and a ‘hypothesis’-matrix. The ‘hypothesis’-matrix reflects sexual-segregation because cells belonging to agents of the same sex are filled with the number 1 and cells of different sexes are filled with zeros. Segregation is thus reflected by a positive correlation.

The spatial direction in which others are located as regards a certain individual (‘ego’) is used as a measure of the degree with which individuals occupy the centre. Using circular statistics [27] the centrality of each individual is calculated for each scan 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. Connecting these points with the origin produces 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 clustering in one direction and indicate lower centrality (i.e. lower 'encirclement'). Thus, greater centrality of higher-ranking agents is reflected in a stronger negative correlation between rank and encirclement.

Differences in behaviour between societies with and without attraction to females are tested using one 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.

### **3 RESULTS**

#### **3.1 EFFECTS ON FEMALE DOMINANCE**

When VirtualMales are attracted to VirtualFemales in NearView, this increases dominance of VirtualFemales over VirtualMales markedly, as shown by the larger number of males being subordinate to VirtualFemales compared to that when 'attraction' is absent (Figure 2A). Simultaneously, the mean dominance value of VirtualFemales is higher and of VirtualMales is lower than in the absence of attraction to females (Figure 2BC). Consequently, the mean dominance values of both sexes converge during attraction. In its absence, however, they diverge over time (Figure 2D).

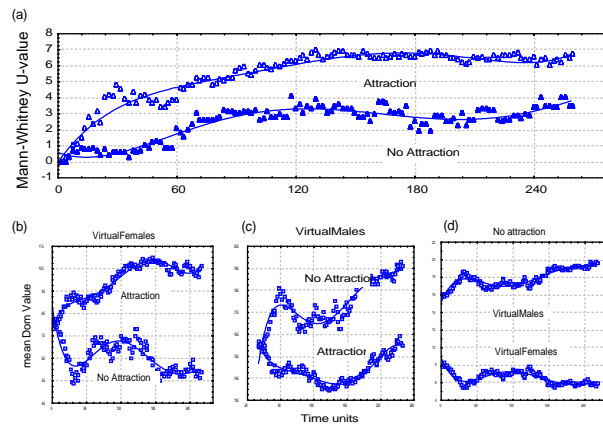
#### **PREVIOUS EXPLANATIONS OF FEMALE DOMINANCE**

How does female dominance over males arise? In earlier models, cohesion (via a steeper hierarchy) and the frequency of interaction between the sexes have been shown to contribute to female dominance [18-20].

Cohesion contributes to female dominance via the accompanying hierarchy, which is steeper than in loose groups [18], as follows. Hierarchical differentiation develops together with spatial centrality of dominants. It appears to arise from the positive feedback between the development of the hierarchy and spatial centrality of dominants. A clearer hierarchy implies that the lowest ranking agents flee from about everyone else. Therefore, they end up at the periphery leaving the dominants in the centre. When agents are thus sorted according to dominance, they will usually meet and interact with partners of close rank. This implies that if a dominance reversal occurs at all, it will only be a minor one. Thus, spatial sorting according to rank stabilises the hierarchy and keeps the differentiation intact. This feedback (clearly leading to bi-directional causation, see Sawyer, same volume) develops more clearly under the spatial constraints and high frequency of interaction of cohesive than of loose grouping. Strong differentiation of dominance values will automatically cause some of these females to obtain a higher dominance position than some males, even

though artificial females start with a weaker tendency to win than males. Conversely, weak hierarchical differentiation will leave artificial females in their initial subordinate position to males.

Besides, female dominance also appears to arise in the presence of a weaker hierarchy, if the sexes interact more often with each other than among themselves [as reflected by a weaker correlation for segregation of the sexes, see 18].



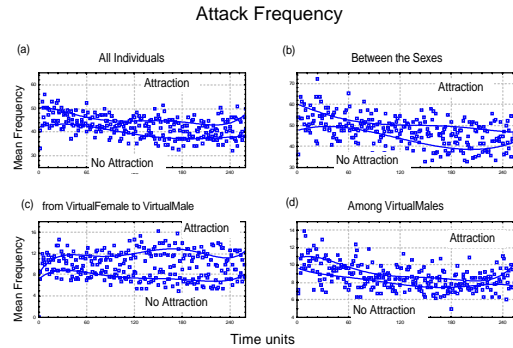
**Fig. 2.** Dominance differentiation for the two societies with and without attraction of VirtualMales to VirtualFemales. (a) Dominance of VirtualFemales over VirtualMales measured by the Mann Whitney U-statistic as the summed countings of the number of males ranking below each female. (b),(c),(d). Mean dominance values calculated over 10 runs for individuals of the same sex.

In summary, in the cases described above, greater female dominance arises from stronger cohesion which goes hand in hand with more marked spatial centrality of dominants and stronger hierarchical differentiation and from weaker sexual segregation.

None of these two processes can, however, explain the present finding of increased female dominance due to male attraction to females, for the following reasons.

First, whether VirtualMales are attracted to females or not, the group cohesion (Mann Whitney U-test,  $n_a = n_n = 10$ ,  $U=46$ ,  $P=0.762$ ), the hierarchical differentiation (Mann Whitney U-test,  $n_a = n_n = 10$ ,  $U=32$ ,  $P=0.174$ ) and the spatial structure (Mann Whitney U-test,  $n_a = n_n = 10$ ,  $U=28.5$ ,  $P=0.103$ ) remain similar. Thus, there is no indication of a stronger social-spatial feedback. Second, adding attraction between the sexes, does unexpectedly, not increase the relative frequency with which the sexes interact with each other and among themselves, as measured by the correlation for sexual segregation (Mann Whitney U-test,  $n_a = n_n = 10$ ,  $U=46.5$ ,  $P=0.796$ ). Obviously, it is a different process that causes female dominance in the present case and therefore, it is necessary to look in greater detail at patterns of aggression.





**Fig. 3.** Mean Attack frequency of the two societies with and without attraction of VirtualMales to VirtualFemales. Mean dominance values calculated for 10 runs for all individuals of the same sex.

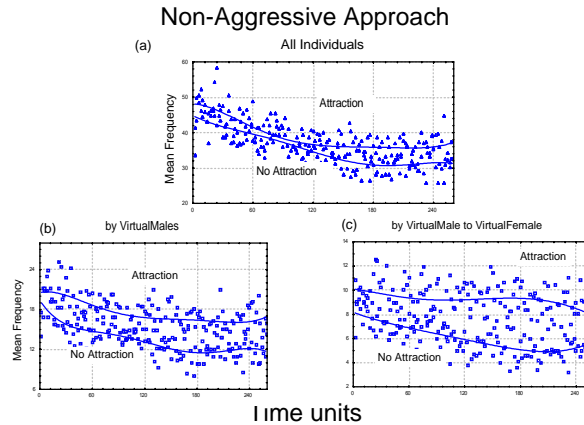
### ALTERNATIVE EXPLANATION FOR FEMALE DOMINANCE

Despite the unchanged cohesion, attraction to VirtualFemales raises the frequency of attack in the group (Mann Whitney U-test, attack:  $n_a = n_n = 10$ ,  $U=0$ ,  $P=0.00016$ , Figure 3a). This fact explains the curious finding that attraction does not increase cohesion. Apparently for the present parameters, stronger cohesion is counter-balanced by the increased frequency with which agents drive each other apart. Note, further, that in contrast to previous results [18] the higher frequency of aggression does not increase spatial structure and differentiation of the hierarchy. The cause of this may be that the movement by VirtualMales counteracts sorting by rank, because they approach any VirtualFemale independently of her dominance.

More specifically, aggression is increased between the sexes both in its absolute frequency and its percentage of total aggression (Mann Whitney U-test, frequency:  $n_a = n_n = 10$ ,  $U=0$ ,  $P=0.00016$ , Figure 3b; percentage:  $n_a = n_n = 10$ ,  $U=21$ ,  $P=0.029$ ). It is this that triggers female dominance as an implication of the rule inbuilt in the model, that the degree with which the outcome of a fight changes the dominance values of both partners, depends on the degree to which the outcome of the conflict was expected. Dominance values of both partners undergo a greater change if, unexpectedly, a lower-ranking agent defeats a higher-ranking one than if, expectedly, a subordinate is beaten by a dominant. As a consequence, defeat of dominants by subordinates produces dominance conversion of the 'sexes' more strongly than expected victories by dominants induce divergence of dominance of both sexes. Since the higher percentage of interaction between the sexes implies a higher percentage of incidental victories of VirtualFemales over VirtualMales at the beginning, attraction will accelerate dominance conversion between both types (the 'sexes').

Greater dominance of VirtualFemales over VirtualMales makes VirtualFemales more aggressive, particularly against VirtualMales (Mann Whitney U-test,  $n_a = n_n = 10$ ,  $U=19$ ,  $P=0.019$ , Figure 3c), than if VirtualMales are not attracted to

them. Note, that this may further enhance their dominance (Kendall Rank Correlation between mean female aggression and dominance,  $n=10$ ,  $\text{Tau}=0.733$ ,  $P=0.003$ ).



**Fig. 4.** Mean frequency of non-aggressive approach of the two societies with and without attraction of VirtualMales to VirtualFemales. Mean dominance values calculated for all individuals of the same sex and for 10 runs.

### 3.2 OTHER CONSEQUENCES

When VirtualMales are attracted to VirtualFemales this also raises the frequency of non-aggressive approach in the group ( $n_a = n_n = 10$ ,  $U=8$ ,  $P=0.0015$ , Figure 4a). Due to their lessened dominance VirtualMales more often approach others (Mann Whitney U-test,  $n_a = n_n = 10$ ,  $U=4$ ,  $P=0.0005$ , Figure 4b) and particularly VirtualFemales non-aggressively (Mann Whitney U-test,  $n_a = n_n = 10$ ,  $U=12$ ,  $P=0.0041$ , Figure 4c).

When VirtualMales are attracted to VirtualFemales, this raises also intrasexual aggression among VirtualMales (Mann Whitney U-test,  $n_a = n_n = 10$ ,  $U=4$ ,  $P=0.0001$ , Figure 3d). Although this needs to further study, it probably comes about via an increased opportunity to meet each other close by when several VirtualMales converge on the same VirtualFemale. Consequently, VirtualMales will more often trespass on each other's personal space and therefore, attack. In line with this, there is also a non-significant trend that VirtualMales more often approach each other non-aggressively (Mann Whitney U-test,  $n_a = n_n = 10$ ,  $U=32$ ,  $P=0.19$ ).

Note that the increased frequency of intrasexual aggression explains why, as mentioned above, the correlation for sexual segregation of interactions remain similar with and without attraction: whereas inter-sexual aggression increases as expected, this is not reflected in a weaker correlation, because it is neutralised by the increase in aggression frequency among VirtualMales.

## 4 DISCUSSION

When in this society of group-living artificial agents, VirtualMales are attracted to VirtualFemales, there are several unexpected consequences.

First, such attraction increases the dominance of VirtualFemales and decreases that of VirtualMales. This is due to the higher frequency of interaction between the sexes and the inbuilt mechanism that unexpected victories and defeats cause a greater change in the dominance values of both opponents than expected outcomes do. This mechanism is based on precise behavioural observations of dominance interactions in bumblebees [28] and seems a plausible assumption for any species. It provides a new mechanism by which female dominance over males increases. Note that this process (together with a steeper hierarchy) will also contribute to female dominance in cohesive groups, because compared to loose groups, the frequency of intersexual interactions and thus also of incidental victories by the weaker sex, will be higher.

Second, VirtualMales behave more often non-aggressively to VirtualFemales. The greater dominance of VirtualFemales makes it more risky for VirtualMales to attack them. Thus, the model presents us with a parsimonious alternative for the usual explanation of the observed male ‘tolerance’ towards females at food sites when females are in their receptive period and males are highly attracted to them. The conventional adaptive explanation for this is, that males increase their number of offspring by exchanging food for sex [5, 6], but the model shows how 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.

Third, VirtualFemales become more aggressive when VirtualMales are attracted to them. Similarly, primate females are described as being more aggressive when in oestrus [e.g. see 6, 29]. Whereas this may be due to their special hormonal state as is traditionally supposed, the model suggests two alternative, more simple mechanisms that may be operative: an increase of encounter frequency with males and, consequently, increased female dominance over males.

Fourth, and unexpectedly, attraction to VirtualFemales makes VirtualMales more aggressive among themselves though they do not want to monopolise VirtualFemales! Although this will be studied in further detail in the near future, it is probably a consequence of the increased frequency of their meeting near VirtualFemales: VirtualMales will more often enter each other’s attack range and actually attack. Similarly, in a combined modelling and empirical study of butterflies [*Euphydryas anica*, 30], male grouping and increased male aggression are suggested to result as a side-effect of male mate-searching behaviour. Male butterflies typically investigate anything that even remotely resembles a female. Such indiscriminate searching causes males to investigate each other. Resulting male-male chases cause a change in the direction of their movement, which, particularly under high density, lead to male aggregations and increased aggression.

Obviously, the model does not represent the complexity and sophistication of real animals. It does not even represent social positive and sexual behaviour. Instead, the model just incorporates the self-reinforcing effects of dominance interactions among agents that are grouping indiscriminately apart from the fact that males move preferentially towards females during certain periods. This simplification is useful,

because the model represents features that are relevant for many animal species and it makes the implications of these assumptions detectable, which cannot be done in studies on real animals due to the many unknown variables. Note that the condition of sexual attraction in the present model concerns attraction to all females, suggesting that all of them are synchronously tumescent. Although this holds for some primate species, in others, female menstrual cycles are not synchronised. The effects of such asynchrony will be studied in a model in future.

Further, I am at present studying the same model for the case where females are attracted to males, whereas males are indifferent. Although this situation hardly applies to any animals in the real world, these models can also represent 'species' that do not exist [31] and allow us to search the 'world of the possible' and thereby, reveal unknown general processes. From the present paper and my former ones it appears that one cannot predict how these changes will affect social structure, in terms of variables such as interaction frequencies, spatial configuration and dominance overlap between the sexes.

In summary, in this and former models, I have presented evidence that inter-sexual dominance may be influenced by the intensity of aggression, by cohesion and by sexual attraction. At first sight, however, a connection of these three variables with intersexual dominance is far from obvious. It seems hardly possible to arrive at this kind of explanations by decomposing behaviour in independent components as is usually done. This shows that individual-based models are indispensable tools to obtain hypotheses how social behaviour, whether in animals or in humans, may emerge from the feedback between changing features of individuals and their group members by self-organisation.

## ACKNOWLEDGEMENTS

I am grateful to Rolf Pfeifer and Bob Martin for continuous support. I like to thank Jaap Hemelrijk for correcting the English. This work is supported by the Swiss National Science Foundation by a grant from the Marie Heim-Vögtlin Foundation and by a grant from the A. H. Schultz foundation.

## REFERENCES

1. Trivers, R.L., *Parental investment and sexual selection*, in *Sexual selection and the descent of man*, B. Campbell, Editor. 1972, Aldine: Chicago. p. 136-179.
2. Magurran, A. and M. Nowak, *Another battle of the sexes*. Proceedings of the Royal Society London, 1991. 246: p. 31-38.
3. Hill, D., Social relationships between adult male and female rhesus macaques: 1. Sexual consortships. *Primates*, 1987. 28: p. 439-456.
4. Yerkes, R.M., *Social dominance and sexual status in chimpanzees*. *Quarterly Review of Biology*, 1939. 14: p. 115-136.
5. Yerkes, R.M., Social behavior of chimpanzees: dominance between mates in relation to sexual status. *Journal of Comparative Psychology*, 1940. 30: p. 147-186.

6. Goodall, J., *The chimpanzees of Gombe: patterns of behaviour*. 1986, Cambridge MA and London: Belknap Press of Harvard University Press.
7. de Waal, F.B.M., *Foodsharing and reciprocal obligations among chimpanzees*. *J. Human Evolution*, 1989. 18: p. 433-459.
8. Hemelrijk, C.K., C.M. Meier, and R.D. Martin, 'Friendship' for fitness in chimpanzees? *Animal Behaviour*, 1999. 58: p. 1223-1229.
9. Gould, S.J. and R.C. Lewontin, *The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme*. *Proceedings of the Royal Society London B*, 1979. 205: p. 581-598.
10. Hemelrijk, C.K., Towards the integration of social dominance and spatial structure. *Animal Behaviour*, 2000, 59, 1035-1048.
11. Hemelrijk, C.K., *Reciprocation in apes: from complex cognition to self-structuring.*, in *Great Ape Societies*, W.C. McGrew, L.F. Marchant, and T. Nishida, Editors. 1996, Cambridge University Press: Cambridge. p. 185-195.
12. Hemelrijk, C.K., *Spatial centrality of dominants without positional preference*, in *Artificial Life VI*, C. Adami, et al., Editors. 1998, MIT-Press: Los Angeles, USA. p. 307-315.
13. Hemelrijk, C. Risk Sensitive and Ambiguity Reducing Dominance Interactions in a Virtual Laboratory. in *Proceedings of the Fourth International Conference on Simulation on Adaptive Behavior. From Animals to Animats 5*. 1998. Zürich: MIT Press.
14. Hemelrijk, C.K., Dominance interactions, spatial dynamics and emergent reciprocity in a virtual world, in *Proceedings of the fourth international conference on simulation of adaptive behavior*, P. Maes, et al., Editors. 1996, The MIT Press: Cambridge, MA. p. 545-552.
15. Hemelrijk, C.K., *Cooperation without genes, games or cognition.*, in *4th European Conference on Artificial Life*, P. Husbands and I. Harvey, Editors. 1997, MIT-Press: Cambridge MA. p. 511-520.
16. Hogeweg, P., *MIRROR beyond MIRROR, Puddles of LIFE*, in *Artificial life, SFI studies in the sciences of complexity*, C. Langton, Editor. 1988, Addison-Wesley Publishing Company: Redwood City, California. p. 297-316.
17. Bonabeau, E., G. Theraulaz, and J.-L. Deneubourg, *Mathematical models of self-organizing hierarchies in animal societies*. *Bulletin of Mathematical Biology*, 1996. 58(4): p. 661-717.
18. Hemelrijk, C.K., Effects of cohesiveness on intersexual dominance relationships and spatial structure among group-living virtual entities, in *Advances in Artificial Life. Fifth European Conference on Artificial Life*, D. Floreano, Nicoud, J-D., Mondada, F., Editor. 1999, Springer Verlag: Berlin. p. 524-534.
19. Hemelrijk, C.K., *An individual-oriented model on the emergence of despotic and egalitarian societies*. *Proceedings of the Royal Society London B: Biological Sciences.*, 1999. 266: p. 361-369.
20. Hemelrijk, C.K., Self-reinforcing dominance interactions between virtual males and females. Hypothesis generation for primate studies. *Adaptive Behavior*, in press.
21. Bernstein, I.S. and C.L. Ehardt, *Intragroup agonistic behavior in Rhesus monkeys (Macaca mulatta)*. *International Journal of Primatology*, 1985. 6(3): p. 209-226.
22. Judson, O.P., *The rise of the individual-based model in ecology*. *Trends in Ecology and Evolution*, 1994. 9: p. 9-14.
23. Schaik, C.P.v., *Why are diurnal primates living in groups ?* *Behaviour*, 1983. 87: p. 120-144.
24. Hogeweg, P. and B. Hesper, *The ontogeny of interaction structure in bumble bee colonies: a MIRROR model*. *Behavioral Ecology and Sociobiology*, 1983. 12: p. 271-283.
25. Sokal, R.R. and F.J. Rohlf, *Biometry: the principles and practice of statistics in biological research*. 2 ed. 1981, San Francisco: W.H. Freeman.
26. Siegel, S. and N.J. Castellan, *Nonparametric statistics for the behavioral sciences*. second ed. *Statistics Series*. 1988, New York: McGraw-Hill international editions. 399.

27. Mardia, K.V., *Statistics of directional data*. 1972, London: Academic Press.
28. Honk, C.v. and P. Hogeweg, *The ontogeny of the social structure in a captive Bombus terrestris colony*. Behavioral Ecology and Sociobiology, 1981. 9: p. 111-119.
29. Michael, R.P. and D. Zumpe, Aggression and gonadal hormones in captive rhesus monkeys (Macaca mulatta). Animal Behaviour, 1970. 18: p. 1-10.
30. Odendaal, F.J., P. Turchin, and F.R. Stermitz, *An incidental-effect hypothesis explaining aggregation of males in a population of Euphydryas anicia*. The American Naturalist, 1988. 132(5): p. 735-749.
31. Ray, T.S., An approach to the synthesis of life., in Artificial Life II, Santa Fe Institute, Studies in the sciences of complexity, C.G. Langton, et al., Editors. 1991, Addison-Wesley, CA: Redwood City. p. 371-408.
32. Hemelrijk, C. K. 1997 Cooperation without genes, games or cognition. In *4th European Conference on Artificial Life* (ed. P. Husbands & I. Harvey), pp. 511-520. Cambridge MA: MIT-Press.
33. Huberman, B.A. and N.S. Glance, *Evolutionary games and computer simulations*. Proceedings of the National Academy of Sciences of the United States of America, 1993. 90: p. 7716-7718.
34. Goss, S. and J.L. Deneubourg, Autocatalysis as a source of synchronised rhythmical activity in social insects. Insectes Sociaux, 1988. 35(3): p. 310-315.
35. Hogeweg, P. and B. Hesper, *A model study on biomorphological description*. Pattern Recognition, 1974. 6: p. 165-179.
36. Galef, B.G.J., Imitation in animals: history, definitions, and interpretation of data from the psychological laboratory., in *Social learning: Psychobiological and biological perspectives*, T. Zentall and B. Galef, Editors. 1988, Erlbaum: Hillsdale, New Jersey. p. 3-28.