

FEMALE CO-DOMINANCE IN A VIRTUAL WORLD: ECOLOGICAL, COGNITIVE, SOCIAL AND SEXUAL CAUSES

by

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Summary

In male-dominant primate species, females are sometimes dominant to some or all males of a group. In this paper, we show a number of variables that increase female dominance over males in a model called DomWorld. This model is relevant, because its results have shown to resemble those of typical egalitarian and despotic macaques. Variables that increase female co-dominance are intensity of aggression, group cohesion, a clumped distribution of food, a similar diet for the sexes and sexual attraction (by one sex to the other, but not mutually). We explain that in these cases female co-dominance increases due to more interactions between the sexes (under certain conditions), and as a consequence of all factors that increase the development of the hierarchy (*i.e.* a higher number of interactions, more interactions per sex, a higher intensity of aggression and a clearer spatial structure). We suggest model-guided studies of female dominance in real animals.

Introduction

Groups of many animal species contain adults of both sexes. Usually individuals of the sex with the larger body size are dominant to those of the smaller sex and outcompete them. However, in primates, such as vervets, macaques, squirrel monkeys, talapoin despite the females' markedly smaller body size they are sometimes dominant over males (Dixson *et al.*, 1973; Wolfheim,

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1977; Loy, 1981; Bramblett *et al.*, 1982; Johnson *et al.*, 1982; Chapais, 1983; Janson, 1984; Bernstein & Ehardt, 1985a; Smuts, 1987). Systematic studies of the occurrence of female dominance over some males (so-called female co-dominance) in typically male-dominated species are, however, absent. This is remarkable, particularly because female dominance over males occurs relatively often, also in species with little sexual dimorphism, such as in callitrichids, monogamous New world monkeys, gibbons and bonobos (Chivers, 1974; Tilson, 1981; Evans & Poole, 1983; Stanford, 1998). It occurs more frequent than for instance deception, to which complete issues are devoted (*e.g.* see Whiten & Byrne, 1986). The aim of the present paper is to develop a starting point for a theory to explain such unexpected female dominance in typically male-dominant species.

For this we acknowledge that dominance is not a fixed trait. Although some argue that the position of an individual is an internal, inherited characteristic that is fixed (Ellis, 1991), this is contradicted by studies of others (Chase *et al.*, 2002). It depends on, for instance, the order of introduction of individuals in the group (Bernstein & Gordon, 1980), the composition of the group (Chase *et al.*, 2002), and immediately preceding events of victory and defeat (Chase *et al.*, 1994; Hsu & Wolf, 1999). The effects of victory and defeat are self-reinforcing, so that after winning or losing a dominance interaction the chance to win or lose again increases. This is called the winner-loser effect (Chase, 1974). Such self-reinforcing effects have been shown empirically in many animal species (ranging from insects to humans). In a model, called DomWorld, it is shown that even if individuals are completely identical at the start, over time a dominance hierarchy develops. The model consists of a world in which agents merely group and compete if others are close by. The effects of victory and defeat are self-reinforcing (Hemelrijk, 2000b).

DomWorld is of interest because its results closely resemble those of real animals, such as primates. For instance, when in this model the value of only one variable is increased (in casu intensity of aggression, from mild aggression, such as slapping, to intense aggression, such as biting), 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 spreads out (which in turn reduces the frequency of aggression); simultaneously, a spatial structure develops with dominants in the centre and subordinates at the periphery and

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 before the fight. Therefore, the spatial structure stabilises the hierarchy and helps it to develop. Thus the development of the hierarchy and the spatial structure are mutually reinforcing each other. 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 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, b; de Waal, 1991; Hemelrijk, 1999b).

Remarkably, intensity of aggression also influences female dominance over males: At a high intensity, female dominance appears to be greater than at a low intensity (Hemelrijk, 1999b) and this corresponds to the greater female dominance described for fiercely aggressive despotic females over maturing subadult males by Thierry (1990a). Thierry argues that it may be due to the stronger coalitions among females against (sub-adult) males in despotic rather than egalitarian societies. In DomWorld, however, this is due to the steeper hierarchy at a high intensity (because some females become very high in dominance and some males very low). Note that species specific intensity of aggression is an unusual factor to relate to female dominance; usually other characteristics are studied that directly relate to power — such as body size and coalitionary support received (*e.g.* see Parish, 1994). However, DomWorld has shown that this unusual factor and also others, such as group cohesion (Hemelrijk, 1999a) and male attraction to females (Hemelrijk, 2002a), contribute to female dominance.

Because of its resemblance to biological systems, we will use DomWorld to study the effects of further factors on female dominance over males. We will look at social, cognitive and environmental characteristics. We study in the model how ecology influences female dominance (via cohesion and diet) and what happens during sexual attraction if the initiative to approach the opposite sex is either mostly the male's, or mostly the female's or equally strong in both sexes and what happens when female attractiveness is either synchronous or asynchronous. Further, we study the effect of the level of cognition involved in the perception of another's dominance (through direct

observation in 'Perceivers' and through memorised experiences in 'Estimators'). We will explain through what processes all these variables influence female dominance over males. We will discuss potential examples of corresponding effects in real animals and give suggestions for model-guided comparisons of real animals.

Methods

The model

The model is individual-oriented and event-driven (see Judson, 1994). Hemelrijk has written it in object-Pascal, Borland Pascal 7.0 and it was transferred to Borland Delphi by Stefan Schläpfer. 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 (Hemelrijk, 2000a). Agents have an angle of vision of 120 degrees and their maximum perception distance (MaxView) is 50 units. 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 before activation from a uniform distribution. Here, a random regime is combined with a biologically plausible timing regime (see also Goss & Deneubourg, 1988): 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 has advantages (such as increased safety); on the other, grouping implies competition for resources, and this drives individuals apart (*e.g.* van Schaik, 1983).

In the basic model of DomWorld this is represented by two sets of rules, concerned with attraction and with competition for resources that are not specified. In the derived model, *i.e.* EcoDomWorld, food is represented also and satiated agents aggregate like in the basic model because they are attracted to each other. Hungry agents, however, meet others because they visit the same food source. Here, competition is specific, in that it concerns food only. We will discuss these models in turn.

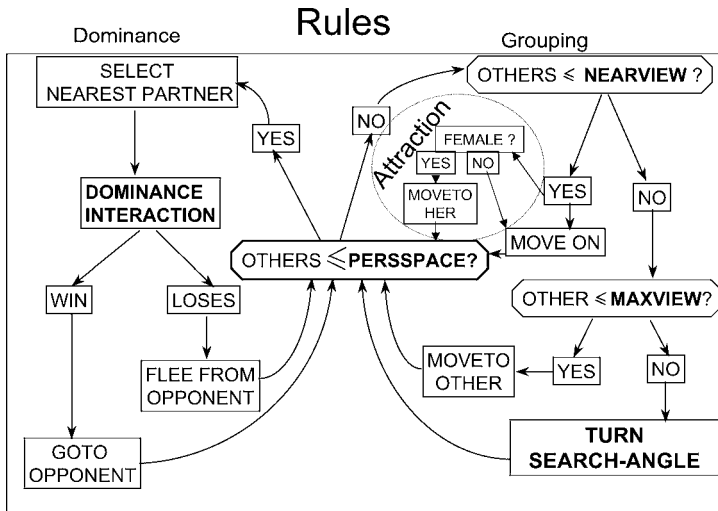


Fig. 1. Flow chart for the behavioural rules of agents. Encircled part (with dotted line and labelled 'Attraction') is the behavioural rule for attraction to females. This rule is only operative during sexual attraction.

Basic DomWorld

Grouping and competition are represented in the model by a set of rules that are graphically displayed in Fig. 1 (see Hemelrijk, 1999b) and parameter values are shown in Table 1. The resources about which the agents compete are not specified.

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 Table 1), then — in runs without 'sexual attraction' — it continues moving one unit in its original direction. In case of 'attraction', however, agents of one sex approach an agent of another sex over one unit distance when they observe it in nearView (see 'attraction' in Fig. 1).
3. If its nearest neighbours are outside NearView, but within its maximum range of vision (= MaxView, see Table 1), the agent moves one unit towards them.
4. If an agent does not perceive other agents within MaxView, it looks around for them by turning a Search angle at random to the right or left.

DomWorld with food, EcoDomWorld

Food, in the form of trees, is distributed in the world in three ways: uniformly, randomly and as clusters (in three degrees). In all three cases the total number of food sources remain the same (36). One food source initially consists of 20 units of energy. After it is fed upon,

TABLE 1. *Default values of parameters of both models*

Parameter	Description	Females	Males
DomWorld			
# of agents		5	5
InitDom basic	Initial DomValue in basic DomWorld	16	32
InitDom eco	Initial DomValue in Eco DomWorld	12	24
StepDom	Scaling factor for fighting intensity	0.8	1
FleeingDistance	After losing an interaction	2	
Perspace	Close encounter distance	2	
Nearview	Medium Distance	24	
Maxview	Maximal viewing distance	50	
SearchAngle	Turning Angle for finding others	90°	
EcoDomWorld			
# of trees		36	
Initial energy of Tree	Initial Energy value	20	
Max energy of Tree	Maximum energy value	50	
Growth Steps		0.2	
Initial Energy of Agent		20	
Hunger threshold	See text	35	
Starving threshold	See text	5	
Energy Loss/time-unit		0.5	
# of insects		72	
Food value of insect		1	

re-growth occurs with an exponential growth rate with steps of 0.2 until a maximum energy level of 50 is reached. Agents lose a fixed amount of energy per time-period (0.5 units).

The agents are supplied with the following rules (Fig. 1).

1. If the agent's energy level is below 35, it searches for food in PersSpace with a certain probability. (When the energy level decreases from 35 to 5 the probability to search for food increases linearly from 0% to 100%, so that below 5 the agent always searches for food.)
 - a. If it finds food of sufficient quality and no-one is close by in PersSpace, it eats it. If there are others in its PersSpace, however, it may first initiate a dominance interaction. After defeating the opponent it chases it away, after losing from it, it flees from it as in the basic model of Figure 1.
 - b. If it does not find food of sufficient quality in its PersSpace, it looks for it at a larger distance, *i.e.* in its NearView. If it finds food there, it moves one step towards the food source.
 - c. If the food quality is too low, or there is no food in NearView, the agent searches for food at an even larger distance, *i.e.* in MaxView. If it finds it, it moves one step in the direction of the nearest food source. If there is no food, the agents turns over a SearchAngle to find it.

2. If the agent has enough energy, it looks for others in its Perspace,
 - (a) if it sees others, it is 'content' and stays put.
 - (b) If it does not see anyone in its PersSpace, it looks for others in NearView. If it finds agents there, it moves one step forwards in its original direction.
 - (c) If it does not find others in NearView, it searches others in MaxView. If it finds others there, it moves towards the one closest by, if not, it turns over a SearchAngle to find others.

To reflect diet differences between the sexes, insects are added to EcoDomWorld. At the beginning of each period 72 insects are distributed randomly, but close to trees. At the end of each period all the remaining insects die. Females prefer to eat insects (energy value of 1) to fruits from trees, males do not eat insects at all (inspired by Halperin, 1979; Cords, 1986).

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. Dominance interactions may be initiated when agents encounter each other nearby, but 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).

Two types of agents (Perceivers and Estimators) are distinguished: Perceivers directly observe the dominance rank of others; Estimators are cognitively more sophisticated agents with memory-based dominance perception (Hemelrijk, 1996a, b, 2000b).

Direct perception by 'Perceivers'

Interactions between agents with direct perception is modelled after Hogeweg & Hesper (Hogeweg & Hesper, 1983) 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 in which the probability to attack decreases according to the risk of suffering defeat in line with experimental studies (Hemelrijk, 1998; Hsu & Wolf, 1999), 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 and moves away two steps (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 :

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

Here w_i is the outcome of a dominance interaction initiated by agent i ($1 = \text{winning}$, $0 = \text{losing}$). 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:

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

The 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 Table 1). 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 0.001.)

Victory 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.

Indirect perception by ‘Estimators’

During indirect, memory-based dominance perception, agents (*i.e.* Estimators) recognise others individually and remember their personal experience with each of them. Dominance interactions are based on the so-called SKINNIES of Hogeweg (1988) and the risk-sensitive strategy by Hemelrijk (2000b).

Each agent has a ‘mental representation’ of the dominance value of each group-member and of itself, $Dom_{i,i}$ and $Dom_{i,j}$. For instance, in a group of 10 agents, agent number 1 saves its record of its own winning tendency $Dom_{1,1}$ and of each of its group-members 2 to 10 under, respectively, $Dom_{1,2}$, $Dom_{1,3}$, \dots , $Dom_{1,10}$.

Whenever the agent meets another in its PersSpace, it first consults its memory to establish whether it might win or lose a dominance interaction with this particular opponent (the so-called risk sensitive strategy). To this end it performs the same dominance interaction as described in equation (1), but now in its ‘mind’ and based on the ‘mental impressions’ it has of its own dominance and that of the other. After losing this mental battle, it moves away without challenging the opponent and it lowers its opinion about its own dominance and increases the impression it has of that of its opponent following equation (2), but since these interactions occurred only in its mind, they do not change how the opponent thinks about itself and others. After winning such a ‘mental battle’, ego updates its dominance values and it starts a ‘real’ fight. It initiates a real fight by displaying its expectance to win (which in

humans may be reflected by ‘self-confidence’) in the form of its updated relative dominance rank (D_i) and the partner displays its value in return (D_j), that is:

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

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

Note that the ‘expectancy to win’ or ‘self-confidence’ depends on the experience the agent has had with a particular opponent. Thus agents differ in their mental image of the dominance of a certain individual.

The conflict is decided as described under equation (1) for the perceivers, but using D_i and D_j instead of Dom_i and Dom_j .

Updating experiences involves two sets of equations, one equation for the agent itself and one for the opponent and this needs be done also for the opponent.

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

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

$$w_j := abs(w_i - 1)$$

$$Dom_{j,i} := Dom_{j,i} - \left(w_j - \frac{Dom_{j,j}}{Dom_{j,j} + Dom_{j,i}} \right) * StepDom_i$$

$$Dom_{j,j} := Dom_{j,j} + \left(w_j - \frac{Dom_{j,j}}{Dom_{j,j} + Dom_{j,i}} \right) * StepDom_i$$

In what follows, the initiation of a dominance interaction is referred to as ‘attack’ for short.

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, 1985b), aggression of artificial males is designed in the model to be more intense than that 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 (see Table 1), but all individuals of the same sex start with the same ability.

As regards sexual attraction, we study three cases where the urge to approach the opposite sex is either mostly the male’s, or mostly the female’s or equally strong in both sexes. Here, artificial individuals of one sex are attracted to all agents of the opposite sex independent of their identity (implemented as a preferential approach of one step by agents of one sex in the direction of those of the other sex rather than those of the own sex, see encircled part of Fig. 1). To reflect the seasonality of sexual behaviour, attraction operates only during

certain runs (as is the case when tumescence of females is synchronised, such as in species with seasonal reproduction) and it is absent in others. For male attraction to females, we also experiment with asynchronous attractiveness of females, in which case a different female is attractive each subsequent interval (with interval lengths of 5, 13 and 52).

Measurements

During a run, every change in spatial position and in heading direction of each agent is recorded. 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. At intervals of two time-units (400 activations), the overlap between the dominance-hierarchies of VirtualMales and VirtualFemales and the degree of rank-differentiation are measured as follows.

At the start of each run, all VirtualMales received a dominance value that was twice that of VirtualFemales, but during a run some VirtualFemales became dominant over (some or all) VirtualMales. We estimate the degree of dominance of VirtualFemales over VirtualMales 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. Complete female dominance, which implies that all females are dominant over all males, corresponds to an U -value of 25 ($\#females * \#males$). Equal dominance between the sexes occurs if females are on average dominant to half of the males, thus $U = 5 * 2.5 = 12.5$.

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.

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 average 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. Thus clearer centrality of dominants is represented by a stronger negative correlation between the average vector of the direction of others and rank.

To exclude a possible bias brought about by transient values, behaviour is characterised per condition on data collected after time-unit 200.

Significance tests between conditions are omitted if significance is obvious, because differences between average values are large and standard errors are very small. Tests are only performed if differences between conditions are unclear by eye.

Experimental set-up and data-collection

Here, the same parameter setting (Table 1) is used as in former studies (Hemelrijk, 1999a, 2000a).

The present study is confined to a population of ten agents including five VirtualFemales and five VirtualMales.

Several conditions, such as different distributions of food, different diets, different ways to perceive dominance and several ways of sexual attraction, are compared. For each condition (clumping of food (3*), diet (2*), cognition (2*) and sexual attraction (7*)) 40 runs are conducted, resulting in a total of $14 \times 40 = 560$ runs.

Results

Former results: intensity, cohesion and sexual attraction

In former studies, we have shown that female dominance over males increases due to higher intensity of aggression (Hemelrijk, 1999b) and due to stronger cohesion of grouping (Hemelrijk, 1999a) via an increase in the gradient of the hierarchy, *i.e.* the differentiation of the hierarchy measured by the coefficient of variation of the dominance values (Figs 3, 4). Further, it may increase through sexual attraction via more interactions between the sexes (Hemelrijk, 2002a). We will shortly discuss these results before progressing with new material.

As regards the hierarchical gradient, when a hierarchy becomes steeper, this automatically implies larger variation among females and among males in dominance value and therefore, some females will be higher in Dom-value than some males.

Intensity of aggression promotes hierarchical development and female dominance in two ways (Fig. 2A, B, C). If intensity of aggression is high, single conflicts have more impact and thus the hierarchy becomes steeper (via the high StepDom value, see formel 2 and Fig. 3A). This is further strengthened by the more marked spatial structure (Fig. 3B). This structure reduces the size of the dominance reversals, because agents mainly interact with those of similar dominance due to their spatial proximity.

Further, cohesion promotes female dominance (Fig. 2D). It does so through the increased development of the hierarchy (Fig. 4A) and via the higher frequency of meeting among agents and the stronger spatial structure with dominants in the centre (Fig. 4B).

Upon implementing sexual attraction in DomWorld (as an increased tendency of a male to move one step towards a female rather than a male upon encountering someone in its nearView), it appears that sexual attraction automatically increases female dominance over males as a side effect (Hemelrijk, 2002a). This happens even though the degree of cohesion, spatial centrality of dominants and hierarchical differentiation is the same as without

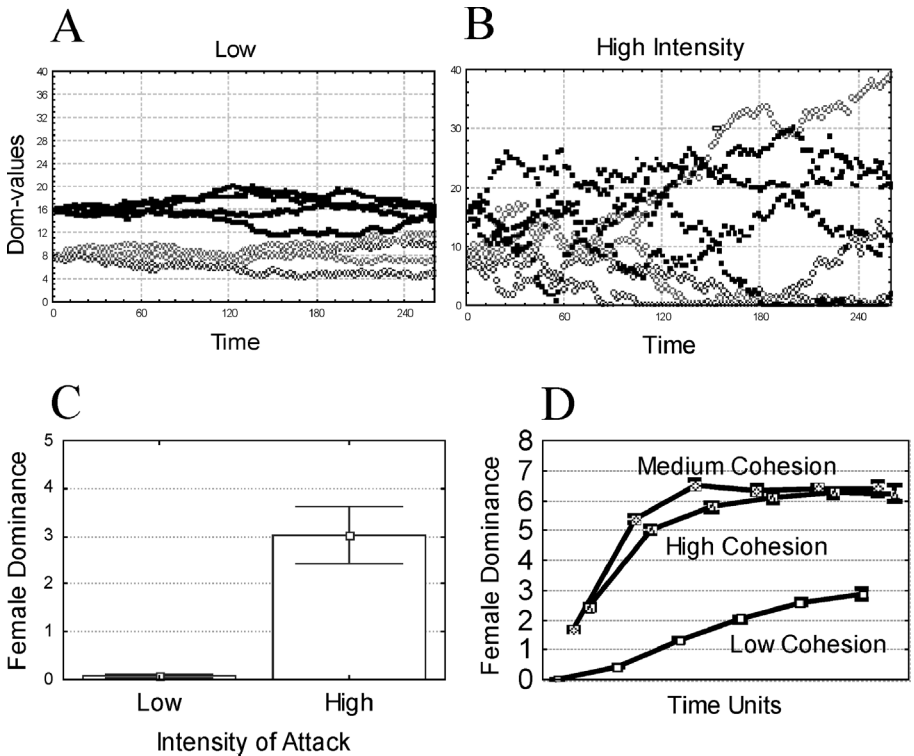


Fig. 2. Female dominance over males, intensity of aggression and cohesion. Development of dominance values over time of 4 males (black dots) and 4 females (open circles) in a single run chosen at random at (A) a low intensity of aggression and (B) a high intensity. Female dominance over males measured by the Mann-Whitney U -test for (C) low and high intensity (mean \pm SE) and (D) three degrees of cohesion.

sexual attraction in this case. It is merely a consequence of the (absolutely and relatively) increased frequency of interaction between the sexes, because through this females may be victorious over males more often during sexual attraction than at other times. This is 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. Thus, a higher percentage of interactions between the sexes will lead to a relatively increased number of victories of females over males and this will accelerate female dominance.

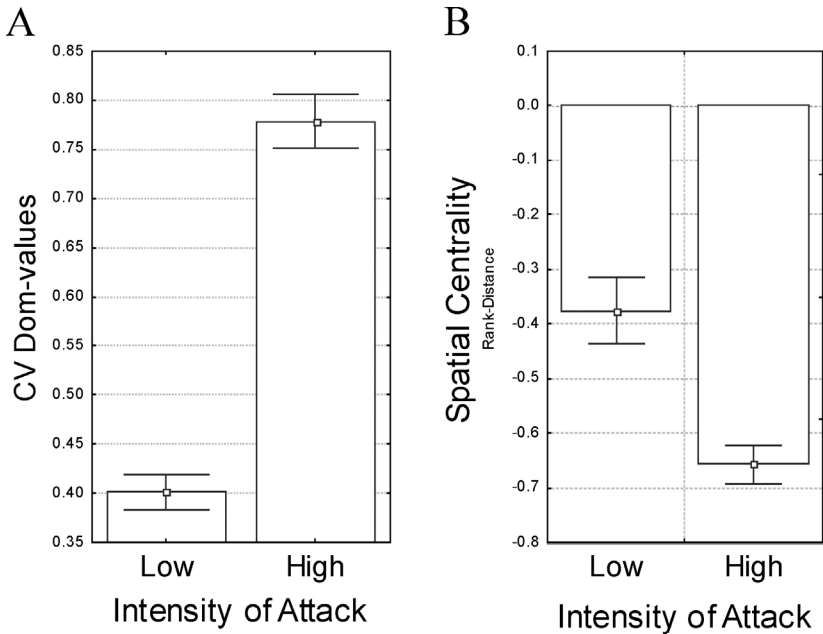


Fig. 3. Effects of intensity of aggression on (A) the hierarchical gradient measured by the coefficient of variation of dominance values and (B) spatial structure (mean \pm SE over 10 runs).

Female dominance does not increase at a low intensity, because the hierarchy of the females is differentiated weakly (see Fig. 2A). Consequently, females that start low in dominance remain low in rank and therefore, more frequent inter-sexual dominance-interaction during sexual attraction does not help to increase their dominance, because their chance of defeating males is almost negligible. Besides, even if females beat males as a rare event, its effect is smaller than at a high intensity of aggression.

New results

Asynchronously versus synchronously attractive females

In some animal species females are sexually attractive (tumescient) synchronously, but in others they are tumescent asynchronously. We compare the effects of both conditions on female dominance. Female dominance over males is approximately similar whether they are attractive synchronously or asyn-

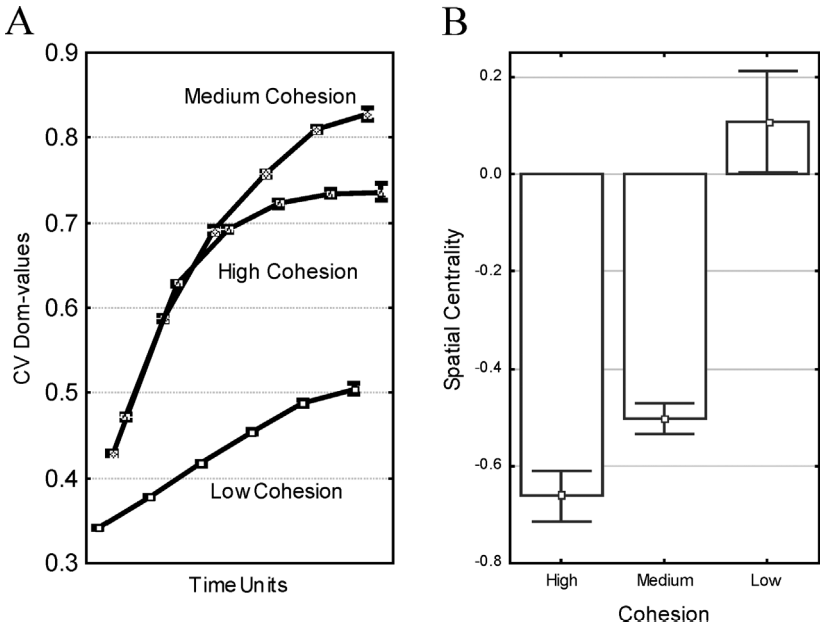


Fig. 4. Effects of different degrees of cohesion (high, medium and low) on (A) hierarchical differentiation and (B) spatial structure (mean \pm SE over 40 runs at StepDom = 1).

chronously (Fig. 5A). The process leading to increased female dominance differs, however, under both conditions. This happens as follows.

If single females are attractive in turn, many males cluster close to a single female. Consequently, the frequency of male-male interactions is increased markedly, but the frequency of interaction between the sexes and among females remains similar to that when females are not attractive to males (Fig. 5B). Due to the higher frequency of interactions among males, the male hierarchy differentiates stronger than without attraction (Fig. 5C) and this causes some males to become subordinate to some females.

In contrast, when females are synchronously attractive, interactions between the sexes are increased significantly, among males they remain similar and among females they are decreased slightly, but significantly compared to the situation without attraction to females (Fig. 5B, Mann-Whitney U -tests among males, $N_{1,2} = 40$, $U = 598.5$, $p = 0.053$, among females $U = 291$, $p < 0.000001$, and between the sexes, $U = 16$, $p < 0.00001$). Thus, if attraction is synchronous, female dominance increases merely due to the higher frequency of interactions between the sexes. This leads to more op-

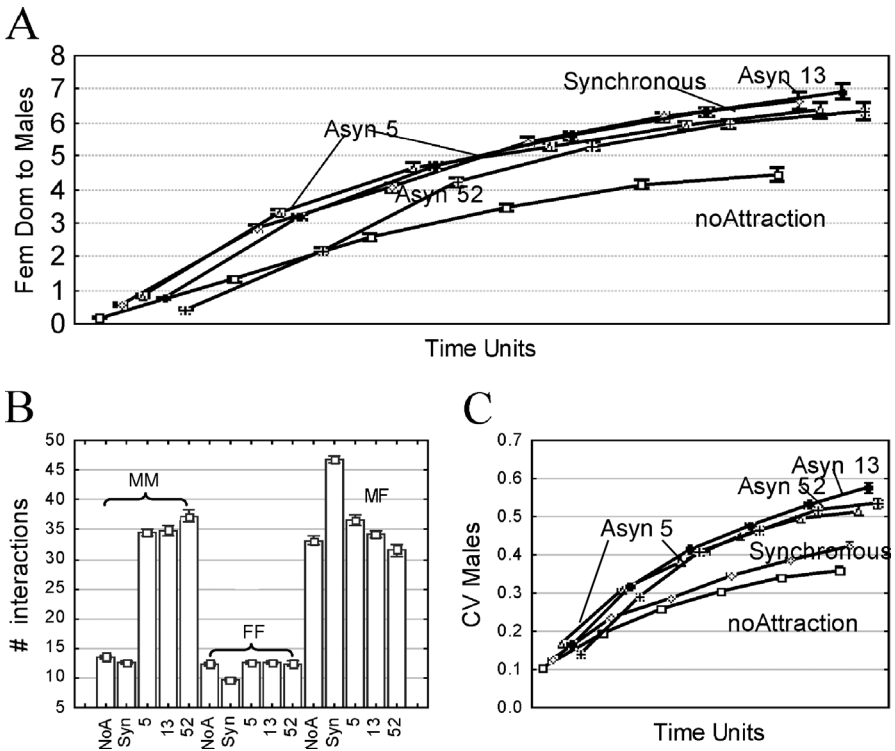


Fig. 5. Mean and SE's (over 40 runs) of effects of sexual attraction to females that are attractive synchronously or asynchronously on (A) female dominance (measured by the Mann-Whitney U -test), on (B) the frequency of interactions among males, among females and between the sexes and on (C) the differentiation of the male hierarchy (coefficient of variation of dominance values).

portunities for low ranking females to win unexpectedly from high-ranking males. Once this happens dominance values of females increase by a larger amount than if females defeat lower-ranking agents.

Note that all these results remain similar if we correct for the number of interactions for the different conditions by running the settings for sexual attraction shorter so that it comprises the same number of interactions as the situation without attraction.

Mutual and unidirectional attraction to the opposite sex

Only rarely attraction is reversed, *i.e.* females are attracted to males rather than the other way around and more often, both sexes are mutually attracted

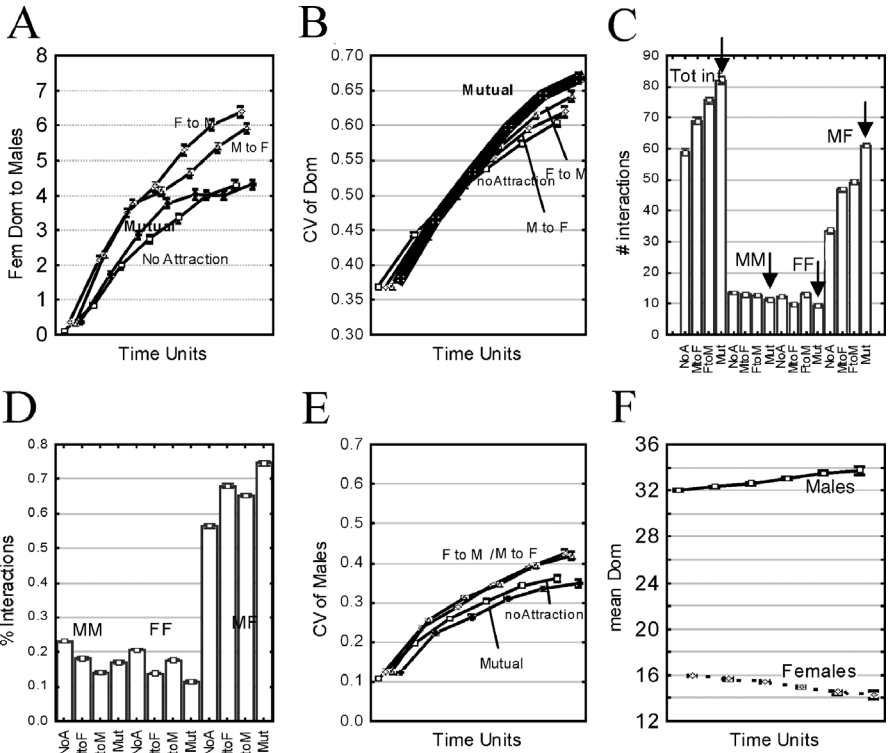


Fig. 6. Mutual and unidirectional sexual attraction and their effects on (A) female dominance (measured by the Mann-Whitney *U*-test, mean \pm SE), (B) hierarchical differentiation, (C) frequency of interactions in total, among males, among females and between the sexes (mean \pm SE), (D) percentage of total number of interactions, (E) hierarchical differentiation among males, and (F) mean dominance of males and of females during mutual attraction (mean \pm SE).

to each other. The effect each form of sexual attraction has on female dominance is shown below: female dominance is increased (compared to that during the absence of sexual attraction) only if one sex is attracted to the other (be it males or females), but not if both sexes are mutually attracted (Fig. 6A). This is remarkable; because during mutual attraction the hierarchical differentiation is similar to that during unidirectional attraction (Fig. 6B) and the frequency of aggression in total and between the sexes is highest (Fig. 6C), which usually stimulates female dominance.

However, during mutual attraction female dominance is not strengthened, because interactions among males as well as among females appear

to be reduced compared to what happens without such attraction (Mann-Whitney U -test, among males, $U = 360$, $p < 0.0001$, among females, $U = 267$, $p < 0.0001$), whereas during unidirectional attraction intra-sexual interaction is reduced less. It is not reduced compared to the situation in which attraction is lacking (in case of female attraction to males: Fig. 6D, Mann-Whitney U -test, among males, $U = 656.5$, $p = \text{NS}$ and even increased among females, $U = 545$, $p = 0.14$) or it is reduced only among females (male attraction to females: among males, $U = 598.5$, $p = \text{NS}$, among females, $U = 291$, $p < 0.0001$). Consequently, due to the strong reduction in intra-sexual interactions, the male hierarchy differentiates least during mutual attraction (Fig. 6E). Therefore, males do not develop low dominance values, but remain high in dominance and thus, they will usually defeat females. Further, the high frequency of interactions between the sexes reinforces their differences only and on average they grow further apart: male dominance increases and female dominance decreases (Fig. 6F).

This is different from what happens during unidirectional attraction. During unidirectional attraction (Fig. 6C), inter-sexual interactions are less frequent than during mutual attraction (Mann-Whitney U -test, male attraction to females $N_{1,2} = 40$, $U = 8$, $p < 0.0001$, female attraction to males $U = 22$, $p < 0.0001$) and interactions among individuals of the same sex (particularly among males) are more frequent than during mutual attraction either among males only (Mann-Whitney U -test, male attraction to females, among males $N_{1,2} = 40$, $U = 556$, $p = 0.019$, among females, $U = 785$, $p = 0.89$) or among males as well as females (female attraction to males, among males, $U = 496.5$, $p < 0.005$, among females, $U = 147$, $p < 0.0001$), as is also clear from the percentage of interactions within and between the sexes of the total number of interactions (Fig. 6D). This arises, because individuals of the sex that is attracted to the other meet each other close to their source of attraction during unidirectional attraction and therefore, interact often among themselves. Consequently, some males sink low in dominance and some females rise so that inter-sexual interactions may incidentally lead lower-ranking females to win from higher-ranking males and this increases female dominance.

Thus, for females inter sexual interactions are helpful to increase female dominance only if females already have a certain probability to defeat males anyhow. This likelihood is enhanced if there are more interactions among individuals of the same sex.

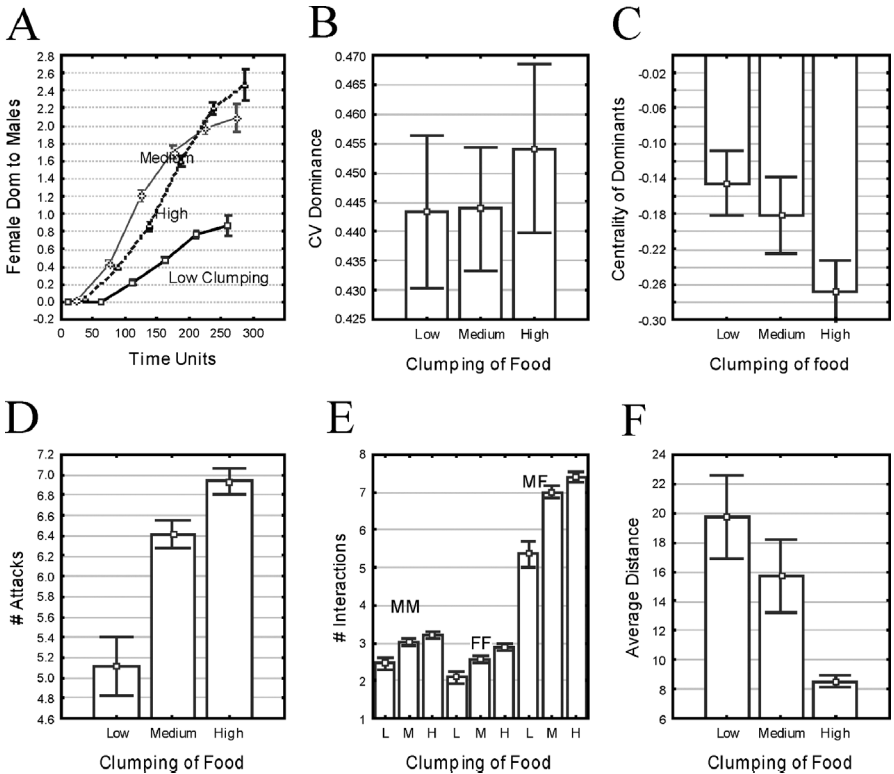


Fig. 7. Degree of clumping of food and (A) female dominance measured by the Mann-Whitney U -value, (B) the gradient of the hierarchy, (C) spatial centrality of dominants (D) total frequency of interaction/aggression, (E) number of interactions within and between the sexes, (F) average distance among group members (mean \pm SE).

Note that all these results remain similar if we correct for the number of interactions under different conditions by running the settings for sexual attraction for the same number of interactions as take place without attraction.

Food distribution and diet

The effect of cohesion is visible in EcoDomWorld where agents group as a consequence of being attracted to the same food source. Female dominance is stronger in groups of high and medium density than in groups of a low density, *i.e.* groups that are loose (Fig. 7A). This can be explained, because the gradient of the hierarchy is slightly steeper for higher degrees of clumping although variation is huge (Fig. 7B) and spatial structure is stronger (Fig. 7C).

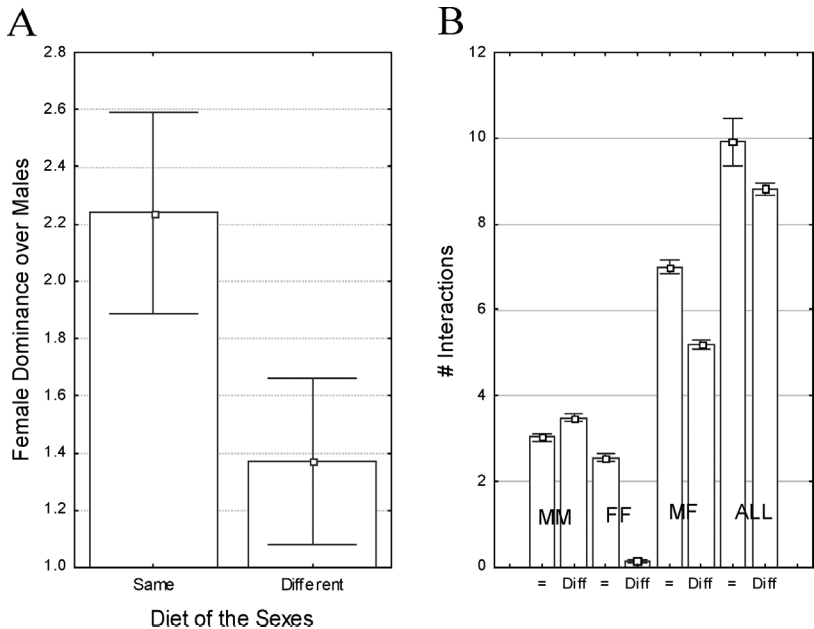


Fig. 8. Effect of diet differences between the sexes on (A) female dominance over males, and (B) number of interactions per sex, between the sexes and in total. Same: both sexes have same diet. Different: females eat insects also, but males do not.

Further, the frequency of aggression in total (Fig. 7D) and the frequency of interactions (aggressive and neutral) between the sexes is higher (Fig. 7E) due to the smaller average distances among agents (Fig. 7F).

Further, the similarity or difference in diet of both sexes influences female dominance. Suppose that the sexes differ in their diet and males eat fruit only (about which they compete), but females prefer to eat insects rather than fruits. Note that about insects there is no competition, because they cannot be monopolised. In this case, female dominance decreases (Fig. 8A) due to a lower frequency of interactions among females, between the sexes and in total (Fig. 8B).

Dominance perception: directly visible or memory-based

Also, the way in which dominance is perceived (directly or via memorised experiences) influences female dominance: it is higher among the cognitive simpler agents, the Perceivers (Fig. 9A). Female dominance increases faster

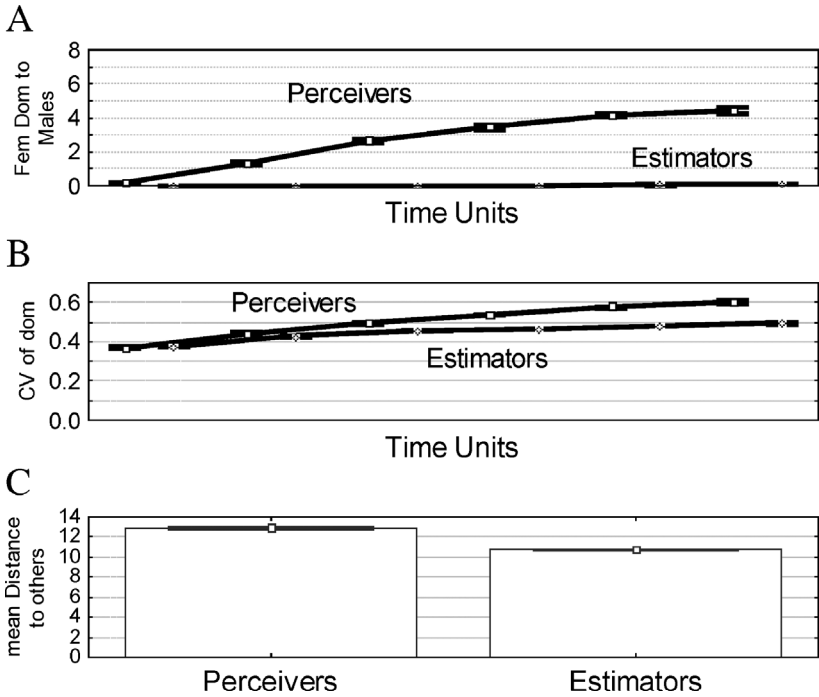


Fig. 9. Effects of perception of rank (directly by Perceivers and through memory by Estimators) on (A) female dominance (Mann-Whitney U -value), (B) hierarchical differentiation, and (C) average distance among agents (mean \pm SE).

among Perceivers than Estimators, because every change in Dom-value is directly visible to everyone. Among Estimators, however, in order to know that a female has increased her dominance, each Estimator-agent needs to interact with her personally. Thus, since individual Estimators vary in the experience they have with each group member, they acquire different opinions about the dominance-value of each other. Therefore, the gradient of the hierarchy is weaker for Estimators than Perceivers (Fig. 9B). Different opinions may cancel each other out as reflected in the average shown in the figure.

Note that the development of female dominance and the hierarchy is slower among Estimators even though their frequency of interactions is greater per time unit due to their closer aggregation (Fig. 9C). Note that Estimators remain closer together due to the weaker development of the hierarchy.

Discussion

Theoretical issues

The aim of the present paper has been to develop a starting point for a theory to explain the unexpected occurrence of female dominance over some males in typically male-dominant species. For this we have extended DomWorld with agents of two dominance classes (Hemelrijk, 1999b). In DomWorld, we have shown that female dominance increases if there is an increase in intensity of aggression (Hemelrijk, 1999b), cohesion (Hemelrijk, 1999a), and degree of clumping of food. Further, female dominance increases if both sexes have the same rather than a different diet, if one of the sexes is attracted to the other, and if agents perceive each other's dominance directly rather than from memorised experiences. Although in these cases female dominance over males increases, it remains a weak form of co-dominance, because on average each female dominates less than half of the males (*i.e.* the U -values remain on average below 12.5).

The mechanisms by which female dominance over males increases are, on the one hand, factors that lead to a stronger differentiation of the hierarchy per sex (such as direct perception of dominance, a higher intensity of aggression, a clearer spatial structure, more interactions in total and specifically more intra-sexual interactions) and, on the other hand, factors that make the values of both sexes more equal (such as a higher frequency of interactions between the sexes does if the dominance values of both sexes are not too different).

Remarkably, mutual attraction (in contrast to unidirectional attraction) does not increase female dominance, although it increases the total number of interactions. This arises, because mutual attraction causes a decrease in the number of intra-sexual interactions. Consequently, low-ranking females almost exclusively meet high-ranking males, and therefore, they have no chance to defeat them at all. In contrast, if they were meeting other low ranking individuals more often, this might increase their dominance to the extent that they may benefit from inter-sexual interactions by defeating males. This finding is similar to what happens in egalitarian societies (Hemelrijk, 2002a). Here females do not benefit in dominance from a higher frequency of inter-sexual interactions either, because their dominance is too low. This is low because due to low intensity of aggression their hierarchy hardly differentiates despite a high frequency of interaction among females.

Unexpectedly, if dominance is perceived directly (by body posture, smell or other signs) implying little cognition, females become dominant faster than if dominance of others is learned from experiences with others individually and cognition is more sophisticated. Thus social change is hindered by cognition rather than stimulated by it. In other words, a directly reactive system adapts faster to a new environment than a system does by learning (and, of course, genetic changes by mutation are slower again). The impediment to change of learning may remind us of the conservative influence that traditions may have on human behaviour.

Obviously, we have discovered a number of variables for which female dominance over males increases. Note however, that female dominance never went beyond weak co-dominance with males (U -value remained < 12.5). Further, we only studied the model for an equal sex ratio and without that (low-ranking) agents have the possibility to migrate. What happens if sex ratio's are unequal and agents are allowed to migrate, we will report on in future. Further, in various animal species, such as 'female-bonded' primates (Wrangham, 1980) in which females remain in their natal group for life and where males migrate at adulthood, females are attracted to females also. Upon studying accordingly simultaneous attraction to females by males and females in DomWorld, female dominance appears to resemble that during unidirectional attraction. The number of interactions among females is higher, however, and between the sexes is lower than without specific attraction.

Further, DomWorld obviously does not reflect the complete behaviour of real monkeys. Instead, it merely reflects certain behavioural processes: those of grouping and competition. EcoDomWorld adds to this a food distribution and feeding behaviour.

Empirical issues

Despite the model's simplicity its results have biological relevance, because the behavioural rules of the agents are based on those apparent in real animals and the collective patterns resemble those of real monkeys. We will illustrate this for the effects of intensity of aggression, cohesion and food distribution.

For instance, regarding intensity of aggression: aggression of despotic macaques is more intense and females remain dominant to sub-adult males longer than among egalitarian species (Thierry, 1990a).

Further, regarding group cohesion in different species of chimpanzees (*i.e.* bonobos and common chimpanzees), groups of bonobos are more dense (Stanford, 1998), and female dominance in bonobos is greater than in common chimpanzees (both species are similar in sexual dimorphism of body size). This may happen via a higher total number of interactions and also via a higher percentage of inter-sexual interactions among bonobos, because groups of bonobos more often contain both sexes than those of common chimpanzees do. Greater dominance over males in females of bonobos than females of common chimpanzees is usually attributed to a higher tendency to communally attack males among females of bonobos than common chimpanzees (Parish, 1994). However, this has not been shown statistically and if it would be found, a higher frequency with which females support each other against males may also be a consequence (rather than a cause) of females being higher in dominance than males. For, if females are dominant to males already, they will perceive less risks to attack males and therefore, they will do so more easily (Hemelrijk, 2002b).

More interactions between individuals of both sexes, may increase not only the dominance of females, but also that of low-ranking males that are maturing: During the birth season maturing males were subordinate to adult females, but during the sex season they became dominant. In the next birth season they fell back again to subordination (Johnson *et al.*, 1982). In line with DomWorld, increased dominance of subadult males during the sex season may be due to their higher frequency of interaction with higher-ranking adult females.

Regarding clumping of food sources this is supposed to lead to contest competition and in turn, to make societies despotic in real animals (*e.g.* see van Schaik, 1989). Similarly, if females prefer to feed on insects this reflects scramble competition and is associated with a flatter hierarchy in real animals too. Obviously, the sexes differ in more aspects than mentioned here (for instance, females care for their offspring whereas males do not), these differences will tend to decrease contact between the sexes and thus decrease female dominance over males.

These findings lead to hypotheses that are testable in real animals. In real animals, however, usually several variables change at a time and it is often impossible to study effects of single variables. For instance, in one and the same group intensity of aggression differs over time depending on the season by being higher during the sex season (Drickamer, 1975). Thus,

following DomWorld, we would expect greater female dominance during the sex season for two reasons, because sexual attraction and intensity of aggression are increased both.

Further, it is of interest to study the effect of various distributions of food on female dominance. Note that here again, a higher degree of clumping of resources may influence both: compactness of grouping and intensity of aggression. Also, one may compare related species with synchronous tumescence and with asynchronous tumescence, but, for instance, in macaques this is often associated with differences in intensity of aggression, because species with low intensity of aggression, such as *Macaca tonkeana*, show non-seasonal asynchronous tumescence, whereas those with high intensity of aggression, such as *Macaca mulatta*, are tumescent synchronously (Thierry, 1997). There is one intermediate case of Barbary macaques (*Macaca sylvanus*); its society is relatively egalitarian and tumescence is seasonal.

Female dominance is important for several reasons: it limits the extent to which males may be able to coerce females (Smuts & Smuts, 1993). This is of interest in the context of sexual conflict, *i.e.* when the wishes of both sexes are incompatible (Krebs & Davies, 1997). DomWorld shows that if males are the ones that mainly initiate sexual approaches females may become 'protected' against males automatically by their increased dominance, without that we need invoke any separate mechanisms. Further, the degree of female dominance is important in a sociological context of 'emancipation'. The results of the model may apply to 'emancipation' not only between males and females but between any classes of different dominance, such as the young and the older, students and faculty etcetera.

In sum, with the help of models like DomWorld, we may be able to learn more about the dynamics of female dominance over males in species in which males are typically dominant.

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