Self-organised dominance relationships: a model and data of primates

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Self-organised dominance relationships: a model and data of primates

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1) Introduction

Aggression and dominance

Conflicts among individuals are common in the animal kingdom; they arise whenever animals live in groups. Conflicts can originate regarding access to specific resources (such as food, mates, or territories: *e.g.* Wilson, 1975; Packer & Pusey, 1982; Clutton-Brock, 1989; van Schaik, 1989; Anderson, 1994); yet they also occur without a specific cause (Pusey & Packer, 1997). Over time, dominance relations with constant winners and losers develop between group members. Although the existence of 'dominance' has been criticised as an artificial construct, and hierarchies have been interpreted as a merely pathological stress response in captivity (Rowell, 1974), today the existence of dominance hierarchies in the animal kingdom is undisputed.

Such dominance hierarchies have been documented in many group living species observed in the field and in captivity (Wilson, 1975; Drews, 1993). However, what 'dominance' really is (the 'concept of dominance') has been discussed extensively in the last decades, and various indicators of dominance have been proposed. For example, the dominance status of an individual could be derived from having prior access to food, from the amount of grooming received or rejected, or from the number of victories in agonistic interactions (*cf.* Drews, 1973). However, applied to one and the same group of animals, different indicators of dominance may yield very different hierarchies, so that these indicators of dominance not always appear to be correlated with each other (*e.g.* Drews, 1973; Noe *et al.*, 1980; Lanctot & Best, 2000; Vervaecke *et al.*, 2000a). Thus, the suitability of an index may depend on the context, for instance, the species that is examined, the observer, or the research question.

After reviewing various interpretations of dominance, Drews (1993) describes the 'essence of dominance' as being the consistent outcome of fights between two individuals, where the winner is considered dominant, and the loser subordinate (Drews, 1993, p. 308). This reflects the notion that dominance is a relation between two individuals, rather than an absolute trait (Bernstein, 1981; Francis, 1988; Drews, 1993). Accordingly, in this thesis 'dominance' will be referred to as the superior fighting capacity of one individual over another.

A main function of dominance relationships is considered to be a way to circumvent conflicts, thus reducing the frequency of aggression and the associated risks (Maynard Smith, 1982; Issa & Edwards, 2006) this is important because escalated, aggressive fights bear a high risk for the individuals involved. The fighters may become injured (*e.g.* Neat *et al.*, 1998), they lose time and energy that could be spent on other activities (*e.g.* foraging), and individuals distract their attention from the environment, hence are prone to being attacked by predators (Jakobsen *et al.*, 1995). However, if subordinate individuals concede to dominant ones without aggression, escalated fights are avoided. Studies indeed show that in artificially composed groups, the initial frequency of aggression is high until a stable dominance hierarchy is established and then it becomes low (Schjelderupp-Ebbe, 1922; Pagel & Dawkins, 1997). Thus, in many species, dominance hierarchies constitute a kind of 'ordering force'.

With dominance being such an omnipresent phenomenon in nature, it is important to understand what makes an individual dominant. Studies show that the dominance of an individual may be influenced in two ways. First, it may depend on asymmetries that are fixed at the time of establishing the dominance relationship (such as age or body size). However, other studies draw a more complex picture: individuals may obtain entirely different ranks if they are repeatedly reassembled in groups (Bernstein & Gordon, 1980; Dugatkin *et al.*, 1994; Chase *et al.*, 2002). This indicates that in addition to fixed traits, dominance depends on factors such as prior fighting experiences: winning a fight increases the likelihood to win again in future fights, and *vice versa* for the loser. Such a winner-loser effect has been demonstrated in many animal species (Hsu *et al.*, 2006). Indeed, models including winner-loser effects show that stable dominance hierarchies can emerge among individuals even if they are all identical at the start (Bonabeau *et al.*, 1996; Van Doorn *et al.*, 2003a; 2003b; Hemelrijk & Wantia, 2005). These findings point out that for the understanding of dominance, models may play an important role.

Regarding the costs and benefits of being dominant, there are contradictory findings. Some studies find large asymmetries between high and low ranking individuals. High ranking individuals obtain the benefits, like a larger share of resources, and consequently have a higher lifetime reproductive success compared to low ranking group members (*e.g.* Clutton-Brock *et al.*, 1984; Ellis, 1995; Pusey *et al.*, 1997; Klinkowa *et al.*, 2005). Low ranking individuals receive smaller shares of food, and may often be unable to reproduce at all (*e.g.* Ulbrich *et al.*, 1996). If such asymmetries occur, the question arises why subordinate individuals accept their fate, being without hope for reproduction. A recent game theoretical approach suggests that subordinates would have to fight so many escalated fights to gain high ranks that the associated cost would be unbearably high (Van Doorn *et al.*, 2003a; 2003b). However, other empirical studies find no, or only weak, asymmetries in cost and benefits between high and low ranking individuals. Reproductive success is distributed evenly among all group members, or may even be biased towards low ranking individuals (*e.g.* Ellis, 1995; Verhulst & Salomons, 2004; Spritzer *et al.*, 2006), and maintaining a high rank may be associated with considerable costs (*cf.* Pusey & Packer, 1997).

However, not only individuals establish dominance relationships; they may also exist between subgroups of individuals, *i.e.* classes of individuals such as old and young, males and females, or different personality types. Furthermore, they may be found between entire groups and species. In terms of dominance relationships between the sexes, males may dominate females (Meder, 1985; Feistner, 1989), females may dominate males (Digby & Kahlenberg, 2002; Waeber & Hemelrijk, 2003), or both sexes may be co-dominant to various degrees (*e.g.* Vervaecke *et al.*, 2000b). Dominant males are able to coerce females to mate with them (Clutton-Brock & Parker, 1995), while dominant females can refuse forced copulations (Smuts & Smuts, 1993), or gain feeding priority (Overdorff *et al.*, 2005). Besides sex, one may also distinguish individuals on basis of their personality type, and observe dominance relations between them. Differences in personality type means that individuals of a single species differ from each other in a number of correlated traits. Personality types have been described in many species, ranging from invertebrates to the great apes (Gosling, 2001; Sih *et al.*, 2004a; 2004b; Réale *et al.*, 2007). In particular, a ’bold’ and a ‘cautious’ personality type have been distinguished. Bold individuals have a low attack latency and high levels of aggression, while cautious personalities have a high attack latency and low levels of aggression (Koolhaas *et al.*, 1999). Dominance relations between these personalities have, for example, been described in birds (Verbeek *et al.*, 1999; Carere *et al.*, 2001) and fish (Dijkstra, 2006).

In addition, dominance relations may exist between groups, where subordinate groups are displaced from feeding sites (Hauser *et al.*, 1986; Dittus, 1987; Takahata *et al.*, 1994; Sugiura *et al.*, 2002). Species may, finally, dominate others species by dislodging them from feeding sites (Eccard & Ylönen, 2003; French *et al.*, 1989; Sushma & Singh, 2006).

Individual-based models and self-organisation

One type of model that enjoys growing attention in the simulation of social systems are the so-called agent-based, or individual-oriented, models[1]. In individual oriented models, artificial (mostly virtual) individuals interact with each other and with the environment according to predefined rules. Individuals are modelled as discrete units that may differ from each other. For instance, and depending on the model in question, in traits such as age, power, capabilities to deal with different situations, degree of saturation, etc. This constitutes a fundamental difference to, for example, ordinary differential equation models that average over many individuals, and that do not incorporate individual differences. One essential feature of individual-oriented models is that global patterns arise due to local interactions among individuals that do not have global knowledge.

Early individual-oriented models were presented by Hogeweg and collaborators as a new heuristic (Hogeweg & Hesper, 1986; 1991). In ecological sciences, individual-oriented modelling today is widely applied (Grimm *et al.*, 2005), while in the social sciences and zoology they are still waiting for the recognition of a broad audience (Bankes, 2002; Hemelrijk, 2002d).

Individual oriented models have a number of advantages. First, such models provide a natural description of a system, because each individual with all its unique characteristics is represented separately. This allows focusing on what researchers of sociality are most interested in: the interactions among individuals (Bankes, 2002, p. 7200). Second, individual-oriented models are flexible, since they may easily be extended by adding further individuals, or levels of complexity. Third, information is available at many levels (single individuals, types, the entire system etc.). Fourth, together with other models they share the advantage of providing data *ad libitum*, *e.g.* many repetitions and experiments can be simulated. Fifth, by analysing a system from the bottom up, rather than from top down, they provide an "*unconventional*" view of, for instance, the evolution of complexity in biotic systems (Hogeweg, 1989). Such a bottom-up approach helps to overcome the difficulties of studying social systems that often are too complex for a top-down approach (like traffic flow, or stock markets).

Flocking models that are based on the bird-oids ('boids') of Reynolds (1987) are an example that nicely illustrates this phenomenon. In these models of bird flocks, there is no global leader that guides the group or keeps individuals together. Rather, single individuals only follow three local rules of: 1) Avoiding collisions with others close by, 2) Alignment with neighbours at intermediate distance, and 3) Grouping with individuals that are further away. From these simple rules swarms emerge: Artificial flocks turn and move in patterns that closely resemble natural flocks of birds, and schools of fish (Huth & Wissel, 1992; Hemelrijk & Kunz, 2005).

Another well-known example of an agent-based model is the socio-economic model "Sugarscape", designed by Epstein & Axtell (1995). In Sugarscape, agents live in a two-dimensional world, where they move around and harvest sugar, on which they feed. The sugar resources at one patch may be depleted, and only re-grow over time, so that sugar is not homogeneously distributed over the world. In a series of experiments the complexity of agents is gradually increased, and a skewed accumulation of wealth (*i.e.* an agent's sugar reservoir), migration, and cultural dynamics emerge. The resulting data and phenomena can be analysed like empirical data. Thus, agent based models can be used for experiments *in silicio* (Epstein & Axtell, 1995).

Common to both examples is that single individuals strictly act according to local rules. Still they show behaviour that appears sophisticated. This emergence of a pattern is

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[1] The terms 'agent based' and 'individual oriented' will be used synonymously throughout this thesis.

called self-organisation. Self-organisation can be defined in several ways; one recent definition is:

> *"Self-organization is a process in which pattern at the global level of a system emerges solely from numerous interactions among the lower-level components of the system. Moreover, the rules specifying interactions among the system's components are executed using only local information, without reference to the global pattern."* (Camazine *et al.*, 2001, p. 8)

Indeed, Bonabeau (2002) concludes that it is mainly the ability to deliver such emergent phenomena that makes individual-oriented models so powerful.

Of all animals, including humans, those best studied with the help of models are probably social insects (*cf.* Camazine *et al.*, 2001). The knowledge about raiding patterns of army ants, the construction of termite mounds, the logistics of pollen and honey in honeycombs, decision making, and task allocation in insect colonies has been greatly extended with the use of such models. Studies of social insects deliver impressive evidence that self-organisation is not an artefact of models, but that it works in real animals, too (Camazine *et al.*, 2001; Boomsma & Franks, 2006). In addition, these advances in the understanding of social insects have been applied to improve optimisation algorithms (Bonabeau *et al.*, 1999) and business solutions (Bonabeau & Meyer, 2001).

However, the complexity of social life is extraordinary not only among insects, but also among primates. Recently, macaques have been suggested to constitute a 'model for social organisation' (Thierry *et al.*, 2004), because the circa 20 species of the genus *Macaca* are closely related, yet they differ considerably in their social behaviour. These differences in behaviour must thus stem from few genetic differences, and they cannot satisfactorily be explained by ecological or environmental conditions, either (Thierry, 2000). This leaves much room for other origins of diversity, such as differences in experience, or self-organisation (Hemelrijk & Wantia, 2005). Due to this variability in behaviour, and together with the fact that the amount of studies published on species of the genus *Macaca* is unmatched in primates, macaques represent a unique source of inspiration not only for empirical research, but also for theoretical biologists interested in the understanding of sociality.

The models DomWorld and GroupWorld

In the present thesis social organisation is studied with the help of two models, called DomWorld and GroupWorld (derived from DomWorld); both are inspired by primates, and in particular by macaques. Both models are very simple and only incorporate grouping and fighting. Dominance relations within groups are explored between categories of individuals (sexes and personality types), and further, it is studied how group composition and dominance style affect the performance of groups in inter-group competition. In the models, dominance is not associated with a fixed trait, but instead it is operationalised as the fighting capacity of an individual, indicated by a variable called dominance value. The dominance value of an agent increases after victories and decreases after defeats (winner-loser effect, above). This effect is self-reinforcing, so that dominance values differentiate in a damped positive feedback, and stable hierarchies emerge (Hemelrijk, 1999d). The main algorithm to describe this self-reinforcing effect is based on detailed observations of a bumblebee colony (Honk & Hogeweg, 1981).

Individuals compete over resources that are not specified in the model; winning could increase physical well-being if one thinks of food items, or the winner may increase its confidence. Thus, a high dominance value may stand for an individual that is physically very strong, or it may be an individual of moderate strength, but with high levels of confidence.

Likewise, a low dominance may result if a physically strong individual has very low confidence, so that it performs badly in a fight (just as A-league soccer teams may lose against highly motivated B-league teams). Since on average individuals with higher dominance values win over those with lower values, dominance is a specific relationship between these two individuals (Bernstein, 1981; Francis, 1988; Drews, 1993).

DomWorld was initially used by Hemelrijk (1996a) to explain patterns of reciprocal grooming in chimpanzees in a parsimonious way. Later, by changing a single parameter alone, namely the intensity of aggression (Hemelrijk, 1999d), the model delivered patterns that emerged through self-organisation, and that resemble those of egalitarian and despotic macaques (Thierry, 1990a; Thierry, 2000). This supports the notion that in closely related species like macaques, large differences in behaviour may not require large genetic differences, but that they may emerge via epigenisis and self-organisation (Thierry *et al.*, 2004).

In subsequent studies, DomWorld has been used to develop further hypotheses regarding the evolution of primate dominance style (Hemelrijk, 2002c), and the emergence of the tolerance of primate males towards females (Hemelrijk, 2002a). Being a minimalist model without assumptions that confine it to a primate context, the model also delivered insight into phenomena of group living animals in general, such as the occurrence of spatial structure without assuming that individuals follow a centripetal instinct (Hemelrijk, 2000b), the differentiation of the behavioural profile of individuals without initial asymmetries (Hemelrijk & Wantia, 2005), or even functioned as a test of various methods to extract linear dominance hierarchies from interaction matrices (Hemelrijk *et al.*, 2005a). Personality types could be simulated via attack strategies in the model (Hemelrijk, 2000b; Hemelrijk & Wantia, 2005).

However, DomWorld only simulates agents of a single group, while in real life groups often closely interact with neighbouring groups. Such inter-group competition may also affect the social life within groups (*cf.* van Schaik, 1989). Therefore, a new model called GroupWorld also has been developed that simulates several groups, and interactions of individuals within as well as between groups. The algorithm for the interactions among individuals is identical to the one in DomWorld, except that in inter-group fights there is no winner-loser effect. For reasons of computational efficiency, there is no explicit representation of space within groups. The spatial structure that may arise in DomWorld due to self organisation (Hemelrijk, 1999d) is accounted for by an algorithm that selects interaction partners. In egalitarian groups, where no spatial structure emerges, interaction partners are selected at random, while in despotic groups that are spatially organised individuals are more likely to be selected for encounters if they have similar dominance. Regarding inter group fights, in real primates high ranking individuals are more likely to participate (Cheney, 1987; Perry, 1996; Kitchen *et al.*, 2004; Cooper, 2004; Majolo *et al.*, 2005). Apparently, high ranking individuals use the ‘power’ that they have within a group also in fights against other groups. Therefore, the dominance values of individuals within groups are also used in fights between groups.

The aim of DomWorld and GroupWorld is to reveal underlying mechanisms of the development of dominance hierarchies. Therefore, they are designed as simplified images of reality. This follows the approach of Axelrod, who argues that models that aim to address fundamental processes should be judged by their fruitfulness, not by their accuracy, and that realistic representation of many details would be unnecessary and even counterproductive. Thus, the purpose of such individual oriented models becomes aiding intuition (Axelrod, 1984, pp. 4, 6).

This thesis

This thesis will follow the approach of Axelrod, using simple models to study primate societies from a new perspective. The aim is to deliver new, proximate explanations, and to direct attention to mechanisms that may not become salient when considering social life in a socio-behavioural framework.

Part I: Female dominance

Part I (chapters 2 – 5) is dedicated to the phenomenon of female dominance, *i.e.* the fact that females may be dominant over some or all males. Female dominance over males has been investigated and reported on mainly in *lemuriformes*, possibly because there it is most conspicuous (in some lemur species, all females dominate all males). However, to a lesser extent, female dominance also occurs in other primate species, but this has never been quantified systematically. This is surprising, because it may have far-reaching consequences for group life: females may receive feeding priority (Waeber & Hemelrijk, 2003), for example by leading the group to food (Erhart & Overdorff, 1999; Overdorff *et al.*, 2005), or by displacing males (Furuichi, 1989). In addition, dominant females may be able to control party composition and mating opportunities (reviewed for bonobos by Parish & de Waal, 2000), or reject attempts of coerced copulations (Smuts & Smuts, 1993). **Chapter 2** provides for the first time an overview of the degree of female dominance in a wide range of primate species. This is accomplished by applying a new measure of female dominance to available empirical studies. The measure is based on the average dominance index (Hemelrijk *et al.*, 2005a) and is easy in computational terms. Furthermore, it takes into account the relation between all group members, which former measures do not incorporate. Therefore, the use of the new measure is advocated. This study shows that in primates, the degree of female dominance varies considerably not only between species (from no female dominance to complete female dominance), but also within species (*e.g. M. mulatta*).

In particular, the intra-specific variation of the degree of female dominance questions the assumption that it could merely be a species-specific trait. However, little is known about the origin of female dominance. Since experiments regarding such complex phenomena as occurrence of female dominance are hardly feasible in real primate groups, here simple models are used to develop hypotheses as to how females may become dominant over males. Most notably, there appears evidence for the correlation of female dominance and the proportion of males in real primate groups (chapters 4 & 5).

In **Chapter 3**, it is shown in the model that a number of factors that previously had not been considered in this context (like food distribution, sexual attraction, and group cohesion) may have an influence on female dominance. In particular, it appears that a high frequency of inter-sexual encounters may increase female dominance, because females that by chance win against males may rise a lot in rank. Also, female dominance is high if the development of the dominance hierarchy is strong, because then some strong females may come to outrank the weakest males (*cf.* Hemelrijk, 1999d).

Aggression between sexes has been observed, but literature on dominance relationships usually concerns either males or females. This may originate from the notion that the sexes compete for different resources (males for mates, females for food, Trivers, 1972), and that consequently competition between the sexes has less influence on dominance than competition among members of the same sex. Therefore, the winner-loser effects could be stronger in intra-sexual than in inter-sexual fights. Yet this has never been investigated. A reason for this may be that it is impossible to estimate the impact that the outcome of a single fight has on the dominance in real animals. **Chapter 4** examines if the winner-loser effect is of different importance in intra-sexual and inter-sexual encounters by switching the winner-loser effect in inter-sexual fights on and off. Here it can be shown that inter-sexual encounters increase female dominance in the model. In addition, this study suggests a method to estimate the importance of inter-sexual self-reinforcing effects in real primates. When this new procedure is applied to empirical data of real macaques, there indeed appears to be support that inter-sexual relations matter for both sexes. Finally, the model indicates a positive correlation between the degree of female dominance and the proportion of males in a group. In fact, in the model the degree of female dominance over males may be influenced in three ways: 1) via winner-loser effects within and between sexes, whereby the effects may differ in strength, 2) via group composition, because this affects the frequency of intra- and inter-sexual encounters, which may have different consequences, and 3) via the steepness of the intra-sexual hierarchies, since an overlap of both hierarchies would result in some females dominating some males. This indicates that the hierarchies of both sexes are always interdependent to a certain extent, even if inter-sexual winner-loser effects are absent.

To test whether female dominance and the proportion of males are also related in real primates, in **Chapter 5** empirical data of 22 primate species are analysed. These data indeed confirm a positive correlation between female dominance and the proportion of males that cannot be accounted for by sexual dimorphism. This shows that female dominance may be influenced by group composition, and, generally, supports the notion that dominance is not a fixed, inert trait.

Part II: Competition within and between groups

Previous studies of dominance style (Hemelrijk, 1999d), and of the relation of attack strategies and personality types (Hemelrijk, 2000b; Hemelrijk & Wantia, 2005) modelled single groups only, while in the real world, groups may interact and compete with each other. The obvious question is, therefore, how different groups perform in competition with each other. To study this, the new model 'GroupWorld' is developed to simulate competition within as well as between groups.

Chapter 6 explores dominance relationships between units other than the sexes, *i.e.* between individuals belonging to different personality types within groups. It elaborates how in the model different personality types, namely a bold type and a cautious type, may coexist within a group. For other species it was suggested that different personalities perform differently well in different contexts, but in primates, there was no hint to this. In a model, I explore the performance of personalities in contexts that have not been addressed experimentally so far, namely competition within and between groups. Results show that the performance of personalities differs per context. Since cautious personalities beat bold ones within groups, yet in competition between groups, those groups with many bold individuals are victorious, one may speculate that coexistence of both types is preserved by selection at different levels (individuals and groups). In contrast, the model does not support another hypothesis, according to which social stability could be higher in mixed groups.

Finally, in **Chapter 7** the influences on the performance of a group in inter-group encounters are investigated. It is often assumed that larger groups are more likely to win, but field studies indicate that size alone cannot explain victory. Therefore, I compare in the model success of groups with different dominance styles, which are supposed to affect a group's performance (van Schaik 1989). Additionally, I study the effect of different sex ratios, since some studies indicate that a high number of males in a group may increase the chance of winning encounters between groups.

Regarding dominance style, I find that under most conditions, groups with more despotic characteristics (such as a high frequency or intensity of aggression) beat more egalitarian ones. This is in contrast to the widely accepted socio-ecological model that predicts egalitarian groups to prevail if competition between groups is high. These results are in line, however, with a recently proposed macaque phylogeny: Thierry *et al.* (2000) assume that the common ancestor of macaques was mildly egalitarian, and that dominance style has evolved from there into two directions, toward extreme egalitarianism and towards mild and extreme despotism. Regarding the sex ratio, our model confirms the assumption that groups with more males have a higher success in competition against groups with few males. In the discussion it is indicated what kind of information should be obtained in future fieldwork to verify the results of the model.

Part I: Female dominance

2) Female dominance: a statistic and data of primates

Together with: Pascal Girod & Charlotte K. Hemelrijk

Abstract

In primates, female dominance over males is known to differ between species, but so far no quantitative description except for the lemurs has been made. The aim of the present study is to present a preliminary quantitative description of female dominance in a broad range of species. For this we use a new statistic that indicates the relative position of adult females in the dominance hierarchy of all adults in the group. We choose this new method because it produces better results than the usual statistic of female dominance, which is the percentage of inter-sexual fights won by females. To compare the performance of both statistics we use a model, called DomWorld, of a social organization that resembles that of primates in several aspects. We quantify female dominance of 23 primate species from 14 genera on the basis of a large dataset of matrices of aggression and winning collected from literature. We discuss results following quantitative and qualitative descriptions by others.

Introduction

In primate groups females may benefit from dominance over males in several ways: by feeding priority (Waeber & Hemelrijk, 2003; Pochron et al., 2005), by the reduction of harassment, and by the ability to reject copulation with males (Smuts & Smuts, 1993). Although benefits are manifold and would therefore apply to many species, studies of female dominance have almost exclusively been confined to species of lemurs of Madagascar, where female dominance is often complete. Even among lemur species, however, female dominance appears to differ between species (Pereira & McGlynn, 1997; Radespiel & Zimmerman, 2001) and between groups (Overdorff *et al.*, 2005). To increase our understanding of female dominance over males in primates in general, it is important to know more about female dominance in anthropoid primates of which so far we know little (Kappeler, 1993). One of the aims of this paper is to present a preliminary quantification of female dominance over males in a broad range of species. For this, we need a statistic that is robust and easy to use. Therefore, the other aim of this paper is to introduce such a method. We compare the performance of two methods in a model. Subsequently, we use the best one to describe female dominance over males among 23 primate species from 14 genera. Data are matrices of aggression and of winning that have mostly been collected from literature. We compare our results to qualitative and quantitative descriptions of others.

The paper is divided into two sections. First, we compare two statistics of female dominance. Second, we quantify female dominance in empirical data of primate species.

Comparison of two statistics

Up until now, female dominance has been measured as the percentage of inter-sexual fights won by females (Pochron *et al.*, 2005; Digby & Kahlenberg, 2002; Radespiel & Zimmerman, 2001; Kappeler, 1993). The percentage of victories may, however, not be informative enough, because it ignores the quality of the opponent (dominance rank) who is beaten by a female in a fight. Therefore, we also quantify female dominance as the relative dominance position of females in the hierarchy compared to that of adult males in a group, computed as a standardised Mann Whitney U test. Here, female dominance ranges from 0 (no female dominance at all) via 0.5 where males and females are of equal dominance (co-dominance) to 1 (complete female dominance). To calculate this measure, we first infer the dominance hierarchy of all adults in the group using the average dominance index, a method that we developed at an earlier date (Hemelrijk *et al.*, 2005b).

We test the performance of both statistics by means of a model as an independent test; the reason is that in contrast to the real world, the model allows us not only behavioural observations of dominance interactions, but informs us also about the internal power, or dominance value, of individuals of both sexes. The model, called DomWorld (Hemelrijk, 2000b; Hemelrijk, 2004), consists of agents that group and perform dominance interactions. We chose this model because it shows the changes of power that arise from the self-reinforcing effects of victory and defeat, similar to those that have been observed in many animal species (*e.g.* see Bonabeau *et al.*, 1996). As well, it reproduces a number of phenomena observed in primate social organisations (Hemelrijk, 1999d; Hemelrijk *et al.*, 2003; Hemelrijk, 2002b). We calculate the 'actual' female dominance in the model from the internal fighting capacity reflected in the dominance values of the agents of both sexes. Using a Pearson correlation, we compare the 'real' female dominance in the model to the degree of female dominance as measured according to both statistics using as input the matrices of winning or aggression based on dominance interactions that take place among the artificial agents. The statistic that leads to strongest correlation is best because it measures female dominance closest to the ‘actual’ female dominance. Since female dominance may differ between various group sizes, types of societies, sex ratios and degrees of sexual dimorphism, we perform these correlations for each of these scenarios.

The Model

A brief summary of the model (called DomWorld) must suffice (for a more complete description see Hemelrijk, 1999d; 2000b; 2002a). This mechanistic model is based on two essential aspects of social life. It consists of a homogeneous virtual world inhabited by agents provided with no more than two tendencies: 1) to group and 2) to perform dominance interactions. Why agents actually group (whether to avoid predators or because resources are clumped) is not specified and irrelevant to the model. The same holds for dominance interactions. They reflect competition for resources (such as food and mates), but these resources are not specified.

Whenever an individual does not see another agent close by (within its personal space), grouping rules come into effect. The agent starts looking for others at greater and greater distances (of 24 and of 50 units). If, even then, no one else is in sight, it turns over an angle of 90 degrees in order to rejoin its group. In this way individuals tend to remain in a group.

If, however, an agent spots another agent within its personal space (4 units), a dominance interaction may take place.

The likelihood that an agent begins an aggressive interaction depends on the risks involved: it increases with its chance to defeat its opponent. This chance depends on the relative capacities of both agents to defeat each other, *i.e.* the relative dominance values. This is the so-called ‘risk-sensitive attack strategy’ (Hemelrijk, 2000b).

If a dominance interaction actually takes place, agents *i* and *j* observe each other’s capacity of winning, *i.e.* their dominance values Dom_i and Dom_j. The probability of winning is greater for the one higher in rank, and this is proportional to the Dom-value of agent *i* relative to that of its opponent *j* (see (1)). To allow for dominance reversals, a stochastic effect is introduced so that if the relative dominance value of an interacting agent is greater than a random number (drawn from a uniform distribution), then agent *i* wins ($w_i = 1$), or else it loses ($w_i = 0$):

$$w_i = \begin{cases} 1 \quad \text{if} \quad \dfrac{\mathrm{DOM}_i}{\mathrm{DOM}_i + \mathrm{DOM}_j} > \mathrm{RND}(0,1) \\ 0 \quad \text{else} \end{cases} \qquad \textit{(1)}$$

To reflect the self-reinforcing effects of victory and defeat, dominance values are updated by increasing the dominance value of the winner and decreasing that of the loser by the same amount:

$$\mathrm{DOM}_i = \mathrm{DOM}_i + \left(w_i - \frac{\mathrm{DOM}_i}{\mathrm{DOM}_i + \mathrm{DOM}_j} \right) * \mathrm{STEPDOM} \qquad \textit{(2)}$$

$$\mathrm{DOM}_j = \mathrm{DOM}_j - \left(w_i - \frac{\mathrm{DOM}_i}{\mathrm{DOM}_i + \mathrm{DOM}_j} \right) * \mathrm{STEPDOM}$$

This positive feedback is ‘damped’ because a victory of the higher ranking opponent reinforces its relative Dom-value only slightly, whereas the (unexpected) success of a lower ranking agent increases its relative dominance value by a greater change, thus equalising their dominance values. This is in agreement with detailed behavioural studies of bumble bees by

Honk & Hogeweg (1981). To keep Dom-values positive, their minimum value is, arbitrarily, set at 0.001. The change in Dom-values is multiplied by a scaling factor, called StepDom, which varies between 0 and 1 and represents the intensity of aggression (see experiments). High values imply a great change in Dom-value when updating it, and thus indicate that single interactions (*e.g.* involving biting) may strongly influence the future outcome of conflicts. Conversely, low StepDom-values represent low impact (*e.g.* threats or slaps).

Winning an interaction entails chasing the opponent over a distance of one unit 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 (of 2 units).

Experiments

Groups of agents contain males and females. Females in some primate species are of equal size as males, *e.g. Lemur catta*, but in many other species females are smaller, *e.g.* among macaques (Smith & Cheverud, 2002). Therefore, the sexes in the model may or may not differ in their initial capacity of winning. In case of sexual dimorphism 'females' initially have a lower dominance value than 'males' (initial Dom-value = 16 instead of 32) and in the absence of sexual dimorphism the initial dominance of both sexes is equal (initial Dom-value = 24). In all cases we suppose that females differ from males in their muscle structure, and that their aggression is less intense than that of males (*e.g.* see Bernstein & Ehardt, 1985b) which we reflect by a lower intensity of aggression for females than for males in the model (females have 80% of the intensity of aggression of the 'males'). Groups consist of 10 or 20 individuals in order to reflect groups of adults of both sexes among numerous primate species, both in captivity and under natural conditions. Since species differ in terms of their sex ratio, we also test three different sex ratios, namely groups with 20%, 50% or 80% of the adults being females in the group. In order to resemble species with a difference in intensity of aggression - such as found in primates, for instance between egalitarian and despotic macaques (Thierry, 1990a)- we test all settings for a high and a low intensity of aggression (StepDom = 1 and StepDom = 0.1). Per setting, we have conducted 40 replicates. In total, this study is based on (2 group sizes * 2 StepDom-values * 2 sexual dimorphisms in initial Dom-value * 3 sex ratios)* 40 replicas = 24 * 40 = 960 runs (see Table 1).

At the start of a run, when individuals have only been activated a few times, the hierarchy is hardly differentiated and there are many dominance reversals (Hemelrijk & Gygax, 2004). Later on, after many activations, approximately from period 200 onwards, the hierarchy is more stable. The run ends at period 260. We study dominance during the supposedly stable phase from period 200 till 260, thus over 60 periods.

Statistics of female dominance over males and their comparison

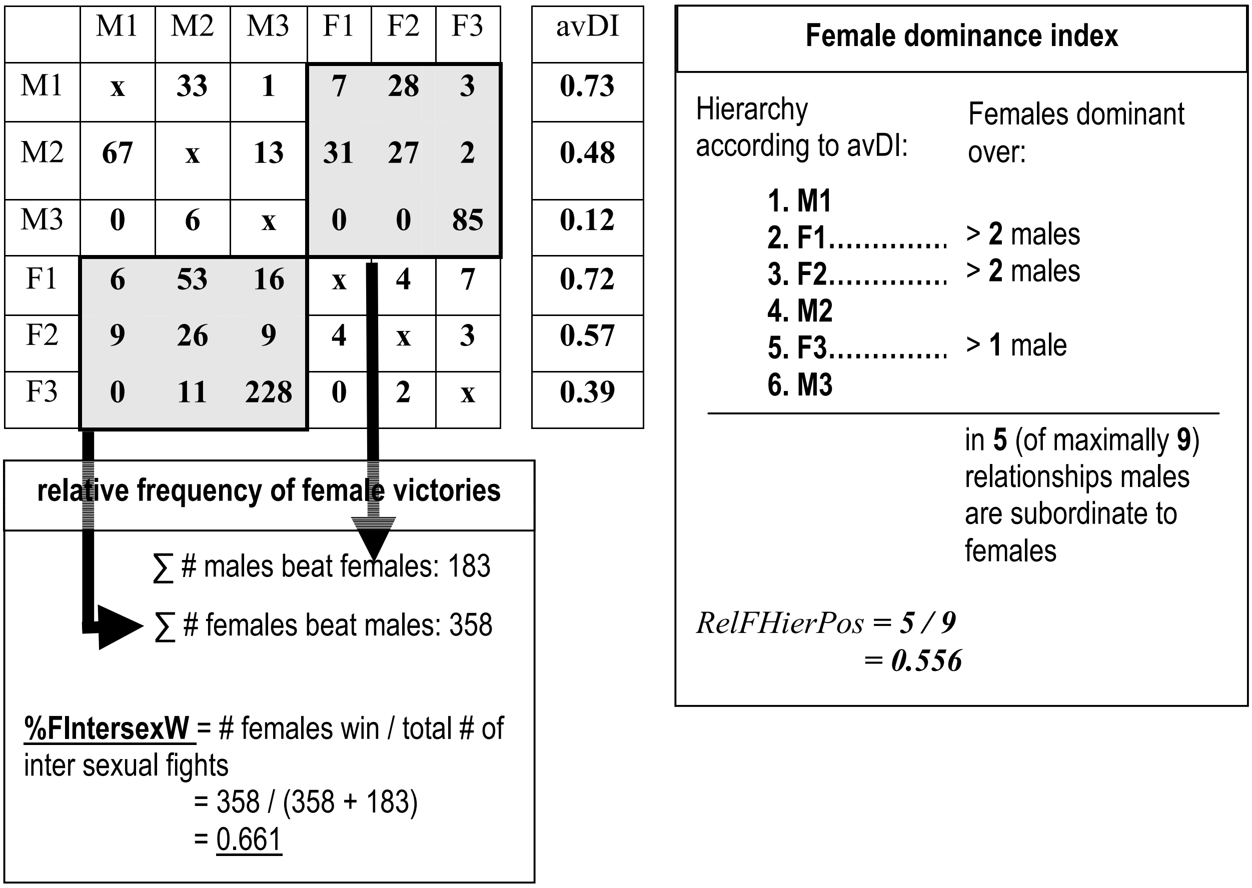
We compare the 'real' dominance of females over males based on their dominance values in the model to that as computed by each of the two statistics on the basis of a matrix of aggression or winning. The comparison is made by correlating (Pearson correlation) each of the statistics with the actual female dominance per scenario for each of the replicas. The stronger the correlation, the more the statistic reflects the 'real' female dominance in the model.

We will first explain the computation of the 'real' female dominance and next, that of female dominance inferred from matrices of aggression.

As the Dom-values of the agents in DomWorld give the real order of the agents of both sexes in the hierarchy, we use this to calculate the degree of 'actual' female dominance as the relative position of females in the adult hierarchy as a standardised Mann Whitney U-statistic (Siegel & Castellan, 1988). For this purpose the number of males ranking below each female is counted. The value of the statistic is computed as the sum of these counts and is divided by its maximum value for a specific sex ratio and group size (see Figure 1). If all males are dominant to all females, the female dominance is zero. In case of complete female dominance this implies that all females are dominant over all males. In a group of 10 agents with an equal number of males and females this corresponds to an absolute value of 5 * 5 = 25 (#females * #males) and a standardised value of 1. Equal dominance between the sexes occurs when females are on average dominant over half of the males, thus U = 5*2.5 = 12.5 and the standardised value of the position of females in the hierarchy is 0.5. We also tried measuring the 'actual' female dominance over males by the average female dominance value divided by that of females plus that of males. This appeared not suitable, because its value may vary even if females dominate the same number of males.

To estimate the degree of female dominance on the basis of the matrix of interactions, first the dominance order of males and females in the hierarchy must be derived. For this, several methods exist. Since in our earlier comparative analysis of five statistics the average Dominance Index (avDI) proved to be the best one (Hemelrijk *et al.*, 2005b), we use this statistic here. The Dominance Index is calculated for each pair of individuals as the ratio of the number of conflicts an individual has beaten a particular opponent, divided by the total number of conflicts with that particular partner. Subsequently, per individual we calculate an individual's average dominance index with all group members, but whenever a pair does not interact at all it is excluded from the calculation of the average. A higher average dominance index indicates a higher dominance position. Once the hierarchy is established, it is used to calculate the relative position of females in the dominance hierarchy using the standardized Mann-Whitney-U-Value as mentioned above (see Figure 1).

The alternative statistic is the usual measure of female dominance, namely the ratio of female victories over males divided by all interactions between the sexes (Figure 1).



	M1	M2	M3	F1	F2	F3	avDI
M1	**x**	**33**	**1**	**7**	**28**	**3**	**0.73**
M2	**67**	**x**	**13**	**31**	**27**	**2**	**0.48**
M3	**0**	**6**	**x**	**0**	**0**	**85**	**0.12**
F1	**6**	**53**	**16**	**x**	**4**	**7**	**0.72**
F2	**9**	**26**	**9**	**4**	**x**	**3**	**0.57**
F3	**0**	**11**	**228**	**0**	**2**	**x**	**0.39**

relative frequency of female victories

∑ # males beat females: 183

∑ # females beat males: 358

%FIntersexW = # females win / total # of inter sexual fights
= 358 / (358 + 183)
= 0.661

Female dominance index

Hierarchy according to avDI:	Females dominant over:
1. M1	
2. F1.............	> **2** males
3. F2.............	> **2** males
4. M2	
5. F3.............	> **1** male
6. M3	
	in **5** (of maximally **9**) relationships males are subordinate to females

RelFHierPos = ***5 / 9***
= ***0.556***

Figure 1. *Calculation of degree of female dominance. RelFHierPos: the relative hierarchical position of females; %FIntersexWin: the ratio of winning in inter sexual fights by females. For explanation see text.*

a) With Dimorphism

Condition	Pearson correlation of actual female dominance and:	
$\text{InitDom}_{f,m}$ = 16, 32	RelFHierPos	%FIntersex Win
10 agents, $\text{StepDom}_{f,\,m}$; #f, #m		
0.8, 1.0; 2, 8	0.625**	0.102
0.8, 1.0; 5, 5	0.664**	0.342
0.8, 1.0; 8, 2	0.375*	-0.232
0.08, 0.1; 2, 8	-[1]	-[1]
0.08, 0.1; 5, 5	-[1]	-[1]
0.08, 0.1; 8, 2	-[1]	-[1]
20 agents, $\text{StepDom}_{f,\,m}$; #f, #m		
0.8, 1.0; 4, 16	0.664	0.396**
0.8, 1.0; 10, 10	0.470	-0.029
0.8, 1.0; 16, 4	0.325	-0.412**
0.08, 0.1; 4, 16	-[1]	-[1]
0.08, 0.1; 10, 10	-[1]	-[1]
0.08, 0.1; 16, 4	-[1]	-[1]

1. Female agents are not dominant over any males

b) Without Dimorphism

Condition	Pearson correlation of actual female dominance and:	
$\text{InitDom}_{f,m}$ = 24	RelFHierPos	%FIntersex Win
10 agents, $\text{StepDom}_{f,\,m}$; #f, #m		
0.8, 1.0; 2, 8	0.358*	-0.136
0.8, 1.0; 5, 5	0.167	-0.276
0.8, 1.0; 8, 2	0.193	-0.079
0.08, 0.1; 2, 8	0.068	0.046
0.08, 0.1; 5, 5	-0.031	-0.106
0.08, 0.1; 8, 2	-0.114	-0.022
20 agents, $\text{StepDom}_{f,\,m}$; #f, #m		
0.8, 1.0; 4, 16	-0.033	-0.218
0.8, 1.0; 10, 10	0.483**	-0.074
0.8, 1.0; 16, 4	0.113	-0.046
0.08, 0.1; 4, 16	-0.205	-0.237
0.08, 0.1; 10, 10	-0.092	-0.157
0.08, 0.1; 16, 4	0.029	-0.027

Table 1: *Performance of two test statistics (Relative hierarchical position of females and ratio of inter-sexual fights won by females) for groups of 10 agents and 20 agents with (a) and without sexual dimorphism (b). StepDom indicates the intensity of aggression, InitDom is the initial dominance value of each sex (compare sexual dimorphism). RelFHierPos: the relative hierarchical position of females; %FIntersexWin: the ratio of winning in inter- sexual fights by females. #f, #m: number females and males, respectively in the group, the sex ratio. NS = not significant, * = P<0.05, ** = P<0.01, *** = P<0.001 two-tailed.*

Condition	R	Significance
With Dimorphism		
$\text{InitDom}_{f,m}$ = 16, 32		
10 agents,		
$\text{StepDom}_{f,\,m}$; #f, #m		
0.8, 1.0; 2, 8	-0.68	***
0.8, 1.0; 5, 5	-0.67	***
0.08, 0.1; 2, 8	-0.14	NS
0.08, 0.1; 5, 5	-0.02	NS
20 agents,		
$\text{StepDom}_{f,\,m}$; #f, #m		
0.8, 1.0; 4, 16	-0.6	***
0.8, 1.0; 10, 10	-0.72	***
0.8, 1.0; 16, 4	-0.57	***
0.08, 0.1; 4, 16	-0.02	NS
0.08, 0.1; 10, 10	-0.11	NS
0.08, 0.1; 16, 4	-0.24	NS
Without Dimorphism		
$\text{InitDom}_{f,m}$ = 24		
10 agents,		
$\text{StepDom}_{f,\,m}$; #f, #m		
0.8, 1.0; 2, 8	-0.67	***
0.8, 1.0; 5, 5	-0.72	***
0.08, 0.1; 2, 8	-0.12	NS
0.08, 0.1; 5, 5	-0.15	NS
20 agents,		
$\text{StepDom}_{f,\,m}$; #f, #m		
0.8, 1.0; 4, 16	-0.67	***
0.8, 1.0; 10, 10	-0.77	***
0.8, 1.0; 16, 4	-0.55	***
0.08, 0.1; 4, 16	-0.08	NS
0.08, 0.1; 10, 10	-0.06	NS
0.08, 0.1; 16, 4	-0.02	NS

Table 2: *Pearson correlations (over 40 replica) between the frequency with which females attack males and the dominance rank of the males (R-values of average correlation). Using Fisher's r-to-Z-transformation the correlation coefficients were transformed to the corresponding Z-values. The average of the 40 Z-values was subsequently transformed back to the average correlation coefficient r. The p-value was calculated via a Z transformation. Two-tailed statistical significance of the average correlation: NS = not significant, *= P<0.10, * = P<0.05, ** = P<0.01, *** = P<0.001 two-tailed.*

Comparative Results of both Statistics

Results of both statistics (relative hierarchical position of females and their ratio of victories in inter-sexual fights) are correlated with the values of 'actual' female dominance based on the dominance values of the agents.

'Actual' female dominance of the agents appears to be correlated more strongly with the statistic of the relative hierarchical position of females (RelFHierPos) than with the ratio of inter-sexual fights won by females (%FintersexWin, see Table 1). This holds for all group sizes, types of societies and sex ratios, but only in the presence of sexual dimorphism. In its absence, however, correlations are seldom significant (Table 1); the reason for this is unclear, at least there is no systematic relation with the differentiation of the hierarchy.

Discussion Statistics

In general, the ratio of inter-sexual fights won by females appears to be hardly correlated with the 'actual' female dominance in the model. This arises in despotic societies because females attack very low ranking males very often due to the low risk involved, but by such attacks their dominance over males increases only little (Table 2).

Therefore as a statistic of female dominance, we prefer to use the relative dominance position of females in the hierarchy (rather than the ratio of inter-sexual fights won by females). We will use this statistic for the empirical data.

Empirical Data of a broad range of species

Data Collection

Matrices of dyadic agonistic interactions among adult females and males of a mixed social group were collected from the following journals up to and including 2004: *Animal Behaviour* (from 1965), *Behaviour* (from 1948), *American Journal of Primatology* (from 1981), *Primates* (from 1959), *International Journal of Primatology* (from 1980) and *Folia Primatologica* (from 1963). To be added to this analysis, a paper had to include a matrix of frequencies of winning fights or agonistic interactions comprising at least four adult individuals. As well, we added unpublished data collected by Bernard Thierry and Pascal Girod. This resulted in a total of 47 data sets on primate groups belonging to 23 different species and 14 different genera (see Table 3).

Data Analysis

To measure the degree of female dominance in a group, we first derive the hierarchy of the group from a matrix of agonistic interactions (Figure 1). For this, we use the average Dominance Index as described above for the model (Hemelrijk *et al.*, 2005b).

Once the hierarchy is established, the degree of female dominance over males is calculated as a statistic of the relative position in the dominance hierarchy of all females using a standardised Mann-Whitney-U-Value, as explained for the model (see Figure 1). This calculation and that of the average dominance index was performed with the program Matrix Tester v223b developed by Hemelrijk and co-workers; it is available on request.

Note that the relative frequency of victories by females over males may give very different results. For instance, in the example of Figure 1 it is 0.6617, whereas the value of the relative dominance position of females is 0.556.

It should be noted that we ignore the contexts of aggression. Although in former studies, ratios were sometimes calculated per context, this was often not necessary because either individuals mainly fought in one context, such as during feeding (Waeber & Hemelrijk, 2003; Pochron et al., 2005) or the impact of context appeared to be marginal (Radespiel & Zimmerman, 2001).

Species	N	N_F	Female Dominance	Reference
Category 1				
Eulemur fulvus rufus	6	2	0.75	(Ostner & Kappeler, 1999)
Eulemur fulvus rufus	9	3	0.7222	(Ostner & Kappeler, 1999)
Eulemur macaco flavifrons	4	2	1	(Digby & Kahlenberg, 2002)
Hapalemur griseus alaotrensis	4	2	1	(Waeber, 2003)
Hapalemur griseus alaotrensis	5	3	1	(Waeber, 2003)
Category 2				
Callithrix jacchus	4	3	0	(Digby, 1995)
Callithrix jacchus	8	6	0.167	(Digby, 1995)
Callithrix jacchus	8	4	0.625	(Digby, 1995)
Category 3				
Ateles geoffroyi	11	4	0.536	(Anaya-Huertas & Mondragon-Ceballos, 1998)
Category 4				
Cercopithecus aethiops	6	3	0.1111	(Struhsaker, 1967)
Cercopithecus aethiops	7	4	0.25	
Macaca arctoides	6	5	0	(Estrada, 1977b; Estrada, 1977a)
Macaca arctoides	5	4	0	(Rhine, 1972)
Macaca arctoides	5	4	0.25	(Rhine, 1972aRhine, 1972a)
Macaca arctoides	4	3	0	(Rhine, 1973)
Macaca assamensis	19	10	0.205	(Cooper *et al.*, 2005; Bernstein & Cooper, 1999)
Macaca fascicularis	8	7	0	(Butovskaya *et al.*, 1996)
Macaca fascicularis	10	9	0	(Butovskaya *et al.*, 1996)
Macaca fascicularis	16	7	0.825	Sterck, 1997 (??)
Macaca fuscata	9	8	0	(Mehlman & Chapais, 1988)
Macaca mulatta	16	9	0.381	(Sade, 1972)
Macaca mulatta	6	5	0.2	Thierry 1994
Macaca mulatta	11	7	0.25	(Sade, 1967)
Macaca mulatta	10	6	0.417	(Sade, 1967)
Macaca mulatta	12	7	0.457	(Sade, 1967)
Macaca mulatta	11	10	0	(Girod & Hemelrijk, 2002)
Macaca mulatta	6	4	0.625	(Varley & Symmes, 1966)
Macaca nemestrina	17	14	0.214	(Oi, 1990)
Macaca thibetana	19	13	0.167	(Berman *et al.*, 2004)
Macaca thibetana	21	13	0.289	(Berman *et al.*, 2004)
Macaca thibetana	18	10	0.388	(Berman *et al.*, 2004)
Macaca tonkeana	13	10	0.2	Thierry and C.
Macaca tonkeana	8	7	0	(Thierry *et al.*, 1990)
Miopithecus talapoin	8	5	0.867	(Dixson & Herbert, 1977)
Miopithecus talapoin	8	5	1	(Dixson & Herbert, 1977)
Miopithecus talapoin	6	4	1	(Dixson & Herbert, 1977)
Saimiri sciureus	6	5	0.2	(Masataka & Biben, 1987)
Category 5				
Alouatta palliata	18	15	0	(Jones, 1980)
Alouatta palliata	10	8	0	(Jones, 1980)
Gorilla gorilla beringei	6	5	0	(Meder, 1985)
Pan troglodytes	15	3	0.528	Arnhem, 1987 Unstable
Pan troglodytes	22	18	0,1111	Arnhem, 1981 Clear hierarchy
Pan troglodytes	27	22	0.091	Arnhem, 1982 Clear hierarchy
Pan paniscus	6	3	0.5556	(Vervaecke *et al.*, 2000b)
Others				
Mandrillus sphinx	9	7	0	(Feistner, 1989)
Cebus apella	7	4	0.583	(Izawa, 1980)
Semnopithecus entellus	13	11	0.2727	(Sommer *et al.*, 2002)

Table 3: *Empirical studies. N = number of group members, N_F = number of females, Female dominance is measured by the relative hierarchical position of females as the standardised Mann Whitney U statistic.*

Empirical Results and Discussion

As can be observed, the degree of female dominance over males ranges from complete (where it equals 1) in a lemur species (*Eulemur macaco flavifrons*), to nil in gorillas, for instance (*Gorilla gorilla berengei*). In certain species, in particular in rhesus macaques (*Macaca mulatta*) and marmosets (*Callithrix jacchus)*, there is considerable variation in dominance between groups.

The most extensive description of female dominance is the one by Smuts (1987) in which she classifies 5 categories based on the degree of female dominance over males, and the way it is obtained by coalitions among males or females or by sexual dimorphism. Therefore, we present our results in the order of Smuts' five categories in Table 3 and Figure 2.

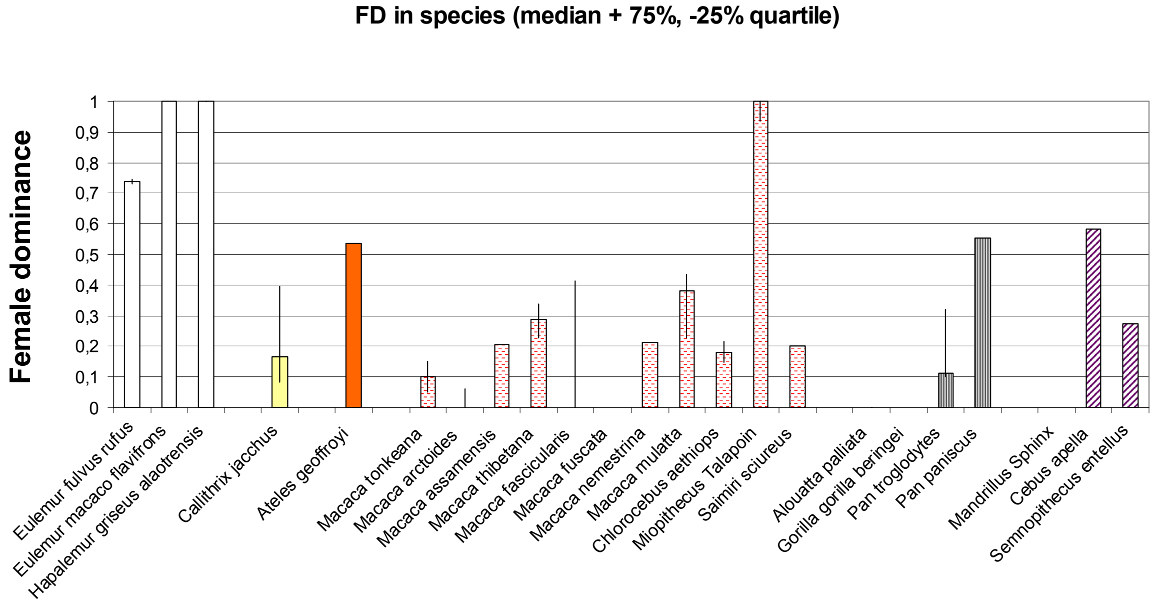


Figure 2. *Female dominance over males in several primate species (median and range of 25-75% of data). Different colours/shading/hatching indicate different categories of Smuts (1987), whereby categories from one to five and a sixth category of unclassified species, are ordered from left to right.*

The first category of Smuts' (1987) classification concerns species in which sexual dimorphism is slight and females are clearly dominant to males. We confirm this in the Malagasy lemurs: in blue-eyed black lemurs, *Eulemur macaco flavifrons,* the alaotran gentle lemurs (*Hapalemur griseus alaotrensis*) and the red fronted lemurs, *Eulemur fulvus rufus*.

Smuts' second category entails species with slight sexual dimorphism, such as common marmosets, *Callithrix jacchus*, in which she and Digby (1995) argue that females and males are equally dominant or co-dominant. This corresponds to a value of 0.5 of the relative position of females in the hierarchy. Although we find these values in the three natural groups studied by Digby, we find a large variation of dominance values and a median value of 0.167. We may explain this as follows. In Digby's study adults consist of breeding and non-breeding individuals. Digby mentions that breeding individuals are dominant to non-breeding individuals. Among the breeding adults the sexes are equal in dominance. Among those that do not breed we observe a weak male dominance. It follows that if the sex ratio among breeders is more female-biased than that among the non-breeders, female dominance will be higher than otherwise. This is confirmed by comparing the three study groups.

Smuts' third category involves species without sexual dimorphism where males are dominant to females through male-male coalitions. She mentions spider monkeys (*Ateles geoffryi*) for this. However, we clearly find co-dominance between the sexes in this species. This may be because the group consisted of individuals that were hand-reared (Anaya-Huertas

& Mondragon-Ceballos, 1998), but on the other hand, it must be noted that female dominance has not been measured quantitatively in former studies and some degree of female leadership in group movements has been reported (Fedigan, 1984). Therefore, it is unclear to what extent our findings differ from former studies.

Fourth, Smuts (1987) distinguishes species where males are larger than females, but in which females sometimes dominate males, possibly through female-female coalitions against males (category 4). We confirm weak female dominance for vervets (*Cercopithecus aethiops*), macaques (*Macaca* spp) and squirrel monkeys (*Saimiri sciureus*), and in the talapoin monkey (*Miopithecus talapoin*). In the last species, however, it appears to be too high. Instead of a value of the relative dominance position of females below 0.5, we find 1.0, that is, complete female dominance. This may be due to the special composition of the group with 3 young males and 5 older females (Wolfheim, 1977). It appears that only a single group of talapoins has been studied in this respect and further studies are clearly needed.

As the fifth category, Smuts classifies species in which female dominance is lacking. Our data confirm this in the gorilla (*Gorilla gorilla berengei*), and the mantled howler (*Alouatta palliata*) (figure 2). However, Smuts mentions it also for all great ape species, but, in line with findings by others (Stanford, 1998), we find co-dominance in bonobos and, further, weak female dominance in common chimpanzees in the colony of Arnhem.

A number of species go unmentioned by Smuts, such as mandrills, langurs and capuchin monkeys. We see that female dominance is absent in mandrills (*Mandrillus sphinx*). This may be expected because of their resemblance to baboons (Smith & Cheverud, 2002) in which female dominance is also lacking. In contrast to the study by Hrdy (1977), Indian hanuman langurs show weak female dominance in single male groups (Sommer *et al.*, 2002). Furthermore, we confirm female co-dominance in the black-capped capuchin, *Cebus apella* (Janson, 1984).

General conclusion

In sum, the relative position of females in the dominance hierarchy (using the standardised Mann Whitney U statistic on the dominance hierarchy inferred from matrices of aggression and winning) suffices to gain an impression of the degree of female dominance. We hope that our statistic of female dominance will be used by others, so that studies of female dominance will be extended to more species and it will help us to elucidate factors that influence the dominance relationship between the sexes.

Acknowledgements

We would like to thank Patrick Waeber and Bernard Thierry for sharing their data on *Hapalemur* and *Macaca* with us, and Bernard Thierry and Matthew Cooper for useful comments on an earlier version. We wish to thank Jamie DeCoster for directing our attention to the r-to-Z transformation of the Pearson correlation and Hanno Hildenbrandt, Jutta Steinhauser and Daan Reid for discussions.

3) Female co-dominance in a virtual world: ecological, cognitive, social, and sexual causes.

Together with: Charlotte K. Hemelrijk & Mark Dätwyler

Behaviour, **140** (10), 1247 – 1273.

Abstract

In male-dominant primate species, females are sometimes dominant to some or all males of a group. In this paper, we present 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, and talapoins, females are sometimes dominant over males despite their markedly smaller body size (Smuts, 1987; Janson, 1984; Wolfheim, 1977; Dixson et al., 1973; Bramblett et al., 1982; Loy, 1981; Bernstein & Ehardt, 1985a; Chapais, 1983; Johnson et al., 1982). 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 (Stanford, 1998; Evans & Poole, 1983; Chivers, 1974; Tilson, 1981). It occurs more frequently 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 assumption is contradicted by studies of others (Chase *et al.*, 2002). It depends on, for instance, the order of introduction of individuals into 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). The model DomWorld shows 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 thus lead to a spreading out of the group (which in turn reduces the frequency of aggression). Simultaneously, a spatial structure develops with dominants in the centre and subordinates at the periphery, with all individuals that are similar in dominance remaining close to each other. 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 can only be a minor one because the opponents were similar in dominance before the fight. As the spatial structure stabilises and further develops the hierarchy, the development of the hierarchy and the spatial structure mutually reinforce each other. In summary, at a high intensity of aggression, the gradient of the hierarchy is steeper, groups are looser, aggression is less frequent, and spatial centrality is greater. In many aspects the results resemble 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; de Waal, 1991; Thierry, 1990a; Thierry, 1990b; Hemelrijk, 1999d).

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, 1999d), and this corresponds to the greater female dominance over maturing sub-adult males described for fiercely aggressive despotic females by Thierry (1990a). Thierry argues that this may be due to the stronger coalitions among females against (sub-adult) males in despotic rather than egalitarian societies. In DomWorld, however, the finding 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, 1999b) and male attraction to females (Hemelrijk, 2002a), contribute to female dominance.

Due to 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. In the model we study 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. In addition, 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. Finally, 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 the master's degree student 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. A continuous world is preferable to a grid world because it represents spatial patterns more precisely (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 (Figure 1).

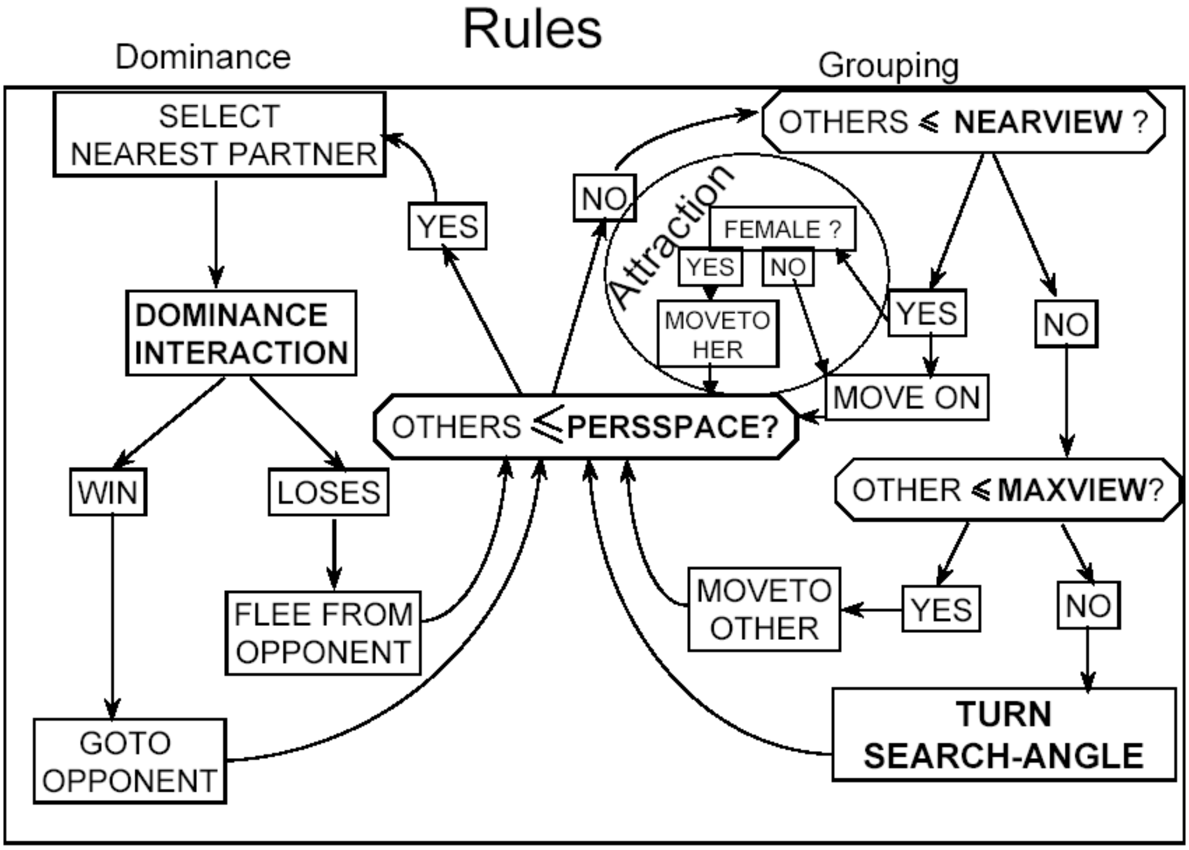


Figure 1. *Flow chart for the behavioural rules of agents. Encircled part (labelled 'Attraction') is the behavioural rule for attraction to females. This rule is only operative during sexual attraction.*

Grouping rules

Usually, group-structure is supposed to be affected by two opposing tendencies: 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, these tendencies are represented by two sets of rules, concerned with attraction and with competition for recourses that are not specified. In the derived model, EcoDomWorld, food is also represented. Satiated agents aggregate, in accordance, with 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.

Basic DomWorld

Grouping and competition are represented in the model by a set of rules that are graphically displayed in Figure 1 (see Hemelrijk, 1999d), and parameter values are shown in Table I. 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 two units farther away under a small random angle.
2. If no other agent 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, agents of one sex approach an agent of another sex over one unit distance when they observe it in NearView (see ‘attraction’ in Figure 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.
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.

	Parameter	Description	Females	Males
Basic 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°	

Eco DomWorld	# 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		0.5
	# of insects		72
	Food value of insect		1

Table I: *Default values of parameters of both models.*

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 remains the

same (36). One food source initially consists of 20 units of energy. After it is fed upon, regrowth 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 (Figure 1).

1. If the agent's energy level is below 35, it searches for food in PerSpace 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 the agent finds food of sufficient quality and no one is close by in PerSpace, it eats the food. If there are others in its PerSpace, however, it may first initiate a dominance interaction. In case of victory, the opponent is chased away, in case of defeat, the agent flees from the opponent as in the basic model of Figure 1.
    b. If it does not find food of sufficient quality in its PerSpace, the agent looks for it at a larger distance, *i.e.* in its NearView. If it finds food there, it moves one unit 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 food there, it moves one unit in the direction of the nearest food source. If there is no food, the agent 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 PerSpace, 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 occur 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 Hemelrijk, 2000b; Bonabeau *et al.*, 1996).

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

Direct perception by 'Perceivers'

Interactions between agents with direct perception is modelled after Hogeweg & Hesper (Hogeweg & Hesper, 1983) and Hemelrijk (1999d), 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 whether 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, the agents display and observe each other’s Dom. Subsequent winning and losing is determined by chance and by values of Dom as follows:

$$w_i = \begin{cases} 1 & \dfrac{DOM_i}{DOM_i + DOM_j} > RND(0,1) \\ 0 & \text{else} \end{cases} \tag{3}$$

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

$$\begin{aligned} DOM_i &:= DOM_i + \left(w_i - \frac{DOM_i}{DOM_i + DOM_j} \right) * STEPDOM \\ DOM_j &:= DOM_j - \left(w_i - \frac{DOM_i}{DOM_i + DOM_j} \right) * STEPDOM \end{aligned} \tag{4}$$

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). 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 group-member 2 to 10 under, respectively, Dom $_{1,2}$ Dom $_{1,3}$, …, Dom $_{1,10}$.

Whenever the agent meets another in its PerSpace, 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. Since these interactions occur only in the agent's mind, they do not change the opponent's notion of 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. The same needs to be done for the opponent.

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

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

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

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

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

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 I), 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 Figure 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 for 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). Therefore, 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 to 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 in visual assessment.

Experimental set-up and data-collection

Here, the same parameter setting (Table I) is used as in former studies (Hemelrijk, 1999b; 2000a). The present study is confined to a population of ten agents including five VirtualFemales and five Virtual Males.

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*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, 1999d) and due to stronger cohesion of grouping (Hemelrijk, 1999b) 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 (Figure 3,4). Furthermore, 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 (Figure 2AB).

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

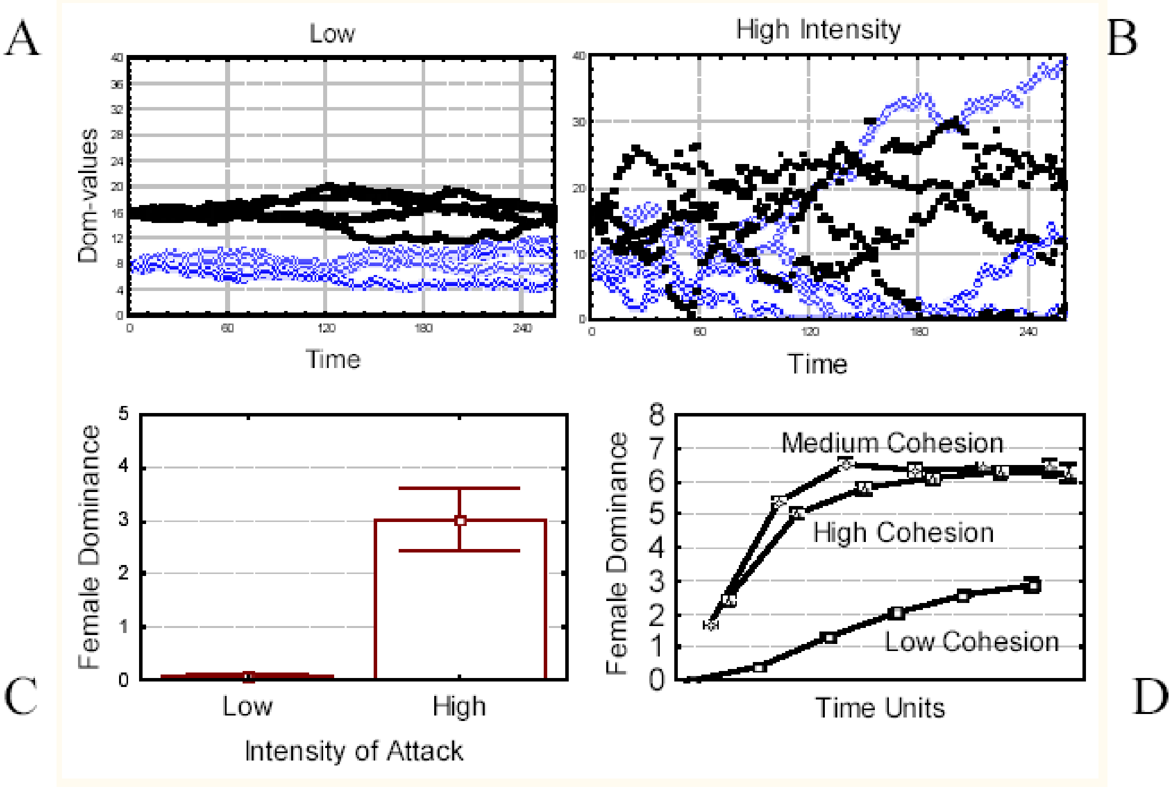


Figure 2. *Female dominance over males, intensity of aggression and cohesion. Development of dominance values over time of 4 males (black dots) and 4 females (open circles) in a single run chosen at random at (A) a low intensity of aggression and (B) a high intensity. Female dominance over males measured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

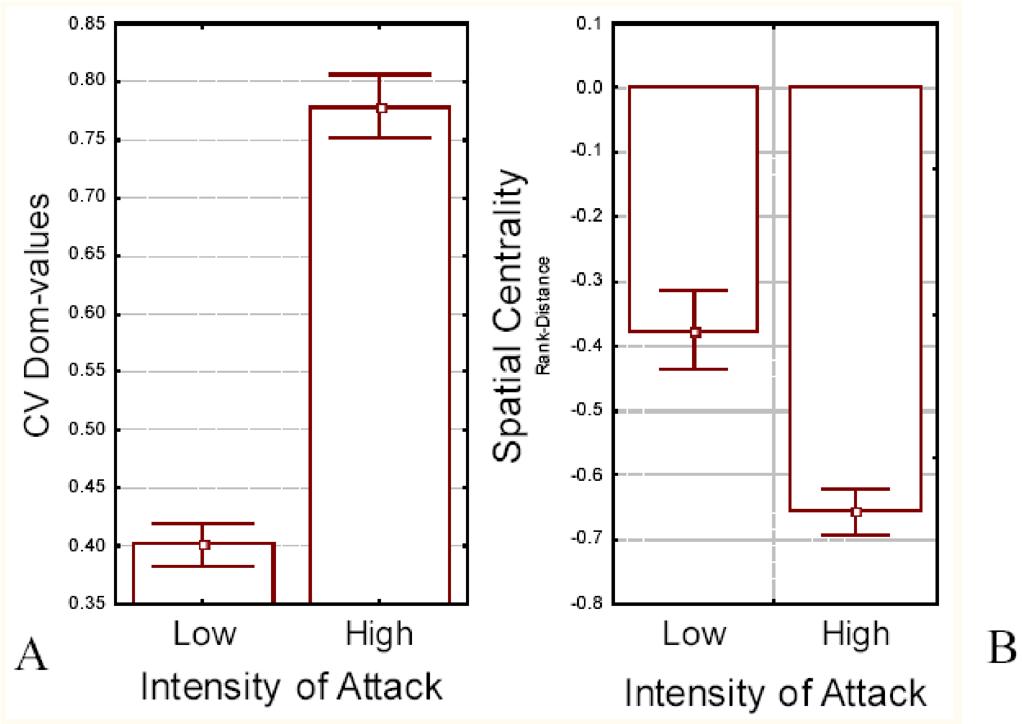


Figure 3. *Effects of intensity of aggression on (A) the hierarchical gradient measured by the coefficient of variation of dominance values and (B) spatial structure (mean ± S. E. over 10 runs).*

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

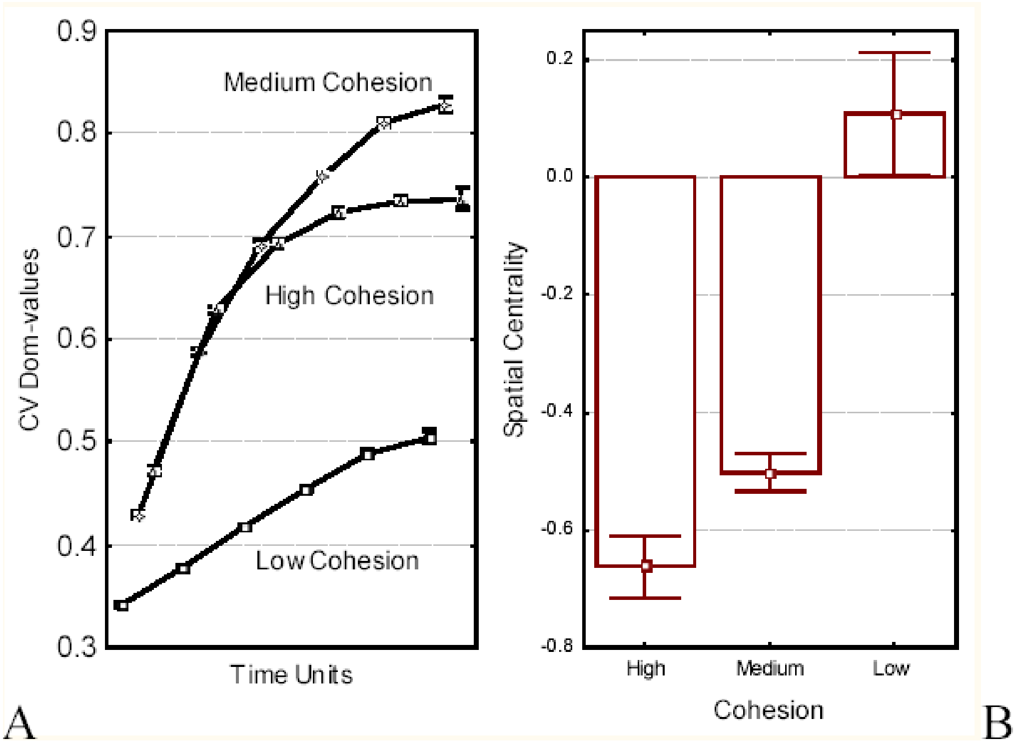


Figure 4. *Effects of different degrees of cohesion (high, medium and low) on (A) hierarchical differentiation and (B) spatial structure. (mean ± S. E. over 40 runs at StepDom =1).*

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). As the degree of cohesion, spatial centrality of dominants and hierarchical differentiation had not been changed, the increase of female dominance must be a consequence of the (absolutely and relatively) increased frequency of interaction between the sexes: The higher frequency of interactions leads to a higher frequency of victories of females over males. This is a consequence of a rule in DomWorld that determines 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, which in turn will accelerate female dominance.

Female dominance does not increase at a low intensity of aggression, because the hierarchy of the females is differentiated weakly (see Figure 2A). Consequently, females that start low in dominance remain low in rank. 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 (tumescent) synchronously, but in others they are tumescent asynchronously. We compare the effects of both conditions on female dominance. It appears that the degree of synchronously and asynchronously attractive females' dominance over males is similar (Figure 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 (Figure 5B). Due to the higher frequency of interactions among males, the male hierarchy differentiates stronger than without attraction (Figure 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 (Figure 5B, Mann Whitney U-tests among males, N1,2=40, U= 598.5, P=0.053, among females U=291, P<0.001, and between the sexes, U=16, P<0.001). Thus, if attraction is synchronous, female dominance increases merely due to the higher frequency of interactions between the sexes. This leads to more opportunities for low ranking females to win unexpectedly from high-ranking males. Whenever this occurs, dominance values of females increase by a larger amount than in the case of females defeating lower-ranking agents.

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

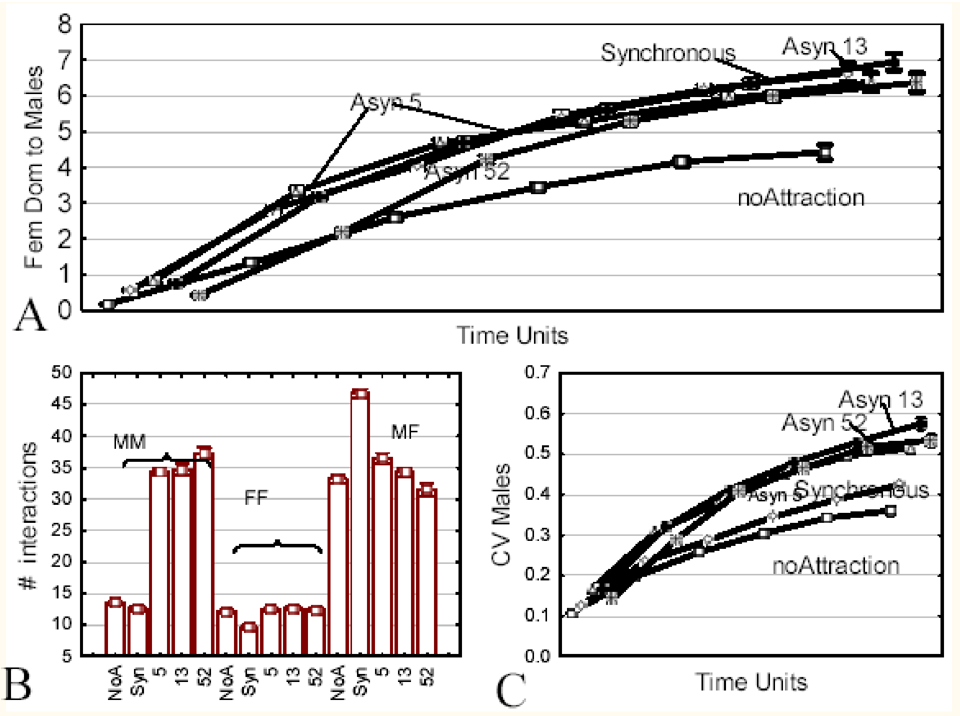


Figure 5. *Mean and S.E.s (over 40 runs) of effects of sexual attraction to females that are attractive synchronously or asynchronously on (A) female dominance (measured by the Mann-Whitney U test), on (B) the frequency of interactions among males, among females and between the sexes and on (C) the differentiation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

Mutual and unidirectional attraction to the opposite sex

Only in rare cases, attraction is reversed, *i.e.* females are attracted to males rather than the other way around. More often, both sexes are mutually attracted 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 (Figure 6A). This is remarkable because during mutual attraction the hierarchical differentiation is similar to that during unidirectional attraction (Figure 6B), and the frequency of aggression in total and between the sexes is highest (Figure 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<0.001, among females, U=267, p<0.001), 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: Figure 6D, Mann Whitney U test, among males, U=656.5, p=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=NS, among females, U=291, p<0.001). Consequently, due to the strong reduction in intra-sexual interactions, the male hierarchy differentiates least during mutual attraction (Figure 6E). Therefore, males do not develop low dominance values, but remain high in dominance and thus will usually defeat females. In addition, 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 (Figure 6F).

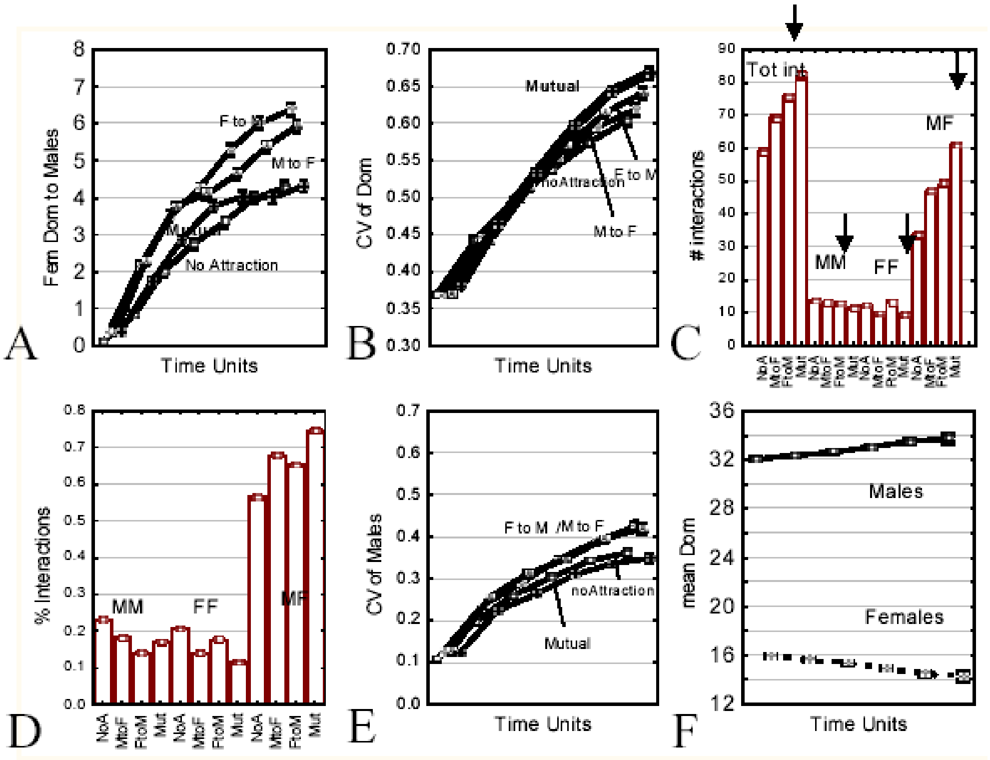


Figure 6. *Mutual and unidirectional sexual attraction and their effects on (A) female dominance (measured by the Mann-Whitney U test, mean ± S. E.), (B) hierarchical differentiation, (C) frequency of interactions in total, among males, among females and between the sexes (mean ± S. E.), (D) percentage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

These findings are different from what happens during unidirectional attraction. During unidirectional attraction (Figure 6C), inter-sexual interactions are less frequent than during mutual attraction (Mann Whitney U test, male attraction to females N1,2=40, U=8, P<0.001, female attraction to males U=22, p<0.001), 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 N1,2=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<0.001). This can also be seen in the percentage of interactions within and between the sexes as compared to the total number of interactions (Figure 6D). This relation is due to the fact that individuals of the sex that is attracted to the other will naturally meet each other frequently close to their source of attraction during unidirectional attraction and, consequently, 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, which in turn 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 from the start. The likelihood of this scenario is enhanced if there are more interactions among individuals of the same sex.

Note that all these results remain similar if we adjust 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 low density, *i.e.* groups that are loose (Figure 7A). This can be explained, because the gradient of the hierarchy is slightly steeper for higher degrees of clumping (although variation is huge, Figure 7B), and spatial structure is stronger (Figure 7C). Furthermore, the frequency of aggression in total (Figure 7D) and the frequency of interactions (aggressive and neutral) between the sexes are higher (Figure 7E) due to the smaller average distances among agents (Figure 7F).

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

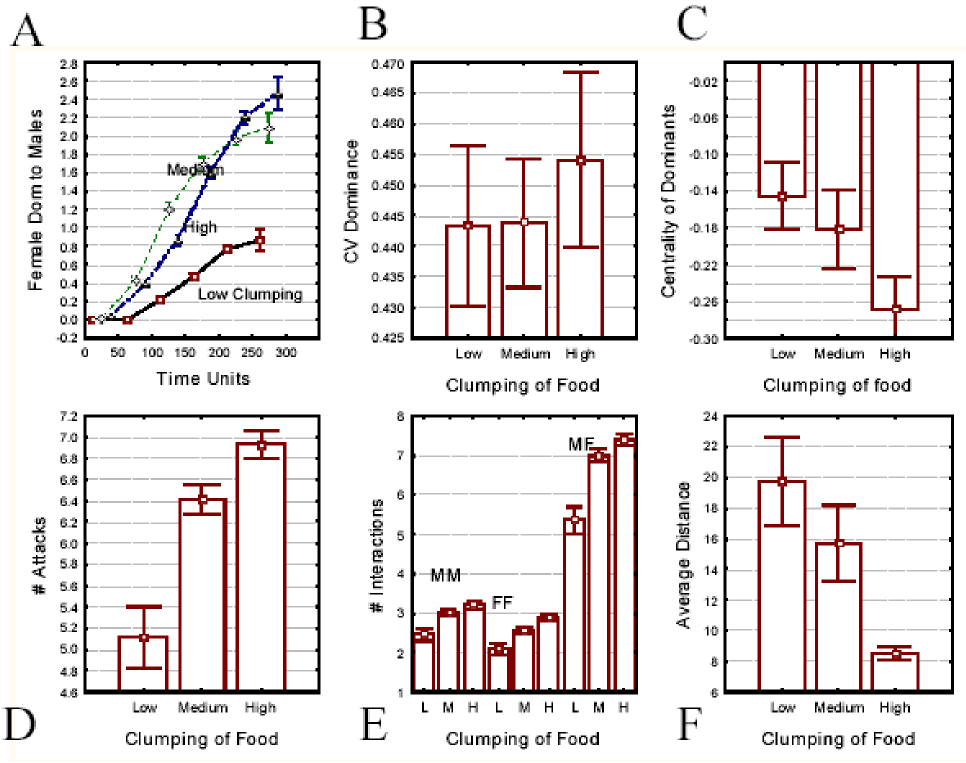


Figure 7. *Degree of clumping of food and (A) female dominance measured by the Mann Whitney U-value, (B) the gradient of the hierarchy, (C) spatial centrality of dominants, (D) total frequency of interaction/aggression, (E) number of interactions within and between the sexes, (F) average distance among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

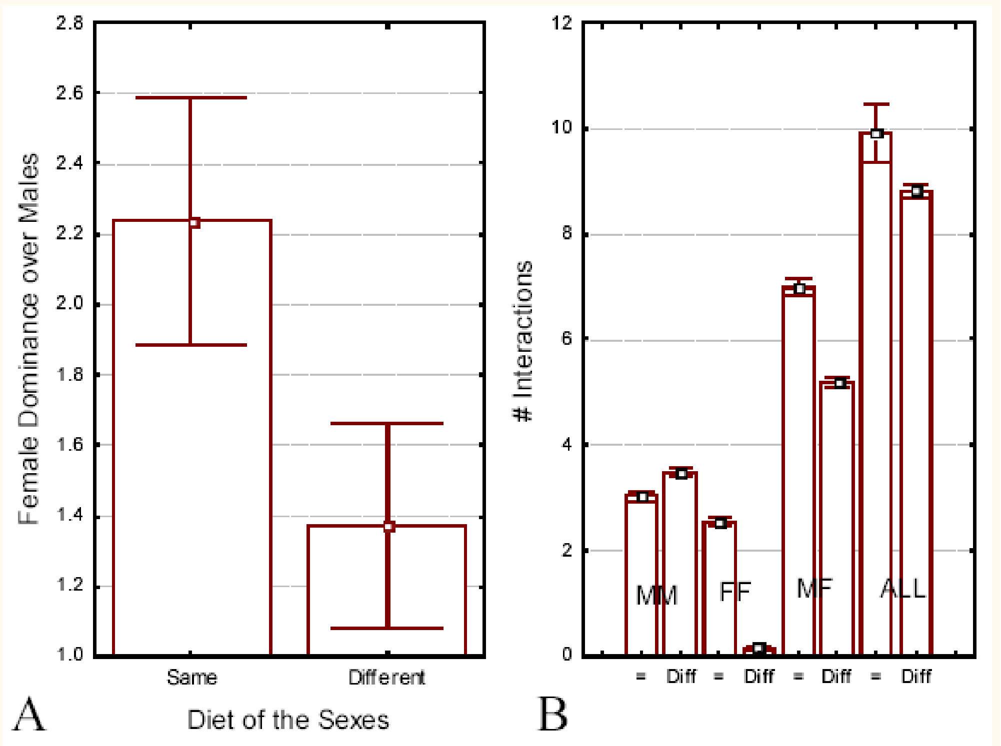


Figure 8. *Effect of diet differences between the sexes on (A) female dominance over males, and (B) number of interactions per sex, between the sexes and in total. Same: both sexes have same diet. Different: females eat insects also, but males do not.*

Dominance perception: directly visible or memory-based

In addition to the above-mentioned points, 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 (Figure 9A). Female dominance increases faster 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 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 (Figure 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 (Figure 9C). Note also that Estimators remain closer together due to the weaker development of the hierarchy.

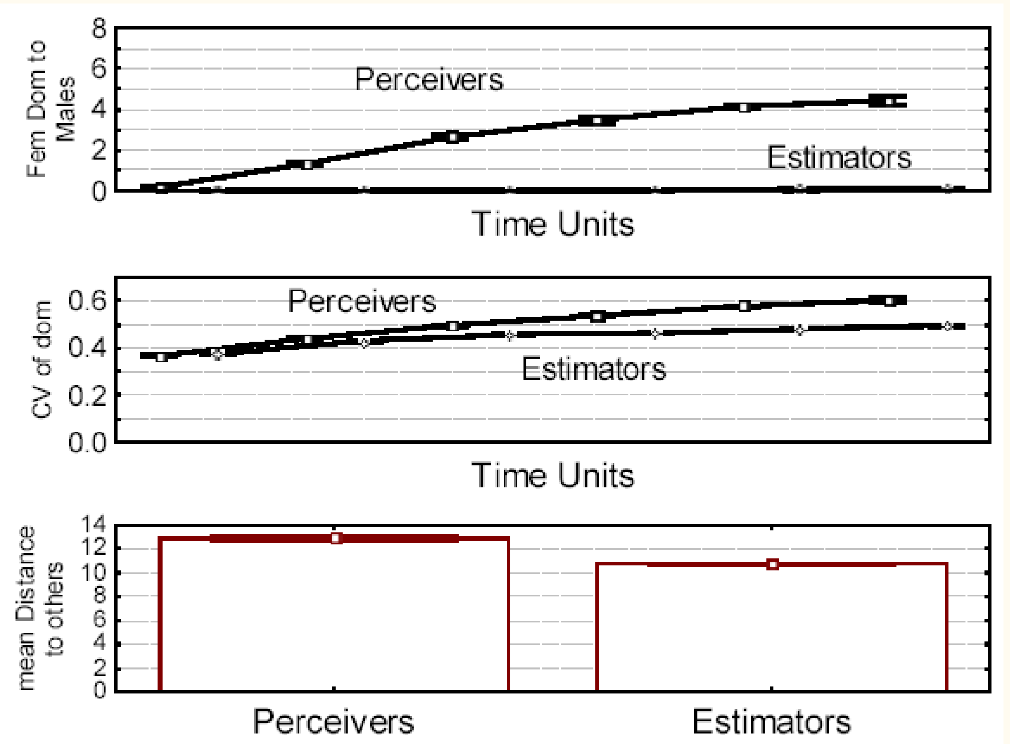


Figure 9. *Effects of perception of rank (directly by Perceivers and through memory by Estimators) on (A) female dominance (Mann Whitney U-value), (B) hierarchical differentiation, and (C) average distance among agents (mean ±S. E.).*

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. To do so we have extended DomWorld with agents of two dominance classes (Hemelrijk, 1999d). In DomWorld, we have shown that female dominance increases if there is an increase in intensity of aggression (Hemelrijk, 1999d), cohesion (Hemelrijk, 1999b), and degree of clumping of food. Furthermore, 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 tend to balance the values of both sexes (such as the influence of a higher frequency of interactions between the sexes 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 does increase the total number of interactions. This is due to the fact that mutual attraction causes a decrease in the number of intra-sexual interactions. Consequently, low-ranking females almost exclusively meet high-ranking males, whom they have no chance to defeat. In contrast, if meetings between low ranking individuals were more frequent, this might increase a low-ranking female's dominance to the extent that she may benefit from inter-sexual interactions by defeating males. This finding is similar to findings 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, and this is 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 does a system that reacts by learning (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 this (low-ranking) agents have the possibility to migrate. What happens if sex ratios are unequal and agents that are allowed to migrate will be reported on in future.

In various animal species, such as 'female-bonded' primates (Wrangham, 1980), in which females remain in their natal group for their lifetime 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.

Obviously, DomWorld 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).

Additionally, 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 subordinance (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.

Furthermore, 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. However, 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.

As regards a possible contribution of differences in the absolute and relative numbers of males and females to differences in the degree of female dominance, see chapter 5.

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 the need to invoke any separate mechanisms. Furthermore, 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 also between any classes of different dominance, such the young and the older, students and faculty *et cetera*.

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.

Acknowledgments

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4) Emergent inter-sexual dominance relations: A model and data of primates

Together with: Charlotte K. Hemelrijk

Abstract

Reports on dominance among group living animals usually concern one sex only. However, for females there are a number of advantages if they have a high dominance relative to males. Therefore, the study of inter-sexual dominance is important. Furthermore, even though the sexes differ in the main items for which they compete, it is questionable whether hierarchies of both sexes should be considered separately, because on a mechanistic level, dominance hierarchies emerge in part due to self-reinforcing effects of winning and losing fights. These occur in both sexes and are, therefore, likely also to be effective in inter-sexual fights. In this paper, we use a model to develop hypotheses about the consequences of inter-sexual winner-loser effects, on the degree of inter-sexual dominance, or female dominance relative to males. Since the adult sex ratio differs between species and groups in primates, we also study effects of the relative number of males in the group. We test these hypotheses on data of real primates. The model consists of grouping individuals that compete, whereby the winning and losing of agonistic encounters has a self-reinforcing effect. In inter-sexual encounters we switch these self-reinforcing effects on and off. We do so for a despotic and an egalitarian dominance style, and for groups with different proportions of males. Results show that if the self-reinforcing effects are switched on for inter-sexual conflicts, 1) the degree to which females dominate males is greater, 2) the hierarchical differentiation among females is higher, and 3) the hierarchical differentiation among females correlates positively with the proportion of males in the group. In contrast, in the absence of self-reinforcing effects of inter-sexual conflicts, the last result is reversed and the hierarchical differentiation among females is negatively correlated with the proportion of males. Unexpectedly, in the model the degree of female dominance over males increases with the proportion of males in the group independent of inter-sexual winner-loser effects, and more so in despotic than in egalitarian groups.

In accordance with the model, we find that in empirical data of eight macaque species, the degree of female dominance increases with the proportion of males in the group. In addition, the correlation between the proportion of males and the hierarchical gradient of females is not significant. These results indicate that in primates inter-sexual effects matter more than previously assumed.

Introduction

Although in many animal species aggression between sexes has been observed, and a bisexual dominance hierarchy can be calculated (Hemelrijk, 2003), reports on dominance relationships usually concern either males or females (for instance, see examples in Drewsbury, 1982; Ellis, 1995). The only exceptions are studies on lemuriformes, where all females are dominant over all males in some species (Kappeler, 1993). It is important to document the relative dominance of females to males, because female dominance over males gives her a number of advantages: Females may receive feeding priority (Waeber & Hemelrijk, 2003), for example, by leading the group to food (Erhart & Overdorff, 1999; Overdorff *et al.*, 2005), or by displacing males (Furuichi, 1989). Furthermore, they may be better able to control mating opportunities (reviewed for bonobos by Parish & de Waal, 2000), and reject undesired attempts of coerced copulations (Smuts & Smuts, 1993). Even though we know from empirical (Smuts, 1987) and theoretical studies (Hemelrijk *et al.*, 2003) that female dominance over males occurs in various degrees (ranging from male dominance via co-dominance to complete female dominance), studies on the relative dominance of females and males are still rare. One reason for this may be that, although there is competition between the sexes, it is rarer than among individuals of the same sex, and possibly weaker, because the sexes compete for different resources: males for mates, females for food (Trivers, 1972). However, it is unlikely that both hierarchies are entirely independent, since dominance ranks are influenced by prior fighting experience: Winning a fight increases the likelihood to win future fights, and *vice versa* for the loser. Such a winner-loser effect has been demonstrated in many animal species, and appears to be effective in both sexes (for a recent extensive review, see Hsu *et al.*, 2006).

Although a connection between self-reinforcing effects and inter-sexual dominance relations was developed in theoretical studies (Hemelrijk, 2002a; 2002b; Hemelrijk *et al.*, 2003), it has never been studied in empirical data. In this paper, we develop hypotheses that can be used to investigate the interdependence of the hierarchy of both sexes in empirical data, and we test them in real primates.

To develop these hypotheses we use a model, called DomWorld. In the model, individuals group and compete. The effects of winning and losing fights are self-reinforcing (Hsu *et al.*, 2006; Hock & Huber, 2006). The model has already been used to study the effects of a number of variables on inter-sexual dominance relations. For instance, the degree of female dominance over males increases at a higher intensity and at a higher frequency of aggression. This is in line with, respectively, findings for despotic macaques compared to egalitarian ones (Thierry, 1990a) and for bonobos compared to common chimpanzees (Hemelrijk, 2002b). Female dominance over males also increases due to sexual attraction, which is consistent with empirical findings in chimpanzees (Hemelrijk, 2003).

In the present paper, we investigate in the model the consequences of differences in strength between self-reinforcing winner-loser effects among individuals of the same sex compared to among individuals of different sexes. We confine ourselves to the extreme cases. Either only intra-sexual, but not inter-sexual, interactions influence dominance, or both inter-sexual and intra-sexual outcomes of fights have the same self-reinforcing effect on dominance. In addition, we vary the proportion of males in the group, because this differs between species and groups also in primates. In our model results we find that with an increasing relative number of males in a group female dominance over them increases and the hierarchical differentiation among females becomes stronger. We use these results as hypotheses to test in real primates, namely macaques, because here we have data from several related species and of two dominance regimes, egalitarian and despotic. These data largely confirm our hypotheses.

Methods

The Model

A brief summary of the model 'DomWorld' follows (for a more complete description see Hemelrijk, 1999c; 2000b; 2002a). The model consists of a homogeneous virtual world inhabited by individuals with two tendencies: grouping and performing dominance interactions. The motivation for individuals to group (whether to avoid predators or because resources are clumped) is not specified and irrelevant to the model. The same holds for the dominance interactions: They reflect competition for resources (such as food and mates), but these resources are not specified.

Individuals remain together via grouping rules. If an individual spots another individual within its personal space, a dominance interaction may take place. The likelihood that an individual begins an aggressive interaction depends on the risks involved. It increases with its chance to defeat its opponent. This is the so-called 'risk-sensitive attack strategy' (Hemelrijk, 2000b).

If a dominance interaction actually takes place, individuals *i* and *j* observe each other's capacity of winning, the probability of individual *i* winning is proportional to its DOM-value, relative to that of its opponent *j* (see formula 1). A stochastic effect is introduced to allow for dominance reversals: if the relative dominance of individual *i* is greater than a random number RND (drawn from a uniform distribution), it wins ($w_i = 1$), otherwise it loses ($w_i = 0$):

$$w_i = \left[\begin{array}{ll} 1 \quad \text{if} & \dfrac{\mathrm{DOM}_i}{\mathrm{DOM}_i + \mathrm{DOM}_j} > \mathrm{RND}(0,1) \\ 0 \quad \text{else} & \end{array} \right. \qquad (5)$$

To reflect the self-reinforcing effects of victory and defeat, DOM values are updated by increasing the DOM value of the winner and decreasing that of the loser by the same amount, scaled by a factor StepDom, which is explained further on:

$$\mathrm{DOM}_i = \mathrm{DOM}_i + \left(w_i - \frac{\mathrm{DOM}_i}{\mathrm{DOM}_i + \mathrm{DOM}_j} \right) * \mathrm{STEPDOM}_i \qquad (6)$$

$$\mathrm{DOM}_j = \mathrm{DOM}_j - \left(w_i - \frac{\mathrm{DOM}_i}{\mathrm{DOM}_i + \mathrm{DOM}_j} \right) * \mathrm{STEPDOM}_i$$

We modelled a 'damped' positive feedback, wherein the (expected) victory of a higher ranking opponent reinforces its DOM-value only slightly, whereas the (unexpected) success of a lower ranking individual increases its DOM-value by a greater change. This is in agreement with a detailed behavioural study of bumble bees (Honk & Hogeweg, 1981). In experiments where inter-sexual interactions were not supposed to influence dominance values, these self-reinforcing effects were omitted during inter-sexual interactions, but retained in intra-sexual interactions.

To keep the DOM-value positive, its minimum value is, arbitrarily, set at 0.001. The change in DOM-value is multiplied by a scaling factor, called StepDom, which varies between 0.1 and 1. High values of StepDom imply a greater change in DOM-value than small values, and thus indicate that single interactions may influence the outcome of conflicts more strongly (*e.g.* involving biting as opposed to threats or slaps). However, although generally high values for StepDom indicate a high intensity of aggression (see experiments), the actual intensity of a fight is given by the change of the DOM-values of both opponents: If a very high ranking individual beats a low ranking one, changes in DOM-values are relatively small even if StepDom is high; one may think of an approach-retreat interaction. Per fight the intensity of aggression is determined by its initiator.

Experiments and the Analysis of the Model

Groups consist of 10 individuals of both sexes. We vary the percentage of males. To simulate species with a different dominance style, we change the intensity of aggression (such as found in primates, for instance between egalitarian and despotic macaque females: Thierry, 1990a). We compare results of despotic societies (with a high intensity of aggression, reflected in the parameter 'StepDom' = 1 for males), and those of egalitarian societies (low intensity of aggression, StepDom = 0.1 for males). Both sexes may have the same dominance value (initial DOM = 24), or, to represent sexual dimorphism of primates (Smith & Cheverud, 2002), 'females' may initially have a lower dominance value than 'males' (initial DOM = 16 and 32, respectively, Hemelrijk & Gygax, 2004). Furthermore, because females have weaker muscles and their aggression is less intense than that of males (*e.g.* see Bernstein & Ehardt, 1985b), the females in the model have 10% of the StepDom-value of the males. We conducted 40 runs per setting. As a control, we tested the degree of hierarchical differentiation (measured as the coefficient of variation of dominance values) in a group of one sex only.

The degree of female dominance is measured as the relative position of females over males in the dominance hierarchy. It is calculated by means of the standardised Mann-Whitney U-Value (*cf.* Hemelrijk *et al.*, 2003): The number of males ranking below each female is counted, then the value of the statistic is computed as the sum of these counts, divided by maximum possible value for a specific sex ratio and group size (Figure 1). It ranges from 0 (no female dominant over a male) to 1 (all females dominant over all males).

At the start of a run, when individuals have only been activated a few times, the hierarchy is hardly differentiated and there are many dominance reversals (Hemelrijk & Gygax, 2004). Later on, after many activations, the hierarchy becomes more differentiated and is more stable. We analyse only the data of this stable phase (*i.e.* from period 200 to 260, whereby one period consists of 20 activations per individual * 10 individuals = 200 activations).

	M1	M2	M3	F1	F2	F3
M1	**x**	**33**	**1**	**7**	**28**	**3**
M2	**67**	**x**	**13**	**31**	**27**	**2**
M3	**0**	**6**	**x**	**0**	**0**	**85**
F1	**6**	**53**	**16**	**x**	**4**	**7**
F2	**9**	**26**	**9**	**4**	**x**	**3**
F3	**0**	**11**	**228**	**0**	**2**	**x**

avDI
0.73
0.48
0.12
0.72
0.57
0.39

Female dominance index

Hierarchy according to avDI: — Females dominant over:

1. M1
2. F1............. **2** males
3. F2............. **2** males
4. M2
5. F3............. **1** male
6. M3

in **5** (of maximally **9**) relationships males are subordinate to females

RelFHierPos = ***5 / 9***
= ***0.556***

Figure 1. *Calculation of degree of female dominance in imaginary data. avDI = average Dominance Index, RelFHierPos = the relative hierarchical position of females. For explanation see text.*

Empirical Data and Analysis

Empirical data have been collected from the following journals up to, and including, 2006: *Animal Behaviour* (from 1965), *Behaviour* (from 1948), *American Journal of Primatology* (from 1981), *Primates* (from 1959), *International Journal of Primatology* (from 1980) and *Folia Primatologica* (from 1963). We confine ourselves to species of the genus *Macaca*, since here the most data are available. To be used in this empirical analysis, data on a group must include a matrix of frequencies of winning fights or agonistic interactions of both sexes comprising at least four adult individuals. We used age-categories as classified by the authors; usually macaques are classified as 'adults' when they are four to five years old. We also include unpublished data collected by Bernard Thierry.

To measure the degree of female dominance in a group, we first deduce the hierarchy of the group from a matrix of agonistic interactions (*cf.* Figure 1). For this, we use the average Dominance Index (avDI), which in an earlier study was shown to be the best measure for this purpose (Hemelrijk *et al.*, 2005b). The Dominance Index is calculated for each pair of individuals as the ratio of the number of conflicts won over a particular partner, divided by the total number of conflicts with that individual. Subsequently, per individual we calculate an individual's average dominance index in relation to all group members; whenever a pair does not interact at all it is excluded from the calculation of the average. The hierarchy is established by ranking individuals: A higher average dominance index indicates a higher dominance position. The relative position of females in the dominance hierarchy is calculated by means of the standardised Mann-Whitney U-Value as explained above for the model (*cf.* Figure 1). This calculation and that of the average dominance index are performed with the program Matrix Tester v223b developed by Hemelrijk and co-workers (available on request). The gradient of the female hierarchy is determined by a normalised David's score (de Vries *et al.*, 2006).

Correlations between female dominance and sex ratio were performed for despotic and egalitarian macaque species separately. We are aware that the notion of despotic and egalitarian species as a characteristic of species has been contested, because the degree of despotism differs between the sexes. However, we have argued elsewhere that despite difference between the sexes in degree of despotism, despotism differs also between species (Hemelrijk & Gygax, 2004). Due to the small sample size of species (n = 4 species of egalitarian and 4 of despotic macaques) it was not possible to correct for the influence of phylogeny with the independent contrast method (Felsenstein, 1985). Therefore, we study the correlation over all groups of despotic species and all groups of egalitarian species. Results over the median values of the 4 species give similar but weaker results. We follow the classification based on female relationships of macaques by Thierry (1990a; 2000), so that *M. fascicularis*, *M. fuscata*, *M. mulatta*, and *M. nemestrina* are rated as despotic, and *M. arctoides*, *M. assamensis*, *M. thibetana*, and *M. tonkeana* as egalitarian (Table 1). Only for *M. mulatta* and *M. arctoides* there were sufficient groups available to perform correlations over groups within species.

Species	***# Individuals***	***# Males***	***# Females***	***Steepness female hier.***	***FemDom***	***Reference***
Despotic						
M. fascicularis	16	9	7	0.562	0.825	(Sterck & Steenbeck, 1997)
M. fuscata	9	1	8	0.793	0	(Mehlman & Chapais, 1988)
M. mulatta	11	1	10	0.036	0	(Girod & Hemelrijk, 2002)
M. mulatta	11	4	7	0.464	0.25	(Sade, 1967)
M. mulatta	10	4	6	0.652	0.417	(Sade, 1967)
M. mulatta	12	5	7	0.721	0.457	(Sade, 1967)
M. mulatta	16	7	9	0.673	0.381	(Sade, 1972)
M. mulatta	7	2	5	0.153	0.2	Thierry, pers. comm.
M. mulatta	6	2	4	0.469	0.625	(Varley & Symmes, 1966)
M. nemestrina	17	3	14	0.501	0.214	(Oi, 1990)
Egalitarian						
M. arctoides	6	1	5	0.802	0	(Estrada, 1977b; 1977a)
M. arctoides	5	1	4	0.738	0	(Rhine, 1972)
M. arctoides	5	1	4	0.814	0	(Rhine & Kronenwetter, 1972)
M. arctoides	4	1	3	0.353	0	(Rhine, 1973)
M. assamensis	23	11	12	0.254	0.205	(Cooper *et al.*, 2005)
M. thibetana	19	6	13	0.475	0.167	(Berman *et al.*, 2004)
M. thibetana	21	8	13	0.494	0.289	(Berman *et al.*, 2004)
M. thibetana	18	8	10	0.769	0.388	(Berman *et al.*, 2004)
M. tonkeana	13	3	10	0.395	0.2	Thierry, pers. comm.

Table 1: *Empirical data.*

Results

The model

First we study a model in which individuals are sexually dimorphic and intensity of aggression is high.

For each sex ratio the average degree of female dominance over males (over 40 runs) appears to be greater when there are inter-sexual winner-loser effects than when they are lacking (Wilcoxon matched-pairs signed-rank test over all sex ratios, n=9, StepDom m/f=1/0.1: t = 45, p = 0.004 two tailed; see dots versus stars in Figure 2). This arises since the dominance values of both sexes are more differentiated in the presence of inter-sexual self-reinforcing effects, because interactions with males cause greater changes in dominance due to the male's higher aggression intensity (StepDom) and their high initial dominance value (dots above stars in Figure 4) and thus lead to a greater range of dominance values of both males and females. Consequently, the highest ranking females become dominant over a few low ranking males. Note that the average absolute dominance values of females and males remain constant independent of self-reinforcing effects in inter-sexual interactions (Figure 3, male values not shown) and merely their variance changes.

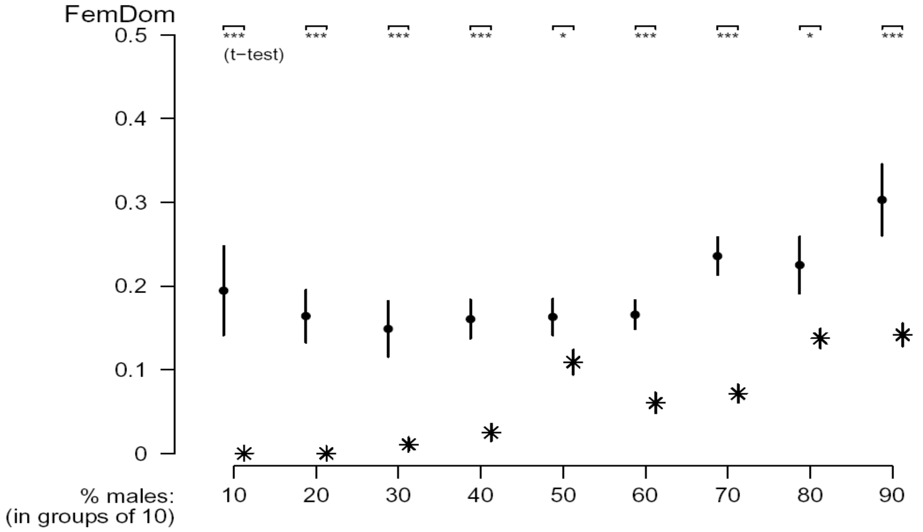


Figure 2*: Mean and standard error of female dominance over males for different sex ratios with and without inter-sexual influence on dominance (InitDom $_{M, F}$ = 32, 16). ● = inter-sexual self-reinforcing effect, * = no inter-sexual self-reinforcing effect. On top, t-test between conditions with and without inter-sexual influence (* = p < 0.05, *** = p < 0.001 two-tailed).*

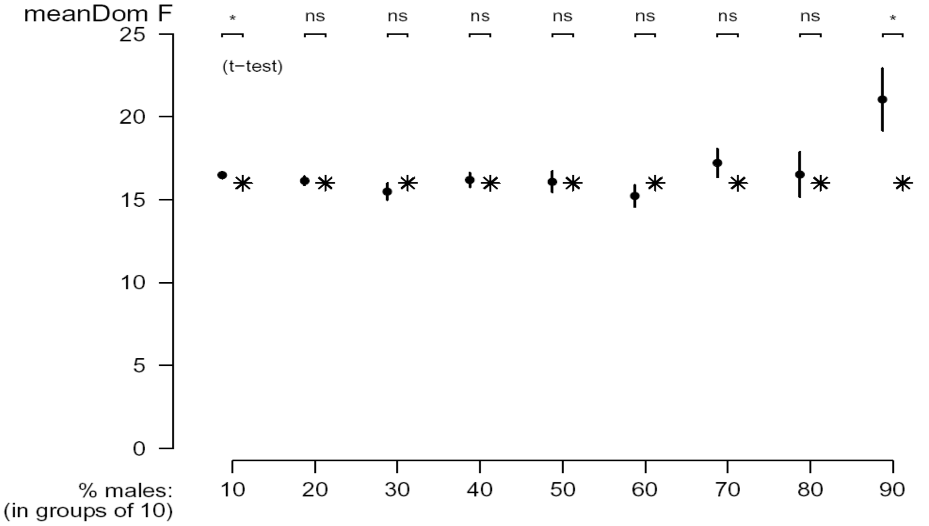


Figure 3*: Mean and standard error of absolute dominance values of females for different sex ratios with and without inter-sexual influence on dominance (InitDom $_{M, F}$ = 32, 16). Females have 10% of the intensity of aggression (= StepDom) of males. ● = inter-sexual self-reinforcing effect, * = no inter-sexual self-reinforcing effect. On top, t-test between conditions with and without inter-sexual influence (NS = 'not significant', * = p < 0.05 two-tailed).*

Second, in the presence of an inter-sexual winner-loser effect, the hierarchical differentiation (and variance) among females and among males increases with the proportion of males within a group (Figure 4, Table 2). In contrast, in the absence of inter-sexual winner-loser effects, the hierarchical differentiation among females decreases with the proportion of males (stars of Figure 4, Table 2). This is due to the fact that the absolute frequency of interactions with self-reinforcing effects per female is lower, because such effects occur only in intra-sexual encounters: if the proportion of males is high, females meet less often in intra-sexual encounters (Figure 5 a). Thus, the direction of the correlation between hierarchical differentiation among females and proportion of males indicates the presence or absence of winner-loser effects between the sexes (positive if there is an inter-sexual winner-loser effect, negative if not). Below we use the direction of this correlation to discover the degree of influence inter-sexual dominance interactions have in real primates.

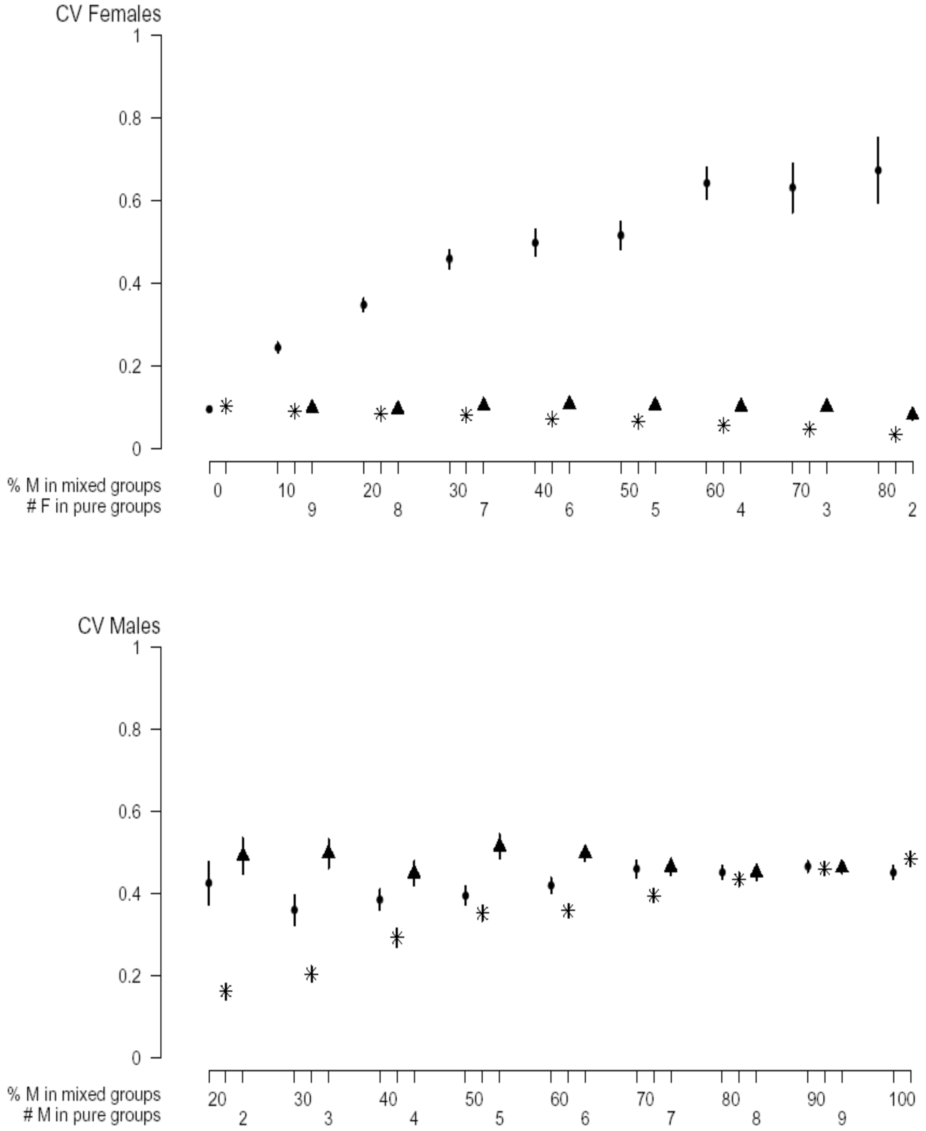


Figure 4: *Mean and standard error of the coefficient of variation (CV) of females (top) and males (bottom) for different sex ratios, with and without inter-sexual influence on dominance. Females have 10 % of the intensity of aggression (= StepDom) of males. ● = inter-sexual self-reinforcing effect, * = no inter-sexual self-reinforcing effect, ▲ = pure 1-sex groups.*

Third, unexpectedly, the higher the proportion of males is in the group, the greater the degree of female dominance over males becomes. This effect is independent of the inter-sexual winner-loser effects (dots and stars, Figure 2, Table 3). In the presence of inter-sexual winner-loser effects female dominance increases due to the fact that the number of interactions with males is larger. This causes a greater differentiation of the dominance values of both females and males (dots in Figure 4, Table 2). In the absence of inter-sexual winner-loser effects, the degree of female dominance is still positively correlated with the proportion of males, because a higher proportion of males still causes an increase of the frequency of intra-sexual interactions per male (Figure 5 a), and thus results in a stronger differentiation of the male hierarchy (Table 2). As the sex ratio becomes more male biased, the increase of the range of the dominance values among males compared to its decrease among females is greater (due to the male's higher intensity of aggression). Thus, a higher number of males in the group causes high ranking females to become more dominant over low ranking males.

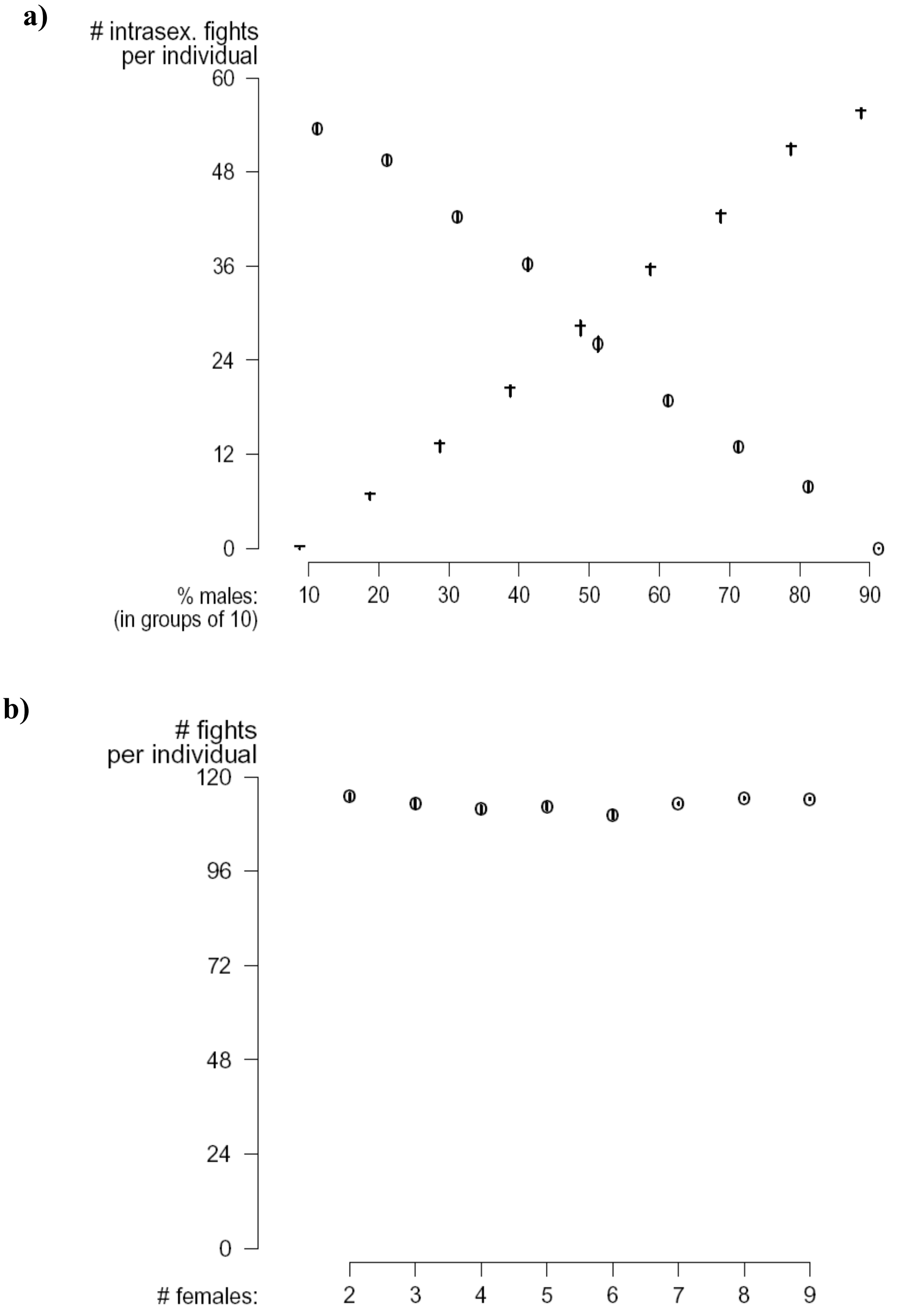


Figure 5*: a) Mean and standard error of the number of intra-sexual fights per male (-) and per female (**o**) for various proportions of males in the group, b) Mean and standard error of the number of fights per female in single sex groups of different sizes.*

Note that in single-sex groups the differentiation of dominance values is independent of the number of individuals, because the average number of interactions per individual remains the same, irrespective of group size (triangles, Figure 4; Figure 5 b). In mixed groups, however, the relative frequency of intra-sexual encounters among males and among females changes with the proportion of males: If the proportion of males is increased, the number of intra-sexual interactions decreases per female, but increases per male (Figure 5 a). Therefore, the coefficient of variation of the dominance of five females is higher when they are in a group with five males than if they are without males in a single sex group (Figure 4). This underlines that the variation of dominance, and, hence, the degree of female dominance over males, is a consequence of the sex ratio, but not of the absolute number of individuals of each sex.

In the absence of sexual dimorphism, female dominance and male dominance is equal and therefore it is not influenced by inter-sexual interactions and the proportion of males (data not shown). At a low intensity of aggression (StepDom = 0.1, egalitarian dominance style) and a great difference in initial dominance between the sexes, there is no female dominance over males, because intra-sexual hierarchies hardly differentiate due to the low impact of each interaction and the absence of social-spatial structure (Hemelrijk, 1999c; 2003). This is only a quantitative difference, but not a qualitative one (Table 3).

Kendall correlation between proportion of males and						
			CV of female DOM		CV of male DOM	
Inter-sexual effects	Sexual dimorphism	Intensity of aggression m / f	Tau	p	Tau	p
present	yes (InitDom m/f = 32/16)	1 / 0.1	0.2648	***	0.1895	***
		0.1 / 0.01	0.2949	***	0.2191	***
	no (InitDom m/f = 24/24)	1 / 0.1	0.2652	***	0.2216	***
		0.1 / 0.01	0.2959	***	0.2301	***
absent	yes (InitDom m/f = 32/16)	1 / 0.1	-0.4265	***	0.4586	***
		0.1 / 0.01	-0.4468	***	0.4286	***
	no (InitDom m/f = 24/24)	1 / 0.1	-0.4339	***	0.4459	***
		0.1 / 0.01	-0.4593	***	0.4443	***

Table 2: *Kendall correlation between the proportion of males in a group and the coefficient of variation (CV) of DOM-values of each sex. m = males, f = females. N = 40 replicates * 9 sex ratios = 360. *** = p < 0.001 two-tailed.*

Empirical Data

In line with the results of the model (Figure 2), the degree of female dominance over males in macaques appears to be significantly positively correlated with the proportion of males in the group over all despotic groups, over all egalitarian groups, and in the despotic species *M. mulatta*, but not so in the egalitarian *M. arctoides* (Table 4). The gradient of the hierarchy, however, is in none of the cases significantly correlated with the proportion of males (Table 4).

Kendall correlation between proportion of males and				
			female dominance over males	
Inter-sexual effects	Sexual dimorphism	Intensity of aggression m / f	Tau	p
present	yes (InitDom m/f = 32/16)	1 / 0.1	0.1759	***
		0.1 / 0.01	0.0157	NS
	no (InitDom m/f = 24/24)	1 / 0.1	0.0169	NS
		0.1 / 0.01	0.0514	NS
absent	yes (InitDom m/f = 32/16)	1 / 0.1	0.4460	***
		0.1 / 0.01	0	NS
	no (InitDom m/f = 24/24)	1 / 0.1	0.0019	NS
		0.1 / 0.01	-0.0101	NS

Table 3: *Kendall correlation between the proportion of males in a group and female dominance. m = males, f = females. N = 40 replicates * 9 sex ratios = 360. NS = 'not significant', *** = p < 0.001 two-tailed.*

Kendall correlation between proportion of males and					
	N	***female dominance over males***		***gradient of female hierarchy***	
		Tau	Significance	Tau	Significance
Macaca (despotic, all groups)	10	0.67	**	0.28	NS
Macaca (egalitarian, all groups)	9	0.68	**	-0.37	NS
Macaca mulatta	7	0.62	*	0.43	NS
Macaca arctoides	4	0.33	NS	- 0.36	NS

Table 4: *Kendall correlation between the median proportion of males, degree of female dominance over males, and differentiation of female hierarchy. NS = 'not significant', * = p < 0.05, ** = p < 0.01 two-tailed. See Table 1 for references.*

Discussion

The model shows a number of new results apart from the fact that at a high intensity of aggression the dominance hierarchy is steep with large differences in power and the society resembles a despotic society in macaques as we showed before (Hemelrijk, 1999c). In the new results, in the first place, the degree of female dominance over males is higher if there are inter-sexual winner-loser effects than if they are lacking. This arises because the differentiation of the dominance among females increases with the number of interactions with males: Since females start with lower dominance than males, an unexpected victory over males has more impact than one over other females (Hemelrijk *et al.*, 2003).

Second, the relation between the hierarchical differentiation among females and the proportion of males in the group depends on inter-sexual winner-loser effects: in the presence of a self-reinforcing effect both are positively correlated, but in its absence both are negatively correlated. This arises because in a group with a higher proportion of males there are relatively more males (with high intensity of aggression) and fewer females (with mild aggression) to interact with, and interactions with a high intensity lead to more differentiation. Testing this finding in real macaques, we find that the hierarchical differentiation among females and the proportion of males are not significantly correlated. Since a non-significant correlation is intermediate between a positive and a negative correlation, we conclude that inter-sexual interactions have an influence on dominance in macaques, but less so than intra-sexual interactions. It is now of interest to study these relationships between hierarchical differentiation and the proportion of males in other taxa also.

Third, surprisingly, in the model the degree of female dominance over males increases with the proportion of males in the group, independent of the presence of self-reinforcing effects of inter-sexual conflicts. This arises because the higher the proportion of males is in the group, the higher the relative number of interactions among males and the stronger their hierarchical differentiation (which has a larger range of values than the hierarchy of females, because of the male's higher intensity). Consequently, some males become very low in dominance, and, hence, subordinate to a few high ranking females. In the model, this effect is stronger at a high intensity of aggression than at a low one, thus, stronger in despotic than in egalitarian societies (due to higher aggression intensity).

In real macaques, this correlation between the degree of female dominance over males and the proportion of males is confirmed, except for the egalitarian species *M. arctoides*. Thus, female dominance may increase due to the higher average intensity of aggression of interactions in a group with more males. These empirical results show that female dominance may be a flexible trait (possibly with the exception of certain species of lemuriformes of Madagascar, Kappeler, 1993). This is also apparent from the intra-specific variation of female dominance between groups of other primate species (Digby, 1995; Overdorff *et al.*, 2005). Recent studies in non-primate species corroborate the plasticity of dominance in general. For example, an individual's dominance may differ depending on whether it is a member of a pair or of a larger group (Chase *et al.*, 2002; Chase *et al.*, 2003; Dijkstra, 2006).

As an alternative to the hypothesis that female dominance increases with the percentage of males due to the winner-loser effect, one may argue that it increases, because with fewer females, males compete more for access to them. This needs to be studied in more detail in empirical studies.

In an alternative view of female dominance, males supposedly concede feeding priority to females in exchange for mating (*e.g.* Stanford, 1998; Pochron *et al.*, 2005). Thus, males permit females to act dominantly as a kind of favour to them. It is more parsimonious, however, to assume that females become dominant over some males due to chance and winner-loser effects.

Obviously, our model is a strong simplification of the real world. For example, we omit kin relations, or migration between groups, which may play an important role in real primates. We do so in order to keep the model minimal. Further, we assume that dominance and winner-loser effect are independent of the identity of the opponents, whereas in real primates, however, individuals may recognise each other. With individual recognition, however, the results of the model remain qualitatively similar, although the development of the hierarchy slows down, and hence, the degree of female dominance too (Hemelrijk, 2000b; Hemelrijk *et al.*, 2003).

Although we used primate data to test the hypotheses generated by the model, the model itself is not primate specific. Instead, we expect that the mechanisms illustrated here may also be effective in other group living animals. It is therefore important to study hierarchies for the whole group also in species other than primates.

In sum, the model shows that the degree of female dominance over males may be influenced in three ways: 1) via winner loser effects within and between sexes, whereby the effects may differ in strength, 2) via group composition, because this affects the frequency of intra- and inter-sexual encounters, which may have different consequences, and 3) via the steepness of the intra-sexual hierarchies, since an overlap of both would result in some females dominating some males. Therefore, the hierarchies of both sexes are always interdependent to some degree, even in the absence of inter-sexual winner-loser effects. In a future publication we will provide further evidence of the impact of group composition on female dominance in a large range of primate species (Hemelrijk, Wantia & Isler, chapter 5 of this thesis).

Acknowledgements

We are grateful to Filippo Aureli, Ton Groothuis, Daan Reid, Jutta Steinhauser, Bernard Thierry, and Elske van der Vaart for comments on an earlier version.

5) The more males, the more dominant are female primates

Together with: Charlotte K. Hemelrijk & Karin Isler

Abstract

Female dominance over males in primates has mainly been studied in species of Lemuriformes of Madagascar, where all females often dominate all males. The present study is the first to analyse female dominance in a much larger range, in 22 species throughout the primate order. It shows that dominance increases with the percentage of males in the group. This correlation is not due to sexual dimorphism, but is due to the percentage of competitive interactions with males. This agrees with predictions based on our previous model of the self-reinforcing effects of winning and losing fights, the so-called winner-loser effect. Similar analyses in other species are needed to indicate the generality of this phenomenon.

Female dominance and group composition

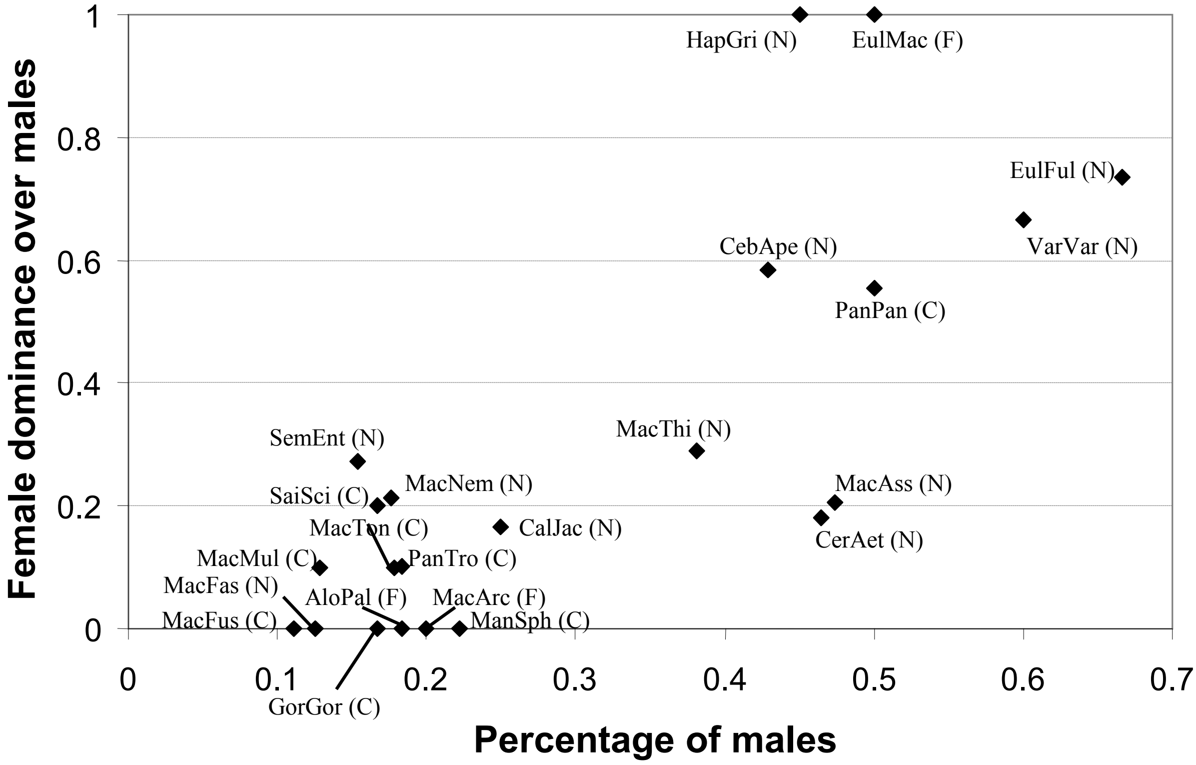
In bi-sexual groups of primates, a greater degree of female dominance over all males may be helpful to females, because females 1) suffer less sexual coercion when they are dominant (Smuts & Smuts, 1993), 2) they may have more freedom in choosing mates (Soltis, 1999), 3) they have more opportunity to lead group movement, and 4) this may result in feeding priority (Erhart & Overdorff, 1999; Overdorff *et al.*, 2005).

Complete dominance of primate females over males is found only among some species of the Lemuriformes of Madagascar (Kappeler, 1993). Without speculating about the evolutionary reasons for this peculiarity, we note that in these species sexual dimorphism is virtually absent. In most other primate species, males are considerably larger than females and such sexual dimorphism naturally impedes female dominance over males. This may be derived from the fact that in species with clear sexual dimorphism there is no female dominance or only for example, the co-dominance in male and female bonobos and the incidental dominance of female over male macaques, vervets and certain squirrel monkeys (Smuts, 1987; Boinski, 1999). However, the correlation with sexual dimorphism has never been studied systematically, nor has female dominance been measured quantitatively in a broad range of species (Smuts, 1987). Therefore in the present study, we measure by means of matrices of aggression female dominance as their relative position in the hierarchy of adults in the form of a corrected Mann Whitney U value (Hemelrijk *et al.*, 2003). This we do for 22 species of primates. Next, we correlate female dominance with the degree of male-biased sexual dimorphism by means of a contrast analysis. This correlation is not significant, when the method of independent contrasts is used to remove effects of phylogenetic relationships (branch length based on Purvis (1995), p =0.678, Table 1). A negative correlation in raw data per species is caused by the special adaptation for female dominance of lemurs, such as their masculinised genitals (Kappeler, 1993). By using the independent contrast method, we make sure that this specialised group does not exert undue influence on the correlations. Thus, unexpectedly, female dominance is not determined by sexual dimorphism.

What else influences female dominance apart from body size? Dominance relations are also affected by the self-reinforcing effects of winning and losing fights (Hsu *et al.*, 2006; Chase *et al.*, 2002). Such self-reinforcing effects imply that, after losing a fight, the loser has a greater chance to be defeated in the next conflict and vice versa, the winner has a greater chance to be victorious in a subsequent encounter. In one of our previous models we have shown that the winner-loser effect may also influence the dominance relationship between the sexes (Hemelrijk *et al.*, 2003).

Among other things, our model predicts an increase of female dominance with an increase in the intensity of aggression and thus with the percentage of males in the group, because males have a higher intensity of aggression. In the present study we test the latter hypothesis, *i.e.* that female dominance increases with the percentage of males in the group. We find that there is a positive correlation between female dominance and the percentage of males in a group (Figure 1, branch length based on Purvis (1995), p =0.002, Table 1).

This correlation may, however, be affected by sexual dimorphism. For instance, in case of strong sexual dimorphism it has been suggested that the number of males in the group tends to be few due to competition among them (Clutton-Brock & Harvey, 1977). However, sexual dimorphism and the percentage of males are not correlated (P=0.631) and when effects of sexual dimorphism are partialled out, the correlation between female dominance and the percentage of males in the group remains highly significant (P=0.001, Table 1). All results remain qualitatively the same if we confine the analysis to the study of groups under natural and captive free-ranging conditions (N=14).



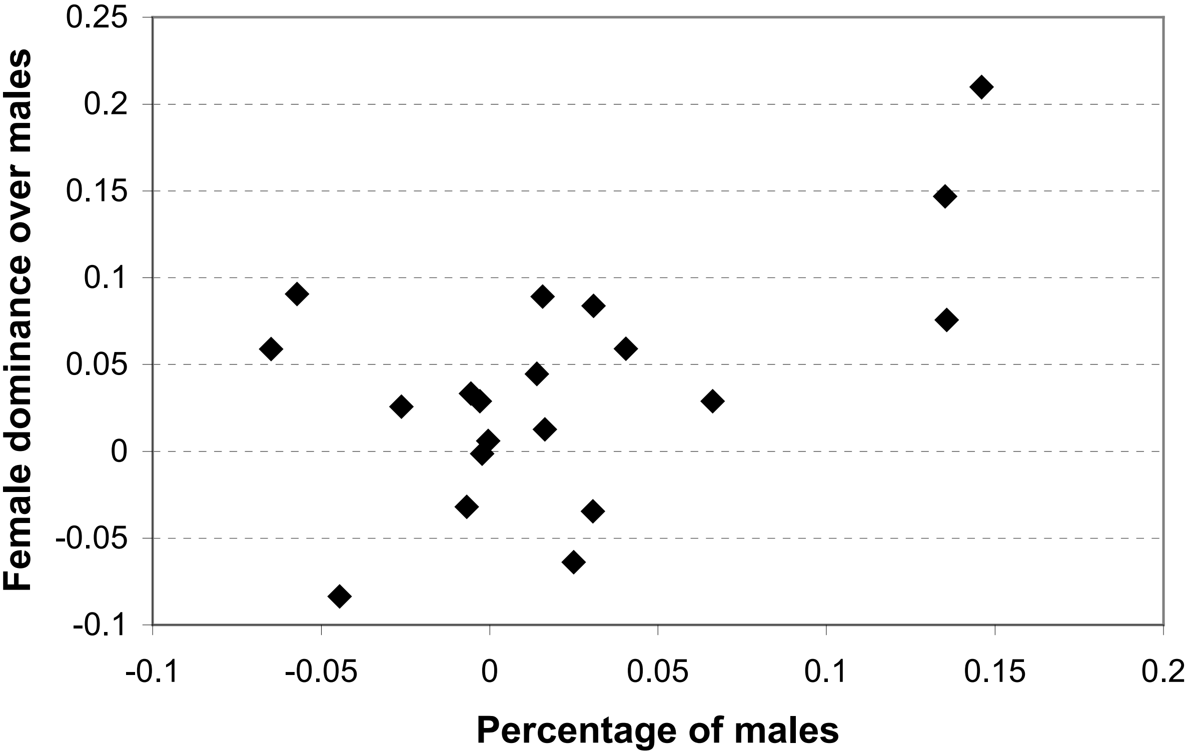


Figure 1*: Female dominance and the proportion of males in a group a) Raw data (medians). AloPal = Alouatta palliata; CalJac = Callithrix jacchus; CebApe = Cebus apella; CerAet = Cercopithecus aethiops; EulFul = Eulemur fulvus rufus; EulMac = Eulemur macaco flavifrons; GorGor = Gorilla gorilla beringei; HapGri = Hapalemur griseus; MacArc = Macaca arctoides; MacAss = Macaca assamensis; MacFas = Macaca fascicularis; MacFus = Macaca fuscata; MacMul = Macaca mulatta; MacNem = Macaca nemestrina; MacThi = Macaca thibetana; MacTon = Macaca tonkeana ManSph = Mandrillus sphinx; PanPan = Pan paniscus; PanTro = Pan troglodytes; SemEnt = Semnopithecus entellus; SaiSci = Saimiri sciureus; VarVar = Varecia variegata. See table 2 for references. Studies under natural conditions are marked (N), free-ranging (F) and captive (C).*

b) Contrast values.

This association between female dominance over males and the percentage of males may be explained in three ways. First, the 'value' of females (and therefore their dominance over males) may increase with their scarcity as a kind of frequency dependent effect (DeBenedictus, 1978). This strengthens the argument of Goodall (1986) who says that during their tumescent period, females are in a good position to bargain. However, this explanation is unlikely to be valid, because the present data set contains few data from a mating season. Further, this hypothesis suggests that female dominance increases with the percentage of competitive interactions among males, but this appears not to be the case in our data (Table 1, last column).

	N[1]	**FemDom – SexDim**	**FemDom – % Males** (Figure 1)	**% Males – SexDim**	**FemDom – % Males** (SexDim partialled out)	N[2]	**FemDom – %IntsWith Males**	**FemDom vs. %IntMM** (only wild/free-ranging)
Raw data								
r^2 (slope)	22	0.269 (neg)	0.616 (pos)	0.150 (neg)	0.549 (pos)	14	0.526 (pos)	0.044 (pos)
p		0.013	<0.0001	0.075	<0.0001		0.003	0.470
Independent contrasts								
r^2 (slope)	21	0.0002 (pos)	0.306 (pos)	0.038 (pos)	0.319 (pos)	13	0.225 (pos)	0.0001 (neg)
p		0.678	0.002	0.631	0.001		0.088	0.941

Table 1: *Regression analyses. Slopes of least-squares regression and p-values for raw data and independent contrasts. [1] : All studies are included. [2] : Only studies on wild and free-ranging colonies are included, because the frequency of interactions is strongly increased in captive conditions. For empirical data see table S1. FemDom= female dominance, SexDim = sexual dimorphism, %Males = percentage of males in the group, %IntsWithMales = percentage of interactions of both sexes with males. %IntMM = percentage of interactions among males.*

Second, the causal arrow may conceivably be reversed, because we are dealing only with a correlation. Therefore, female dominance may not be caused by the percentage of males, but cause it: it allows a higher percentage of males in the group. This may arise when males do not have much to compete for, as has been suggested for hyenas (East & Hofer, 2001). If this were true, we would expect a negative correlation between the frequency of aggression among males and the degree of female dominance over them. We do not find this in our data, however (Table 1, last column).

Third, our previous model (Hemelrijk *et al.*, 2003) suggests that the correlation between female dominance and the percentage of males in the group is due to the winner-loser effect operating in both sexes. In the model a higher percentage of males in the group leads to a higher frequency of interactions of both sexes with males. Therefore, the hierarchy among males develops more strongly, and a few males will rank very low, below some high-ranking females. Due to the large number of males, females will also interact more often with males. Therefore, they have more opportunities to beat higher ranking males by chance, which, due to its unexpectedness, has a greater positive effect on their dominance than the negative effect due to losing. Consequently, this increases their capability to become victorious again. As well, due to the greater number of their interactions with males and the greater intensity in aggression of males, the hierarchy of females differentiates more strongly than when they interact more rarely with males. Consequently, a number of females ascend to a very high rank and therefore above low ranking males. Thus, we expect a correlation between female dominance and the percentage of fights of both sexes with males. This appears to be the case, although the correlation of female dominance with the percentage of interactions with males is only significant in the raw data (P=0.003), and after correction for phylogenetic effects there is only a trend (P=0.088, Table 1). This explanation is also supported by other findings about the relation between aggression and the self-reinforcing processes mentioned above: viz. that female dominance increases at a higher intensity of aggression (Hemelrijk, 1999d) and at a higher number of interactions (Hemelrijk & Wantia, 2005) is supported by empirical studies. In despotic species of macaques in which intensity of aggression is higher, female dominance is more common than in egalitarian species where the intensity of aggression is low (Thierry, 1990a). Furthermore, although bonobos and common chimpanzees exhibit a similar degree of sexual dimorphism, the frequency of aggression among female bonobos is greater (due to their denser and more permanent grouping) and female dominance over males is much more common (Hemelrijk, 2002b).

It is generally acknowledged that intra-sexual dominance varies. For instance, when, as an experiment, a group of male rhesus monkeys was introduced into another group, their dominance relations among themselves appeared to depend on the social context, such as the order of introduction in the group (Bernstein & Gordon, 1980). Thus their dominance was variable. Our present study shows further that female dominance over males appears also to be variable and specifically to depend on social context (Kappeler, 1993). Note that significant correlations between female dominance and the percentage of males in different groups of a single species will only be expected if dominance of one sex over the other is partial - that is, incomplete. For instance, in certain species of Lemuriformes where female dominance is complete, the dominance of females over males cannot increase any further, even if the number of males is increased. As well, the study of species of non-primate taxa also shows that the relative dominance of morphs and personalities may differ depending on the social context, for example if individuals are kept in a pair or a group (Chase *et al.*, 2002; Chase *et al.*, 2003): In cichlids, the relative dominance of two morphs, the red and the blue one (Dijkstra, 2006), differ according to circumstances: whether they are members of a pair or of a group. In great tits this changes the relative dominance of different personalities (bold and cautious). In pairs bold (aggressive) individuals are dominant over cautious (mild) ones (Verbeek, 1996), but in groups we see that the reverse happens (Verbeek *et al.*, 1999). Clearly, we need systematic analyses of both female dominance and type dominance (of morph and personality) in groups of different compositions.

In sum, the results presented here demonstrate that, in line with our previous model, female dominance in primates increases with the percentage of males in the group. This may depend on the winner-loser effect and on self-organisation. Since the winner-loser effect operates in virtually all animal species that live in groups, including humans, our results may be relevant to a broad range of taxa (as long as female dominance is incomplete). To suggest boldly a far-reaching effect, we may expect that changing sex ratios caused by selective abortion in some countries may in the near future produce an increase in female dominance in terms of social power and influence.

Acknowledgements

We would like to thank Elizabeth Erhart, Wolfgang Goymann, Peter Kappeler and Daan Reid for comments.

Species	Condition	# Adults	% Males	SexDim	FemDom	%fights with M	%MM	Reference
Alouatta palliata	f	18	0.167	1.34	0.000	0.479	0.066	(Jones, 1980)
Alouatta palliata	f	10	0.200	1.34	0.000	0.343	0.041	(Jones, 1980)
Callithrix jacchus	n	4	0.250	0.98	0.000	0.438	0.000	(Digby, 1995)
Callithrix jacchus	n	8	0.250	0.98	0.167	0.521	0.000	(Digby, 1995)
Callithrix jacchus	n	8	0.500	0.98	0.625	0.528	0.028	(Digby, 1995)
Cebus apella	n	7	0.429	1.45	0.583	0.486	0.200	(Izawa, 1980)
Cercopithecus aethiops	n	6	0.500	1.43	0.111	0.786	0.625	(Struhsaker, 1967)
Cercopithecus aethiops	n	7	0.429	1.43	0.250	0.500	0.321	(Struhsaker, 1967)
Eulemur fulvus rufus	n	6	0.667	0.97	0.750	1.000	0.732	(Ostner & Kappeler, 1999)
Eulemur fulvus rufus	n	9	0.667	0.97	0.722	1.000	0.882	(Ostner & Kappeler, 1999)
Eulemur macaco flavifrons	f	4	0.500	0.94	1.000	0.917	0.194	(Digby & Kahlenberg, 2002)
Gorilla gorilla berengei	c	6	0.167	2.24	0.000	0.356	0.000	(Meder, 1985)
Hapalemur griseus	n	4	0.500	1.09	1.000	1.000	0.018	(Waeber & Hemelrijk, 2003)
Hapalemur griseus	n	5	0.400	1.09	1.000	0.983	0.133	(Waeber & Hemelrijk, 2003)
Macaca arctoides	f	6	0.167	1.32	0.000	0.153	0.000	(Estrada, 1977b)
Macaca arctoides	c	5	0.200	1.32	0.000	0.075	0.000	(Rhine, 1972)
Macaca arctoides	c	4	0.250	1.32	0.000	0.305	0.000	(Rhine, 1973)
Macaca assamensis	n	23	0.478	1.64	0.205	0.803	0.411	(Cooper *et al.*, 2005)
Macaca fascicularis	n	16	0.563	1.59	0.825	0.639	0.164	(Sterck & Steenbeck, 1997)
Macaca fascicularis	c	8	0.125	1.59	0.000	0.326	0.000	(Butovskaya *et al.*, 1996)
Macaca fascicularis	c	10	0.100	1.59	0.000	0.417	0.000	(Butovskaya *et al.*, 1996)
Macaca fuscata	c	9	0.111	1.37	0.000	0.670	0.000	(Mehlman & Chapais, 1988)
Macaca mulatta	c	11	0.091	1.25	0.000	0.167	0.000	(Girod & Hemelrijk, 2002)
Macaca mulatta	c	6	0.167	1.25	0.200	0.200	0.000	(Thierry, pers. comm.)
Macaca nemestrina	n	17	0.176	1.72	0.214	0.461	0.068	(Oi, 1990)
Macaca thibetana	n	18	0.333	1.43	0.167	0.702	0.090	(Berman *et al.*, 2004)
Macaca thibetana	n	21	0.381	1.43	0.289	0.544	0.083	(Berman *et al.*, 2004)
Macaca thibetana	n	18	0.444	1.43	0.388	0.719	0.124	(Berman *et al.*, 2004)
Macaca tonkeana	c	8	0.125	1.21	0.000	0.141	0.000	(Thierry *et al.*, 1990)
Macaca tonkeana	c	13	0.231	1.21	0.200	0.163	0.007	(Thierry, pers. comm.)
Mandrillus sphinx	c	5	0.200	2.45	0.000	0.231	0.000	(Bout & Thierry, 2005)
Mandrillus sphinx	c	9	0.222	2.45	0.000	0.236	0.000	(Feistner, 1989)
Pan paniscus	c	6	0.500	1.36	0.556	0.971	0.176	(Vervaecke *et al.*, 2000b)
Pan troglodytes	c	13	0.308	1.27	0.111	0.902	0.283	(Hemelrijk & Ek, 1991)
Pan troglodytes	c	15	0.333	1.27	0.091	0.938	0.307	(Hemelrijk & Ek, 1991)
Saimiri sciureus	c	6	0.167	1.18	0.200	0.045	0.000	(Masataka & Biben, 1987)
Semnopithecus entellus	n	13	0.154	1.65	0.273	0.230	0.000	(Sommer *et al.*, 2002)
Varecia variegata	n	5	0.600	0.99	0.667	0.891	0.063	(Overdorff *et al.*, 2005)
Varecia variegata	n	4	0.500	0.99	0.750	0.902	0.024	(Overdorff *et al.*, 2005)

Table 2*: Raw data and references. % of fights with M = proportion of all fights that included males, % MM = proportion of all fights between males.*

Part II: Inter-group competition

6) Coexistence of bold and cautious personality types in primates: A model

Together with: Charlotte K. Hemelrijk

Abstract

In many taxa, individuals of a single group differ from one another in a number of correlated traits, so-called personality types. Usually, bold and cautious types are distinguished from those who are aggressive, for example. It is still unresolved how both types coexist. Although several explanations have been suggested, there is no evidence that they apply to primates. The aim of the present paper is to deliver hypotheses relevant to primates to explain coexistence by using a process-oriented model. We investigate the model in relation to two explanations. First, that each personality differs in its performance in different contexts, *i.e.* in competition within and between groups. Second, that social stability is higher in mixed groups of both types than in pure groups of a single type. As indicators of social stability we take the frequency of aggression, and the stability of the hierarchy.

We use a model, called DomWorld, because it previously showed resemblance with real primate societies, and personality types (bold and cautious). The model only incorporates grouping and fighting, whereby the effects of winning and losing are self-reinforcing. To model encounters between groups, we develop a new model, called GroupWorld, that is based on DomWorld. We simulate bold and cautious personalities as attack strategies. Bold individuals attack always, whereas cautious individuals attack risk-sensitively, *i.e.* only when the chance to win is high. As regards social stability, the frequency of aggression and the stability of the hierarchy both appear to be high in pure bold groups, low in pure cautious ones, and intermediate in mixed groups. Thus, we find no evidence of increased stability in mixed groups. Furthermore, we find that within groups bold individuals usually lose against cautious ones, but in competition between groups, groups with a higher percentage of bold individuals outcompete those with more cautious individuals. Thus, the performance of the personality types differs between contexts and this may support their co-existence. In evolutionary terms, one may speculate that coexistence may be favoured by selection at different levels, that of the individual and of the group.

Introduction

In many species, individuals differ from one another in a number of correlated traits, so-called personality types (*e.g.* Oortmerssen & Busser, 1989; Carere *et al.*, 2001; Thierry, 2004; Capitanio, 2004; Groothuis & Carere, 2005). Personality types have been described in many species, ranging from invertebrates to the great apes (Gosling, 2001; Sih *et al.*, 2004a; 2004b; Réale *et al.*, 2007). In particular, a 'bold' and a 'cautious' personality type have been distinguished: Bold individuals show high levels of aggression, while cautious personalities attack less often (reviewed by Koolhaas *et al.* 1999). Several authors suggest that personality types have been important targets of selection (Oortmerssen & Busser, 1989; Réale & Festa-Bianchet, 2003; Capitanio, 2004; Sih *et al.*, 2004b; Dingemanse & Réale, 2005). However, in primates where both types exist (Clarke & Boinski, 1995) the few indications of performance that exist all point to disadvantages of being extremely bold (Mehlman *et al.*, 1994; Higley *et al.*, 1996; Cleveland *et al.*, 2004; Dingemanse & Réale, 2005). It is thus unclear why both personality types still coexist in a group, and why one type has not displaced the other over time.

For several other species than primates the following explanations for co-existence have been suggested. One explanation is that individuals in mixed groups of bold and cautious personalities experience more social stability and less stress than individuals in pure groups of a single type (suggested for pigs, Hessing *et al.*, 1994; Ruis *et al.*, 2002). Another explanation is that different personality types have been adapted to different contexts. For example, bold individuals appear to be better adapted to phases of migration, whereas cautious ones do better during territorial phases (mice: Oortmerssen *et al.*, 1985; Oortmerssen & Busser, 1989). Further, bold individuals grow faster than cautious ones when food can easily be monopolised, but slower when not, for example in spatially complex habitats (trout: Höjesjö *et al.*, 1998). In addition, fitness may depend on the frequency of a type in a population as hypothesised by Both *et al.* (2005): Individuals of each type may have a high fitness when they are few and low fitness when they are many. As well, fitness of a personality may depend on combination of age and the presence or absence of high predator pressure (bighorn sheep: Réale & Festa-Bianchet, 2003; reviewed by Dingemanse & Réale, 2005). Finally, selection pressure on one or the other type may fluctuate between years (Dingemanse *et al.*, 2004; Réale & Festa-Bianchet, 2003). In all of these examples, context dependent performance facilitates the coexistence of different types.

Since in primates support for any of these explanations for the co-existence of personality types is currently lacking, we need to develop a new hypothesis. The aim of the present paper is to do so in a model. We compare performance between two contexts, namely competition within and between neighbouring groups, because this is of great importance in primates as it influences dominance style and group survival (Hauser *et al.*, 1986; van Schaik, 1989; Takahata *et al.*, 1994; Sugiura *et al.*, 2002). Further, we study whether individuals in mixed groups enjoy more social stability than those in pure ones. Here social stability is indicated by a low frequency of aggression within a group, and a high stability of the hierarchy.

We use a process-oriented model instead of a game theoretic model (Korte *et al.*, 2005; Costantini, 2005; McElreath & Strimling, 2006), because we are interested in mechanisms, rather than the optimisation of strategies.

We use a new model called GroupWorld that simulates several groups with competition within and between them. Interactions within a group are based on a former model called DomWorld, because this has already been shown to generate many features of primate societies and personality types (Hemelrijk, 1999d; 2002a; Hemelrijk & Wantia, 2005). DomWorld consists of individuals that group and compete. The effects of winning and losing fights are self-reinforcing, so that winners have an increased chance to win again, and vice versa for losers. Such winner-loser effects have been demonstrated in a wide range of animal species (Hsu *et al.*, 2006; Hock & Huber, 2006). Bold personality types were simulated as individuals that attack obligately, *i.e.* always (Pagel & Dawkins, 1997), and cautious personalities as risk-sensitive individuals that only attack when the chance to win is high (Jackson, 1991; Datta & Beauchamp, 1991). The behaviour of individuals in the model appears to be similar to that of bold and cautious types in great tits (Hemelrijk & Wantia, 2005; Dingemanse & Goede, 2004): For instance, in the model and in the real bird, bold types developed extreme dominance ranks (high and low, Carere *et al.*, 2001), and on average were superior to cautious individuals (Verbeek *et al.*, 1999). Further, it appeared that by increasing a single parameter (the intensity of aggression) the type of society switches from egalitarian to despotic with traits that resemble societies of despotic macaques (Hemelrijk, 1999d; 2002a). We study success of both types (bold and cautious) in competition within and between groups for different ratios of both types per group. Furthermore, we compare social stability (indicated by a low frequency of aggression and stabile hierarchy) between pure and mixed groups.

Methods

The models

We use a model of a single group, and one of multiple groups.

A single group

Individuals group and compete as described before ('DomWorld', Hemelrijk, 1999d; Hemelrijk, 2000b). Each individual has a variable called 'DomValue', representing its fighting capacity. At the beginning, identical DomValues are assigned to all individuals; DomValues differentiate due to fights in the course of the simulation. Whether or not an encounter of two individuals results in a fight depends on the attack strategy (see below). If a fight takes place, its outcome is determined by following Formula (1).

$$\text{DomRatio}_{\text{initiator}} := \text{DomValue}_{\text{initiator}} / (\text{DomValue}_{\text{initiator}} + \text{DomValue}_{\text{opponent}}) \qquad (1\text{ a})$$

$$\begin{array}{lll} \text{if} & (\mathit{Rand}) < \text{DomRatio}_{\text{initiator}} & : \text{initiator wins} \\ \text{else} & & : \text{initiator loses} \end{array} \qquad (1\text{ b})$$

Rand is a random number between 0 and 1, drawn from uniform distribution. After the fight, the dominance values of both individuals are updated following Formula (2): A winner's DomValue increases, so that it has a higher chance to win again, and vice versa for the loser.

$$\begin{array}{ll} \text{DomValue}_{\text{initiator}} & := \text{DomValue}_{\text{initiator}} + (w - \text{DomRatio}_{\text{initiator}}) * \text{StepDom}_{\text{initiator}} \\ \text{DomValue}_{\text{opponent}} & := \text{DomValue}_{\text{opponent}} - (w - \text{DomRatio}_{\text{initiator}}) * \text{StepDom}_{\text{initiator}} \end{array} \qquad (2)$$

w = 1 if initiator won, w = 0 if initiator lost. 'StepDom' stands for the intensity of aggression: High values of StepDom cause large changes in DomValue, *i.e.* fights are fierce. Since the opponent reacts to the attack of the initiator, the StepDom of the initiator is used for both participants. StepDom has proven to be a crucial parameter in the model. By increasing its value, groups switch from egalitarian to despotic dominance styles, which show great similarity to societies of real primates (Hemelrijk, 1999d). Further, changes in DomValue depend on whether the outcome of the fight is likely: If it is expected (large DomRatio), the fight will only result in small changes of DomValue (Formula 2). This may be seen as an approach-retreat interaction instead of a real fight. If, however, the outcome is unexpected and a low ranking individual beats a high ranking one, the changes in DomValue are large.

Multiple groups

To model encounters between groups, we developed a model called GroupWorld, in which groups of different types are placed next to each other in a circle to avoid border effects. A fixed number of fights within and between groups are performed alternating (for numbers see Experiments). Dominance interactions between individuals of different groups also follow Formulas (1) and (2). However, since in competition between groups of real primates higher ranking individuals are significantly more often involved (Cheney, 1987; Perry, 1996; Kitchen *et al.*, 2004; Cooper, 2004; Majolo *et al.*, 2005) we also implement this in the model: The probability of an individual *k* to engage in encounters between groups, $P_{BG}(k)$, is equal to the proportion of *k*'s DomValue of the summed DomValues of all individuals of the group (Formula 3).

$$P_{BG}(k) \;=\; DomValue(k)\,/\,\sum_{i=1}^{n} DomValue(i) \qquad (3)$$

n = number of group members. In DomWorld, the spatial structure of the group determines who meets whom. To reduce computational costs we did not represent space in the multi-group model, but in order to reflect the effect of space on encounter frequency, at a high StepDom (despotic), we gave individuals a higher chance to meet others with similar DomValues, and at a low StepDom we made them meet others randomly (Hemelrijk, 1999d).

Attack strategies

Bold and cautious individuals differ in the way they are sensitive to risks (Hemelrijk & Wantia, 2005). Therefore, we model bold individuals as those that do not care about risks and always attack others (the obligate attack strategy), whereas cautious individuals are more likely to attack when their chance to win is higher (risk-sensitive strategy). This is implemented as follows: prior to attacking, individuals estimate their chance of winning by performing a 'mental battle', following Formula (1). If they win this mental battle, they initiate a real fight; otherwise they turn and walk away. The outcome of the real fight is determined by re-calculating Formula (1).

Experiments and parameters

We used groups of 30 individuals (instead of 10 in earlier work, Hemelrijk, 1999d) to allow for a large number of group compositions of both types. We also study pure groups of bold or cautious individuals. In DomWorld, one simulation consists of 130 time steps. Per time step individuals are activated 400 times.

In the multi-group model, GroupWorld, eight groups of two different compositions (pure risk-sensitive vs. pure obligate, pure risk-sensitive vs. mixed, or pure obligate vs. mixed) are arranged along a circle, in alternating order. As regards the frequency of fights within and between groups, our parameter settings take into account the finding that in real primates fights between groups are relatively rare (macaques: between 0.3 and 0.64 per group per day, Cooper, 2004) Results remain qualitatively similar if the number of fights within groups varies in the range 100 to 1000, and that of fights between groups lies in the range of 10 to 100 (as long as there are many more fights within groups than between them). Therefore, we use here an intermediate setting in which 500 fights within groups are followed by 50 encounters between groups; this scenario is repeated 128 times per run.

In all simulations, individuals start with an initial DomValue of 24, and unless otherwise mentioned, intensity of aggression is high (StepDom = 1). For all conditions results are based on 50 replicate runs.

Measurements

Within groups, we measure the frequency of aggression of a run during its last time step, when the dominance is established (Hemelrijk & Gygax, 2004).

The stability of the hierarchy is calculated as the Kendall rank correlation between the rank order of individuals' DomValues 25 time steps before the end of the run, and at the end of a run (during the 'stable phase', *cf.* Hemelrijk & Gygax 2004). A high Kendall-Tau-value indicates a stable hierarchy.

The 'winratio' is calculated as the number of fights won by one strategy over the other, divided by the number of all fights between individuals of both strategies. Differences in winning frequency are tested with the X^2 goodness of fit test. We compare per condition the number of victories observed in 50 runs to the number of victories expected by chance.

The differentiation of the hierarchy is determined by the coefficient of variation of the DomValues at the end of a run. A low coefficient of variation indicates a weakly developed hierarchy, whereas a high coefficient of variation indicates a strong development of the hierarchy with few rank reversals (Hemelrijk, 1999d).

Note that through differences in the implementation, the coefficient of variation is greater in the multi-group model than in the single group model (compare Figure 2 and 5). However, this does not affect the main findings.

Results

Performance in different contexts

Which personality type wins depends on the context: Whereas within groups individuals that attack obligately tend to lose (Figure 1), they win in fights between groups (Figure 2).

If we look at a single group of individuals of both personality types, the obligate attack strategy has a lower win ratio than the risk-sensitive strategy for most group compositions (Figure 1 a). This happens because obligate attackers assault all opponents they encounter without discrimination, and consequently often lose against higher ranking individuals. Risk-sensitive individuals, in contrast, specifically attack opponents with lower dominance values, and therefore win more often, only in groups where individuals of one type are very rare, the win-ratio of both types is equal (Figure 1 a). This is because when there are few individuals that attack obligately, their hierarchy is relatively weakly developed (Figure 2), so that there are no individuals with extremely low dominance values to be picked on by risk-sensitive individuals. If we assume that in addition, bold individuals also have a higher intensity of aggression than cautious ones, as may be the case in real animals, risk sensitive individuals win always (obligate attack: StepDom = 1; risk-sensitive: StepDom = 0.1, Figure 1 b). This arises because due to the low intensity of aggression, their hierarchy develops more slowly, and there are less very low ranking individuals that could be easily defeated.

In contrast, in encounters between groups, those groups with more obligate attackers beat those with fewer (Figure 2). This is because in groups with many individuals that attack obligately the hierarchy is more strongly developed (since the frequency of aggression is higher, see below and Figure 5). As a consequence, those individuals that participate in inter-group fights (*i.e.* the highest ranking individuals of a certain group) have higher dominance values than those of groups with more risk-sensitive individuals.

Results are qualitatively similar if we arrange groups on a two-dimensional grid, so that every group competes with four neighbours (data not shown).

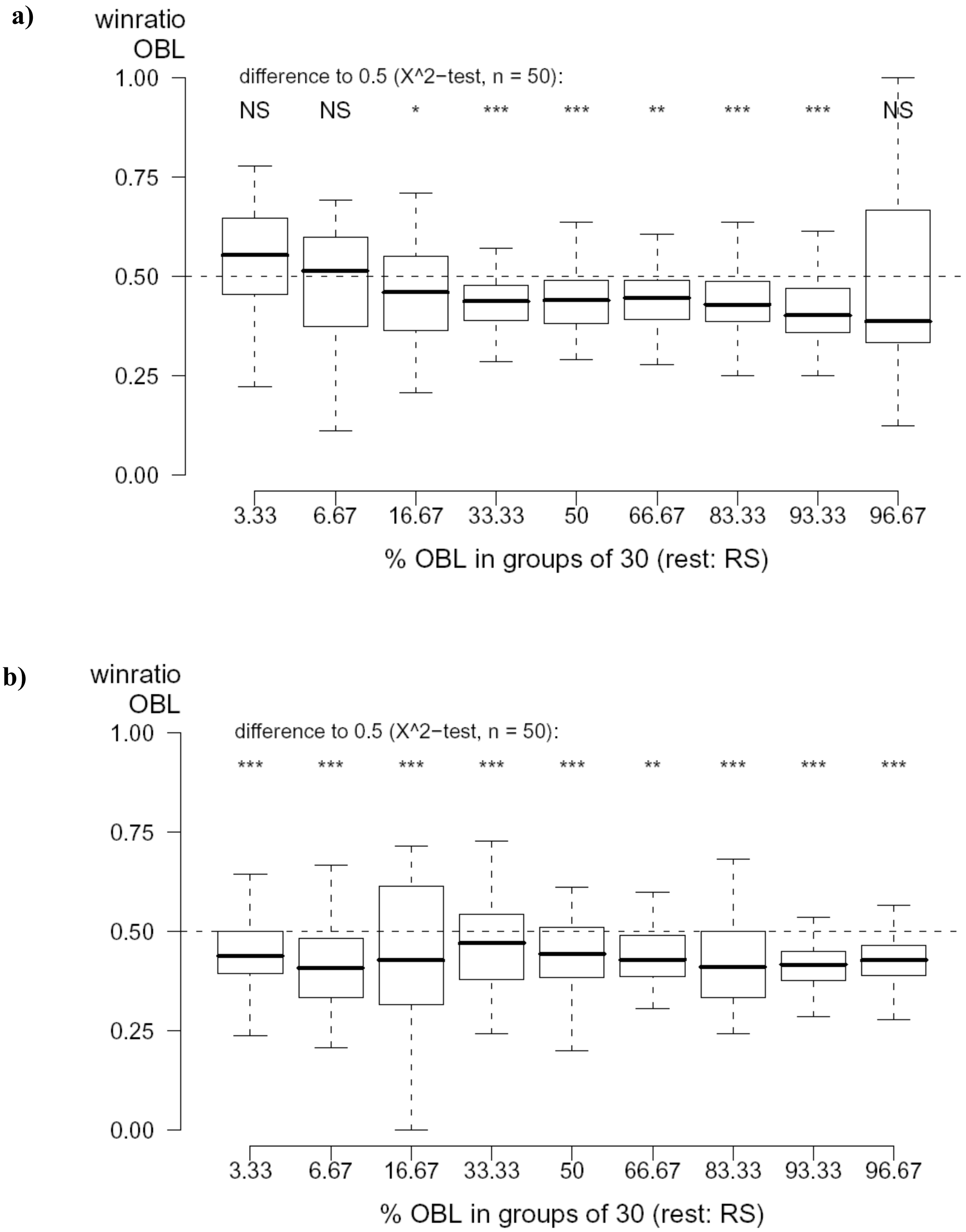
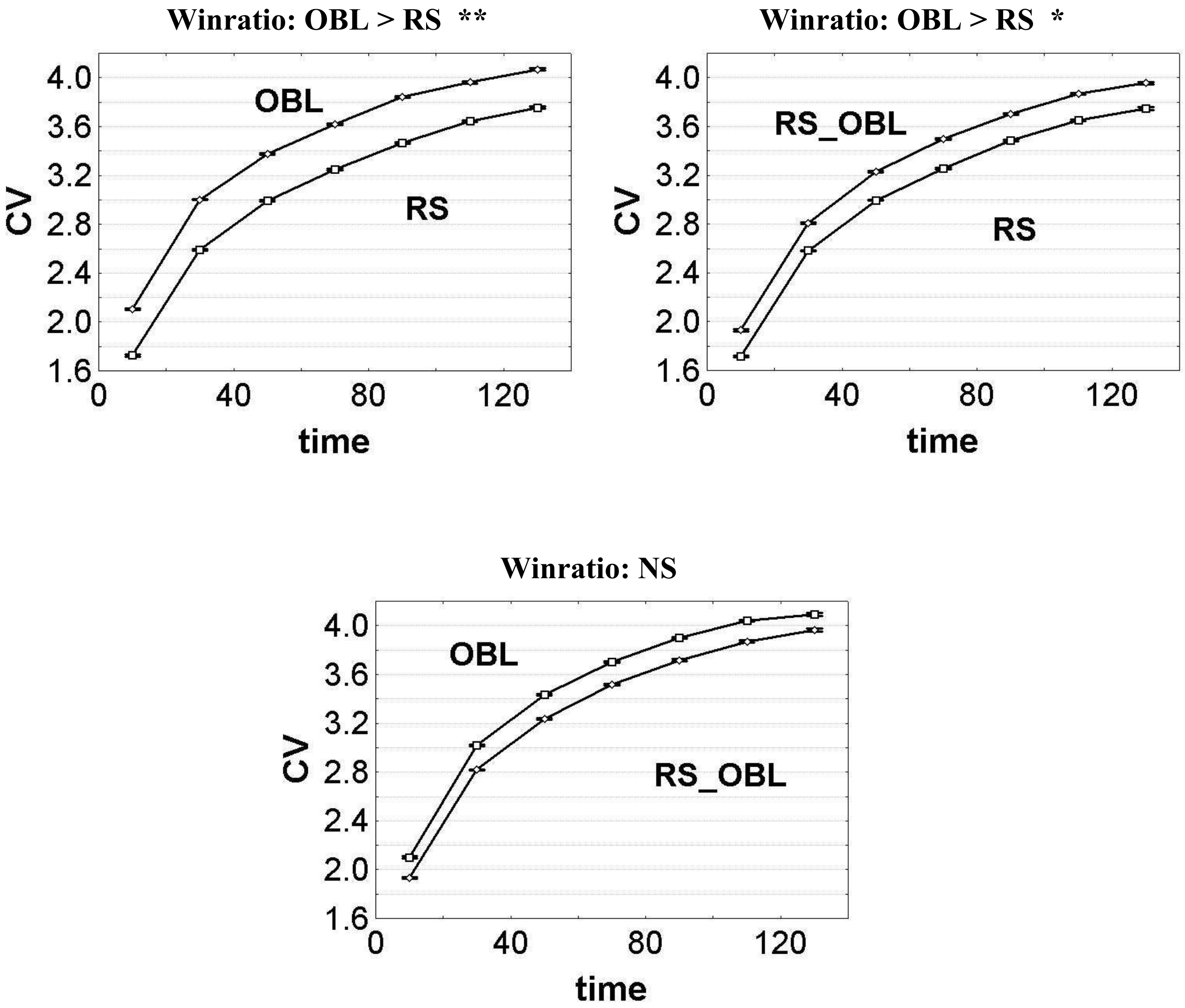


Figure 1*: a) Mean win-ratio of OBL-individuals over RS-individuals for various ratios of risk-sensitive (RS) and obligately attacking (OBL) individuals within a group. b) Ditto when RS-individuals have a low intensity of aggression (StepDom = 0.1). Box = S.E., whiskers = S.D. The dashed line indicates the win-ratio by chance. Significance of the* X^2 *Goodness of fit test:* $*** = p < 0.001$, $** = p < 0.01$, $* = p < 0.05$, *NS = not significant.*



Winratio: OBL > RS **

Winratio: OBL > RS *

Winratio: NS

Figure 2: *Coefficient of variation of DomValues (CV) over time for two competing groups. The winning group is always the one with the higher CV. Means ± S.E. of 50 simulation runs. ** = p < 0.01, * = p < 0.05, NS = not significant (t-test), RS = risk-sensitive, OBL = obligately attacking, RS_OBL = mixed.*

Social stability

The stability of the hierarchy, as measured in terms of rank reversals, is higher when more individuals attack obligately (Figure 3). This is due to the stronger hierarchical differentiation in such groups (Figure 4): When the dominance values of individuals are further apart, rank reversals occur less often. Stronger hierarchical differentiation in turn is a consequence of the higher frequency of attack due to the higher proportion of individuals that attack obligately (Figure 5 a). Consequently, the number of attacks that an individual receives (independent of its attack strategy) increases with the proportion of individuals that attack obligately (Figure 5 b). In contrast, the frequency with which individuals of each type attack others on average does not depend on the group composition (Figure 5 c).

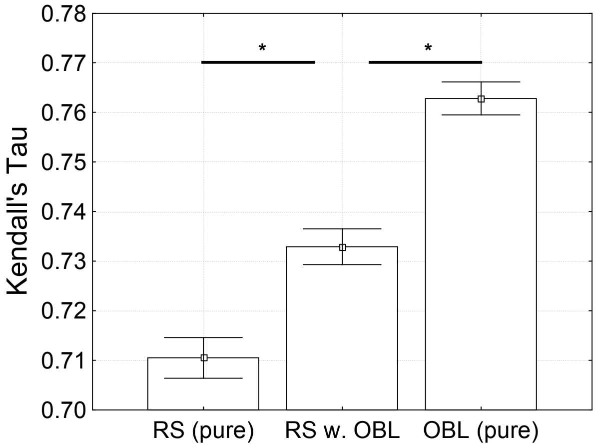


Figure 3: *Rank stability, measured as a Kendall Tau correlation between individual ranks 25 time steps before the end of the run, and in the last time step. Means ± S.E. * = $p < 0.05$ (two tailed t-tests, Bonferroni corrected). RS = risk-sensitive, OBL = obligately attacking.*

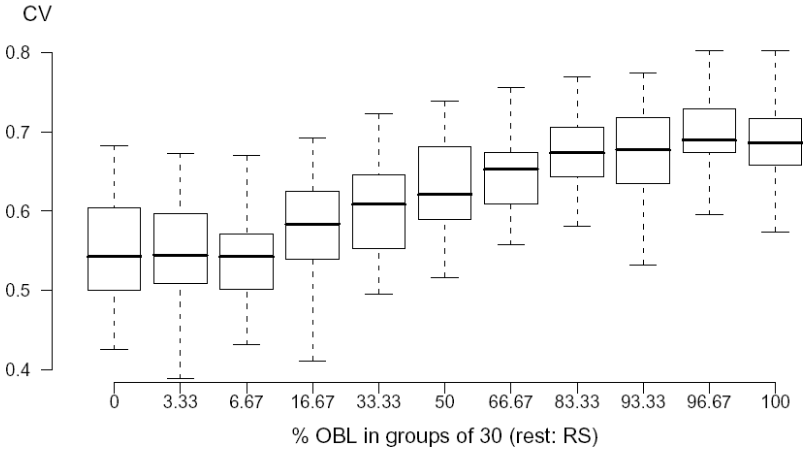


Figure 4: *Mean coefficient of variation of DomValues (CV) for different ratios of risk-sensitive (RS) and obligately attacking (OBL) individuals within a group. Box = S.E., whiskers = S.D.*

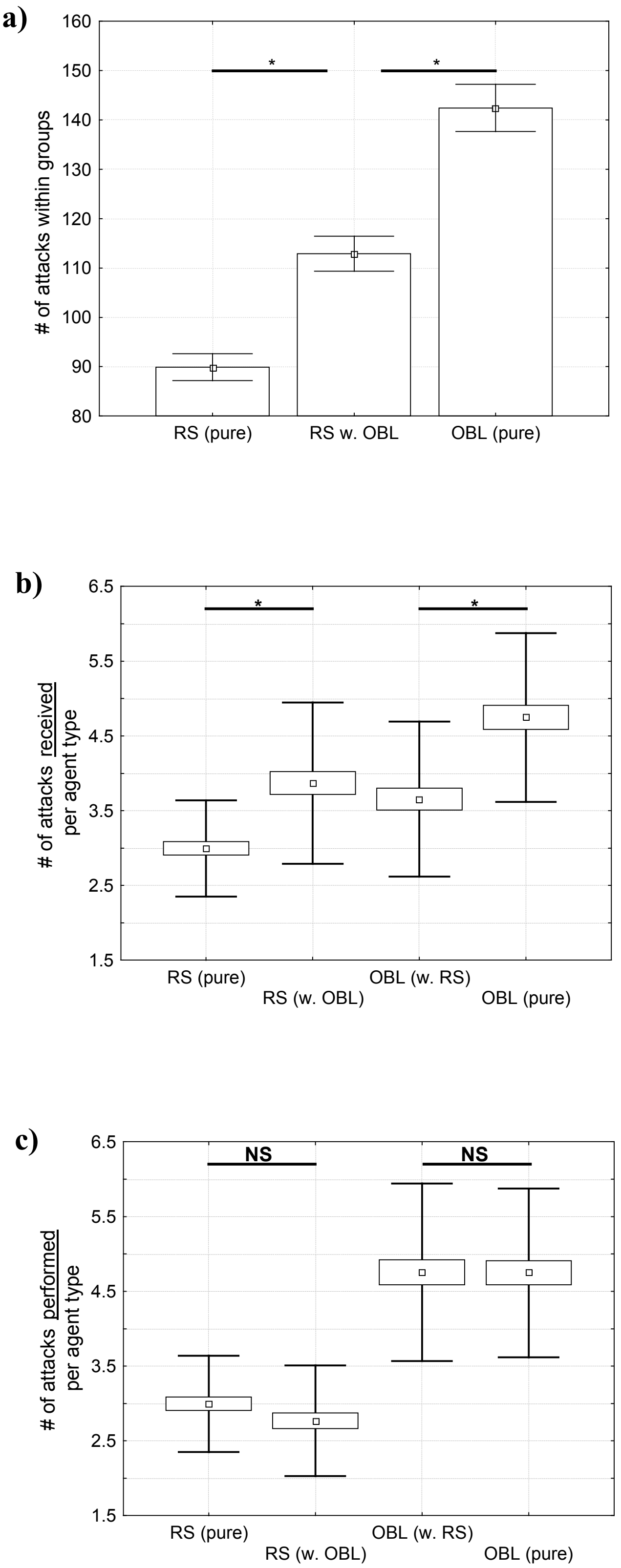


Figure 5: *a) Frequency of attack within groups (means ± S.E.). b) Mean frequency of attack received per individual in different group compositions. c) Mean frequency of attacks performed per individual in different group compositions. All measures were taken at the end of a run. B) and c): box = S.E., whiskers = S.D.*
** = $p < 0.05$ (two tailed t-tests, Bonferroni corrected in a), NS = not significant. RS = risk-sensitive, OBL = obligately attacking.*

Discussion

In terms of the performance of bold and cautious personalities, it indeed differs between contexts. Within groups, individuals that attack obligately lose, but in competition between groups they are victorious. This arises because individuals that attack obligately always fight, irrespective of the power of the opponent. Therefore, they lose often within groups. In contrast, risk-sensitive individuals mostly attack those they are likely to win. However, in competition between groups, groups with more individuals that attack obligately have a higher chance to win due to their stronger hierarchical differentiation, and because high ranking individuals participate more. In sum, within groups risk-sensitive individuals are more often victorious than individuals that attack obligately, but in competition between groups the reverse holds. Thus, our results support the explanation that different personalities may coexist because of different success in different contexts. This is in line with findings of game theoretical models that indicated coexistence of both types if they are adapted to different contexts (Costantini, 2005; Korte *et al.*, 2005; McElreath & Strimling, 2006).

The biological relevance of this hypothesis may be tested empirically by investigating whether also in real animals, in fights within groups bold individuals on average lose against cautious ones, and in fights between groups those with a higher number of bold individuals beat those with fewer of them. In case of positive evidence, coexistence in the model could be explained as a result of multiple level selection: individual selection for cautiousness, and selection at the group level for boldness. Such group selection for bold aggression in primates extends the number of traits on which group selection has been supposed to work. So far, it has been suggested to play only a role in the evolution of supposedly altruistic acts, such as alarm calls and coalition formation (Bradley, 1999).

As regards social stability in a group, in pure groups of bold individuals we find a high frequency of aggression and a stable hierarchy, and of risk sensitive individuals a low frequency of aggression and an unstable hierarchy, whereas in mixed groups, both the frequency of aggression and rank stability are intermediate. Thus, there is no clear advantage to mixed groups. This contrasts with earlier findings, where stress was lower in mixed groups than in pure groups of each personality type (pigs, Hessing *et al.*, 1994; Ruis *et al.*, 2002). Note that individuals that attack obligately 'profit' from being among risk-sensitive individuals, because they receive attacks less often than in pure groups of their own type. Conversely, risk-sensitive individuals are attacked more often when they are in mixed groups. This result partially resembles that of a study on two species of cichlids, the red *Pundamilia nyereri*, that is aggressive, and the blue *P. pundamilia,* that shows only mild aggression (Dijkstra, 2006). Here, like in the model, in mixed groups the red, aggressive species receives less aggression than in pure groups. However, in contrast to the model, the mild, blue species receives aggression equally often in mixed and pure groups. This is a consequence of the preference of red fish to attack individuals of its own species (own-type bias, Dijkstra, 2006). Such a rule is absent in our model.

Of course, real animals, and in particular primates, are much more complex than the individuals in our model: for instance, the bold - cautious dimension is only one of several personality dimensions that are found in primates (*e.g.* Clarke & Boinski, 1995). Further, primates have kin relations, and migrate between groups. We ignored these aspects in order to keep the model minimal. As well, we did not include costs of fighting, since they are hard to estimate in primates. This is also the reason why we did not follow a game theoretical approach, or another type of optimality model, where acts include effects on fitness payoff (Korte *et al.*, 2005). Rather, the aim of our study is to present a simple, conceptual model that helps to develop new hypotheses, with special relevance for primate behaviour, about how different personality types may coexist within a group.

In sum, our model suggests that the performance of both personality types depends on context, namely competition within and between groups and that each type may be maintained by different selection processes, namely at the level of the individual and that of the group. Since we studied contexts that are important to primates, we hope that our findings may in particular contribute to the understanding of coexistence in this taxon.

Acknowledgements

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7) Dominance style of primates through competition within and between groups: A model

Together with: Charlotte K. Hemelrijk

Abstract

In primates, winning inter-group encounters may be essential for group survival. Although large groups are supposed to have higher chances of victory than small ones, this is contradicted by certain empirical studies. Apparently, more factors are needed to explain a group's performance. In the current paper, we use a model to study the effects of other characteristics that have been suggested to affect the outcome of inter-group fights in primates, namely the dominance style, and the number of males in a group. We investigate traits that influence the dominance style, such as the frequency and intensity of aggression, separately and in combination. For this, we use an extended version of a process-oriented, agent-based model that previously showed great similarities with real primates. Since little is known about how inter-group fights are carried out, we compare results of different ways of fighting, *i.e.* individuals fight against other groups in a series of dyads, or as coalitions.

We confirm that dominance style and number of males influence the success of a group. Under most conditions groups with more despotic traits appear to beat more egalitarian ones. This arises due to the greatly developed hierarchy in despotic groups through which some individuals become very powerful. Egalitarian groups are victorious over despotic ones only when egalitarian groups contain a higher number of males, and when a larger number of their group members participates in a coalition against the other group.

These results are in contrast to the socio-ecological model, which assumes that more egalitarian groups outcompete despotic ones. Our results are in line with empirical observations on macaques. In addition, our model supports the hypothesis that the dominance style may have evolved from a mildly egalitarian ancestor into two directions, towards more despotism and towards more egalitarianism. This has been suggested recently for macaques. Finally, we speculate that despotism may be selected at a group level.

Introduction

Success in inter-group encounters is important for primate groups, because groups that lose may be displaced from feeding sites (Dittus, 1987; Vollmer, 1997), and eventually be driven to extinction (Hauser *et al.*, 1986; Takahata *et al.*, 1994; Sugiura *et al.*, 2002).

In fights between groups, larger groups are often expected to beat smaller ones. However, whereas some studies provide evidence for this (Hamilton *et al.*, 1975; Cheney, 1987; Kitchen *et al.*, 2004), others do not (Mehlman & Parkhill, 1988; Perry, 1996; partial support: Sugiura *et al.*, 2000). Thus, size alone does not determine victory. As additional influences on the success of a group in inter group competition were suggested 1) dominance style (van Schaik, 1989), and 2) the number of males in the group (Wrangham, 1980; Fashing, 2001; Cooper *et al.*, 2004).

However, it is difficult to test these influences empirically in real primates, since an experimental set up for studying inter-group encounters repeatedly (and ideally between several different groups) is hardly feasible, and in the field inter-group encounters are relatively rare and difficult to observe. Therefore, we here study the two factors, dominance style and number of males, in a model of competition within and between groups.

We use an extended version of the process-oriented, agent-based model 'DomWorld' (Hemelrijk, 1996a; 1999c), because in former studies, virtual societies in DomWorld developed dominance styles that resemble egalitarian and despotic societies of real macaques (Hemelrijk, 1999a; 1999c). DomWorld consists of a single group in which individuals only group and compete. In the model, the effects of winning and losing fights are self-reinforcing, just as is the case in many animal species (Hsu *et al.*, 2006). By increasing the intensity of aggression alone, from a low value (*cf.* threat displays or slaps) to a high one (*cf.* biting), changes in dominance become stronger. Consequently, a steep dominance hierarchy develops; this is in line with real macaques, where despotic species are characterised by a high intensity of aggression (Caldecott, 1986; Thierry, 1990a; 2000). In the model, other traits typical of a despotic dominance style emerge via self-organisation: some individuals that are beaten frequently are driven towards the periphery, and this results in a spatial structure with dominants in the centre. Simultaneously, aggression becomes asymmetric. However, at a low intensity, groups in the model resemble egalitarian primate societies: due to the weak hierarchy, no spatial structure develops and aggression remains symmetric (Hemelrijk, 1999a; 1999c). Similar results are brought about by increasing the frequency of aggression, whereby groups with a low frequency of aggression resemble egalitarian societies, and those with a high frequency resemble despotic ones (Caldecott, 1986).

The new, extended model 'GroupWorld' is derived from DomWorld. It incorporates both competition in a single group and competition between groups. In terms of the implementation of inter-group fights, we account for the finding that for real primates mostly high ranking individuals participate (Cheney, 1987; Perry, 1996; Kitchen *et al.*, 2004; Cooper *et al.*, 2004; Majolo *et al.*, 2005). Apart from that, little is known of the precise behavioural interactions during encounters between groups of real primates (Cheney, 1987; Cooper, 2004). Therefore, we model fights between groups in three different ways: 1) as a series of single fights, and as fights between 2) coalitions formed by a fixed proportion of group members, or 3) coalitions consisting of the top ranking individuals plus those that are sufficiently similar in dominance to the top ranking one.

In the present study we investigate the inter-group success of groups that differ in their intensity and frequency of aggression. In addition, since despotic species often have a female biased sex ratio (Caldecott, 1986; Ménard, 2004), we also study the influence of sex ratio. These three traits (intensity and frequency of aggression, sex ratio) are tested separately and in combination.

We will relate our findings to the predictions of the socio-ecological model of van Schaik about competition within and between groups, and to recent findings concerning the phylogeny of macaques as suggested by (Thierry *et al.*, 2000).

Methods

The model

The model consists of several groups. We will first describe competition in a single group, and then competition between neighbouring groups.

Competition within a single group

Within their group individuals group and compete as described by Hemelrijk (Hemelrijk, 1999a; 1999c; 2000b). Each individual has a variable called 'DomValue', which represents its fighting capacity or dominance. Individuals are more likely to attack when their chance to win is higher. This is implemented as follows: prior to attacking, an individual estimates its chance of winning by performing a 'mental battle', following formula (1 a). After winning, it initiates a real fight, otherwise it turns over 180 degrees and moves two steps. The outcome of the real fight is determined following formula (1 b).

$$DomRatio := DomValue_{\text{initiator}} / (DomValue_{\text{initiator}} + DomValue_{\text{opponent}}) \qquad \text{(1 a)}$$

$$\begin{array}{lll} \text{if} & (Rand) < DomRatio & \text{: initiator wins} \\ \text{else} & & \text{: initiator loses} \end{array} \qquad \text{(1 b)}$$

Rand is a random number between 0 and 1, drawn from a uniform distribution. After the fight, DomValues of both individuals are updated following formula (2): A winner's DomValue increases, so that it has a higher chance to win the next time, and *vice versa* for the loser.

$$\begin{array}{ll} DomValue_{\text{initiator}} & := DomValue_{\text{initiator}} + (w - DomRatio) * \text{StepDom}_{\text{initiator}} \\ DomValue_{\text{opponent}} & := DomValue_{\text{opponent}} - (w - DomRatio) * \text{StepDom}_{\text{initiator}} \end{array} \qquad (2)$$

$w = 1$ if initiator won, $w = 0$ if initiator lost. 'StepDom' stands for the intensity of aggression: High values of StepDom cause large changes in DomValue, *i.e.* fights are fierce. The StepDom-value of the initiator is used for the interaction. Further, changes in DomValue depend on whether the outcome of the fight is as expected: If a high ranking individual beats a lower ranking opponent, the outcome causes a small change in both DomValues (formula 2). This may be regarded as an approach-retreat interaction rather than a real fight. If, however, the outcome is unexpected and a low ranking individual beats a high ranking one, the change in DomValues is large.

In GroupWorld we omit the representation of the spatial structure within a group for computational reasons. Instead, we choose interaction partners in the same way as in DomWorld: At a high intensity of aggression, we give individuals a greater chance to meet opponents that are similar in dominance value, whereas at a low intensity of aggression they meet at random (Hemelrijk, 1999c).

Competition between groups

As regards inter group fights in real primates, high ranking individuals are more likely to participate (Cheney, 1987; Perry, 1996; Kitchen *et al.*, 2004; Cooper *et al.*, 2004; Majolo *et al.*, 2005). Apparently, individuals use the 'power' that they have within a group also in fights against other groups. Therefore, we use the DomValue of individuals within groups also in fights between groups and we give high ranking individuals a higher probability to interact in fights between groups than low ranking ones. However, since little data is available as to how fights between groups are carried out, we implement three different approaches. First, fights between groups could consist of a series of duels between members of the opposing groups. Which group member participates in a duel is decided with formula 3, with higher ranking individuals being more likely to participate:

$$P_{BG}(k) \;=\; DomValue(k)\,/\,\sum_{i=1}^{n} DomValue(i) \tag{3}$$

$P_{BG}(k)$ = probability of individual k to initiate an inter group fight. n = number of group members. Dominance interactions follow formula (1).

Another possibility is that individuals form coalitions to attack another group. When fights between groups involve such coalitions, the outcome of the fight in the model is determined as before, but instead of using the dominance value, the summed dominance value of all coalition partners for each group is used following formula (4). We model two extreme cases of coalition formation (Figure 1): Either, coalitions consist of a fixed percentage (in our case: 40 %) of the highest ranking individuals of a group. Alternatively, coalitions consist of the highest ranking individual plus those group members whose dominance is similar to that of the top-ranking individual (in our case, whose DomValues fall into the range [0.6*DomMax, DomMax], Figure 1). This results in larger coalitions in egalitarian groups than in despotic ones, which reflects the assumption of the socio-ecological model that in egalitarian groups more individuals participate in group defence than in despotic ones (van Schaik, 1989).

$$sumDomRatio = \frac{\sum_{i=1}^{n(initiatorgroup)} DomValue(i)}{\sum_{i=1}^{n(initiatorgroup)} DomValue(i) + \sum_{j=1}^{m(opponentgroup)} DomValue(j)} \tag{4 a}$$

if (*Rand*) < *sumDomRatio* : initiating group wins
else : initiating group loses (4 b)

Rand = random number between 0 and 1 from uniform distribution, *n*, *m* = number of coalition members of opposing groups.

In all cases we assume that inter-group victories and defeats do not affect DomValues, since they are rare relative to encounters within groups.

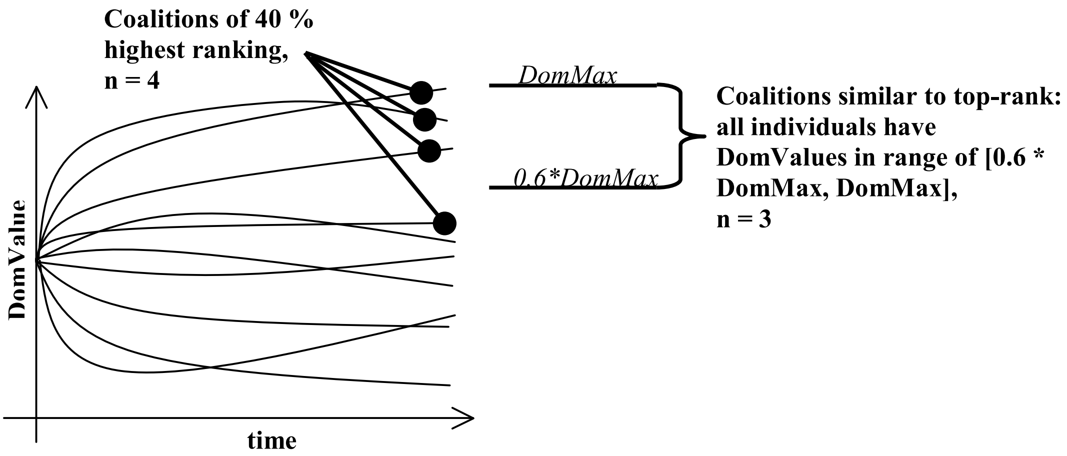

Figure 1: *Participation of individuals in inter group fights if coalitions consist of a fixed percentage of individuals of the highest rank (left), and of individuals with a dominance similar to that of the top ranking individual (right). DomMax = DomValue of the highest ranking individual in a group. Note that the number of coalition members, n, may differ.*

Parameter settings and experiments

For each run, four groups with one parameter setting fight four groups with another parameter setting (Figure 2). Groups with different parameter settings are placed next to each other in a circle to avoid border effects. Parameter settings take into account the finding that in real primates fights between groups are relatively rare (macaques: between 0.3 and 0.64 per day, Cooper, 2004): Unless mentioned otherwise, 500 fights within groups alternate with 50 fights between groups, and this is repeated 128 times. 50 replicas of these cycles of 128 repetitions are run for each set-up. Default parameters are shown in Table 1 a. To simulate sexual dimorphism, which is typical of macaques (Smith & Cheverud, 2002), females in the model have a lower StepDom (80 % of that of males) and initial DomValue (50 % of that of males) (Table 1 a).

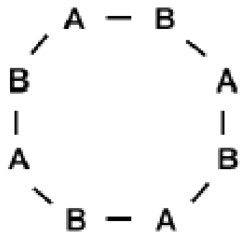

Figure 2: *Arrangement of groups with two different parameter settings (A and B).*

We test groups that differ in intensity of aggression, in frequency of aggression, in the degree of female-bias in adult sex ratio, and combinations of these three aspects (Caldecott, 1986). The parameter settings for extreme despotism and egalitarianism are based on former analyses of the model (*cf.* Hemelrijk, 1999c); those of the intermediate degrees were interpolated. The proportion of females in a group of 80 % females in despotic groups, and 70 % females in egalitarian groups is based on observations of Caldecott (1986) and Ménard (2004) (Table 1 b).

a) Parameter	**Default value**
# of individuals per group	10
Proportion of females	50 %
# of groups	8
StepDom of male	1
StepDom of female	0.8
Initial DomValue of male	32
Initial DomValue of female	16
# encounters within groups	500

b)	**Parameter values**				
Frequency of aggression	Encounters within groups:	0, 100, 500, 1000			
Sex ratio	# of females per group of 10:	1 - 9			
Combination of traits		Egalitarian		Despotic	
	Degree of despotism:	**EE**	**E**	**D**	**DD**
	StepDom of male	0.1	0.2	0.5	1
	StepDom of female	0.08	0.16	0.4	0.8
	# females per group of 10	7	7	8	8
	# encounters in groups	300	600	900	1200

Table 1: *a) Default values of the model. b) Parameter values for different experiments.*

Measurements and tests

We only consider hierarchies in the ‘stable phase’ here, *i.e.* when the dominance values do not differentiate further (from timestep 200 onwards, *cf.* Figures 3b, c, Hemelrijk & Gygax, 2004).

To measure the gradient of the hierarchy we use the coefficient of variation of the DomValues at the end of a simulation. Groups with a steep hierarchy have a high coefficient of variation (Figure 3 b), whereas groups with a weakly developed hierarchy have a low coefficient of variation (Figure 3 c).

The performance of a group is described by the ‘winratio’, *i.e.* the number of fights won by one group, divided by the total number of all fights between both groups.

Differences in winning frequency are tested with the X^2 goodness of fit test. We compare per condition the number of victories observed in 50 runs to the number of victories expected by chance.

Results

When interactions between groups are modelled as a series of dyadic individual encounters, groups with a high intensity of aggression beat groups with a low intensity, and this effect increases with the number of aggressive interactions within a group (Figure 3 a). This arises because a high intensity as well as a high frequency of aggression lead to a strong development of the hierarchy (Figure 3 b, c, *cf.* Hemelrijk 1999 a, c). Since the highest ranking individuals of each group are more likely to participate in inter-group fights, and their dominance value is much higher in groups in which the hierarchy is differentiated more strongly, groups with more differentiated hierarchies (*i.e.* despotic ones) are more likely to win.

Similarly, if a fixed percentage of the highest ranking individuals form a coalition, the groups with a higher intensity of aggression and those with a higher frequency of aggression within the group will win more often (Figure 4 a): Due to the strong development of the hierarchy, the combined power of the coalition members (their summed DomValue) is higher in groups with a high intensity of aggression than with a low intensity (Figure 4 b).

In contrast, if coalitions are formed by those individuals that are similar in dominance to the top-ranking individual (Figure 5 a), at a high intensity of aggression groups are defeated, because due to their steeper hierarchical gradient fewer individuals will participate in the coalition than at a lower intensity of aggression when the hierarchical gradient is weak (Figure 5 b).

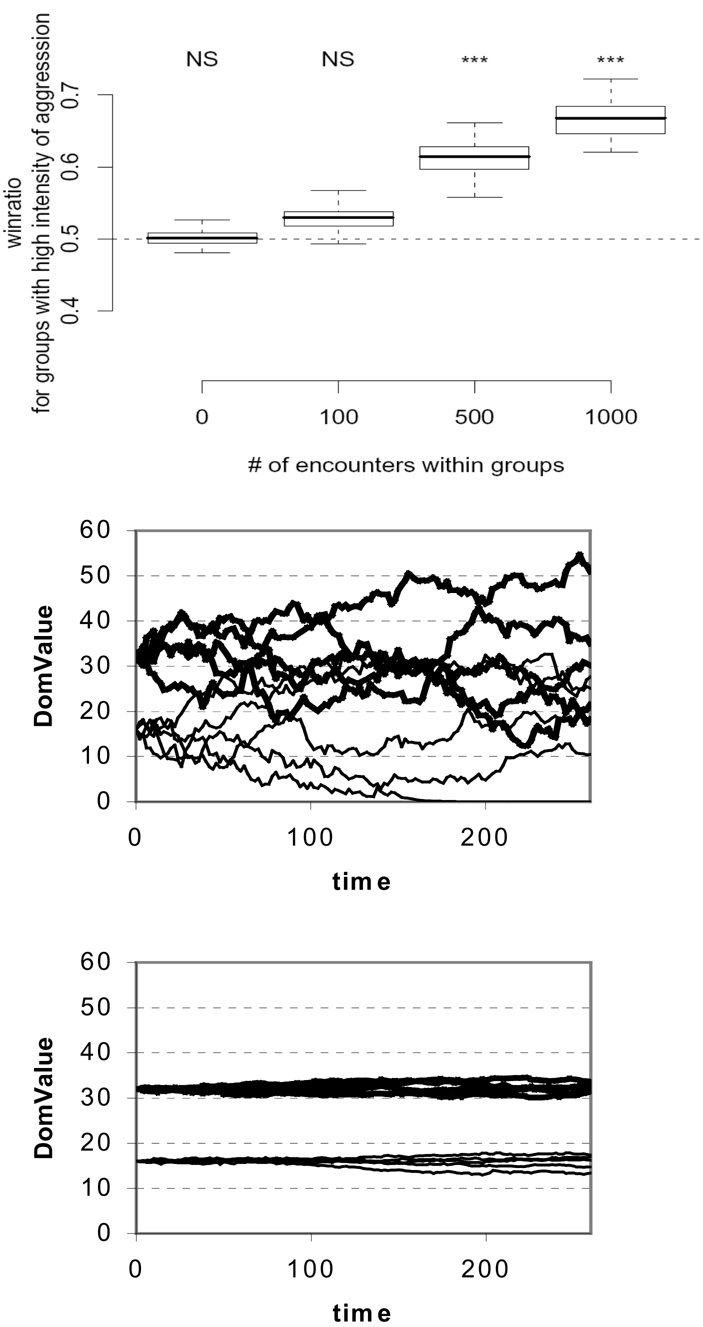

Figure 3: *Dyadic fights. a) Winratio of groups with a high intensity of aggression (StepDom = 1) when competing with groups with low intensity of aggression (StepDom = 0.1) for different frequencies of aggression within groups. The dashed line indicates the winratio by chance. Significance of the* X^2 *Goodness of fit test: *** = p < 0.001, NS = not significant. b) Example of a hierarchy in a group at a high intensity of aggression (StepDom = 1). c) Example of a hierarchy in a group at a low intensity of aggression (StepDom = 0.1).*

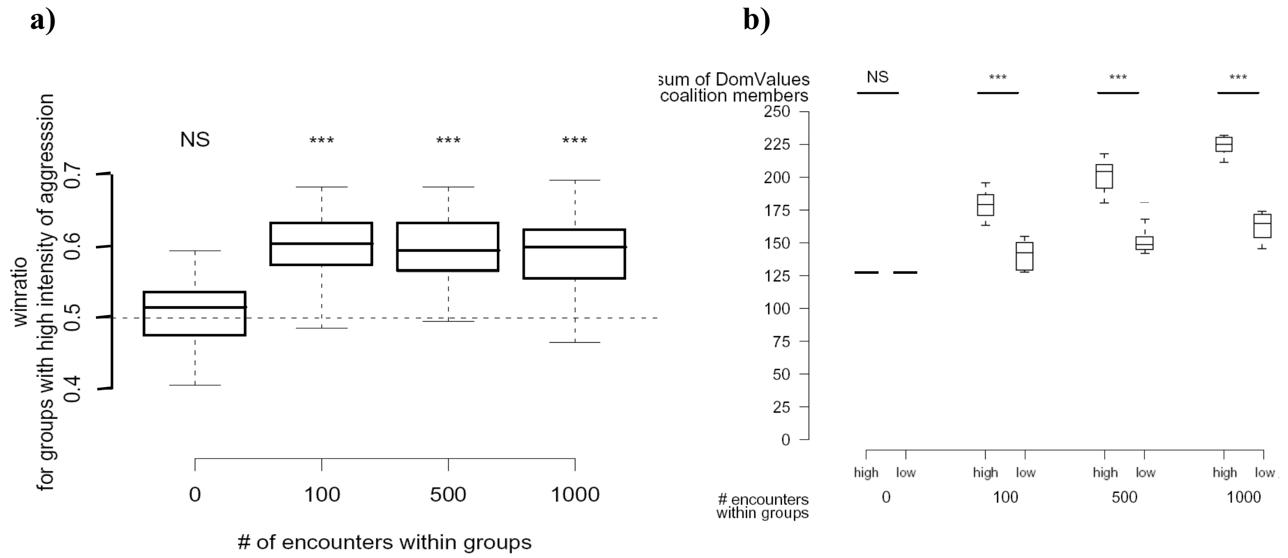

Figure 4: *Coalitions of the 40% highest ranking individuals. a) Winratio of groups with a high intensity of aggression (StepDom = 1) against groups with a low intensity of aggression (StepDom = 0.1) for different frequencies of aggression within groups. The dashed line indicates the winratio by chance. Significance of the* X^2 *Goodness of fit test: *** = p < 0.001, NS = not significant. b) Summed DomValues of all members of a coalition in groups with low and high intensity for different numbers of interactions in groups. Mann Whitney U test (n = 50, *** = p < 0.001, NS = not significant).*

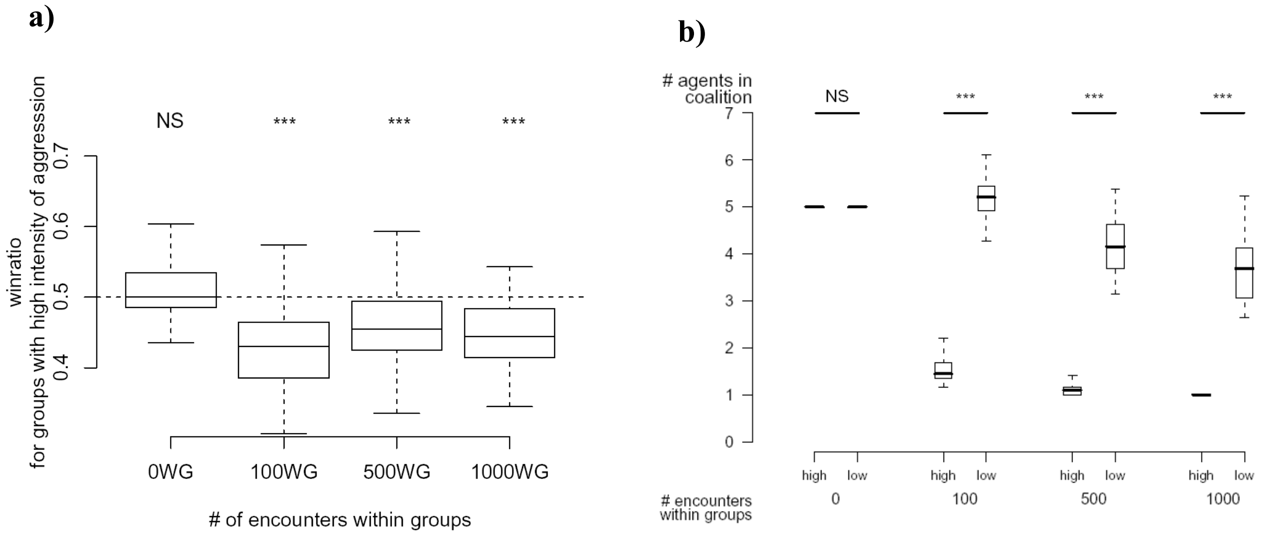

Figure 5: *Coalitions of individuals similar to the top ranking one. a) Winratio of groups with a high intensity of aggression (StepDom = 1) against those with low intensity of aggression (StepDom = 0.1) for a different frequency of aggression within groups. The dashed line indicates the winratio by chance. Significance of the* X^2 *Goodness of fit test: *** = p < 0.001, NS = not significant. b) Number of participants in coalitions in groups with high and low aggression intensity for different numbers of interactions in groups. Mann Whitney U test (n = 50, *** = p < 0.00, NS = not significant).*

As regards the proportion of females in a group, at a high intensity of aggression, a group that contains a higher proportion of females will always lose against one with a lower proportion of females (Figure 6, top). This is due to the fact that, on average, females are lower in dominance than males (Figure 6, bottom).
At a low intensity of aggression, the results are similar but less pronounced (not shown).

We also combined sex ratio and frequency and intensity of aggression, so as to reflect different degrees of despotism as observed in empirical studies (Table 1 b). Extremely despotic groups appear to be victorious over more egalitarian ones in dyadic fights, and in coalitions that consist of a fixed number of the highest ranking individuals (DD vs. D, DD vs. E, DD vs. EE, Figure 7 a, b). This is due to the power of a few strong individuals, even though the winning tendency of these groups is weakened by the participation of a larger number of weak females. In fights between groups with a lower degree of despotism, both groups play even (D vs. E, D vs. EE and E vs. EE, Figure 7 a, b).

If coalitions are formed by individuals whose dominance is similar to that of the top-ranking male, extremely despotic groups may still outcompete mildly despotic and mildly egalitarian groups due to the great DomValue of a few high ranking individuals (DD vs. E, DD vs. D, Figure 7 c). However, mildly despotic groups are more likely to be defeated by extremely egalitarian groups, because the higher dominance of individuals of mildly despotic groups cannot outweigh the higher number of coalition members of extremely egalitarian groups (D vs. EE, Figure 7 c).

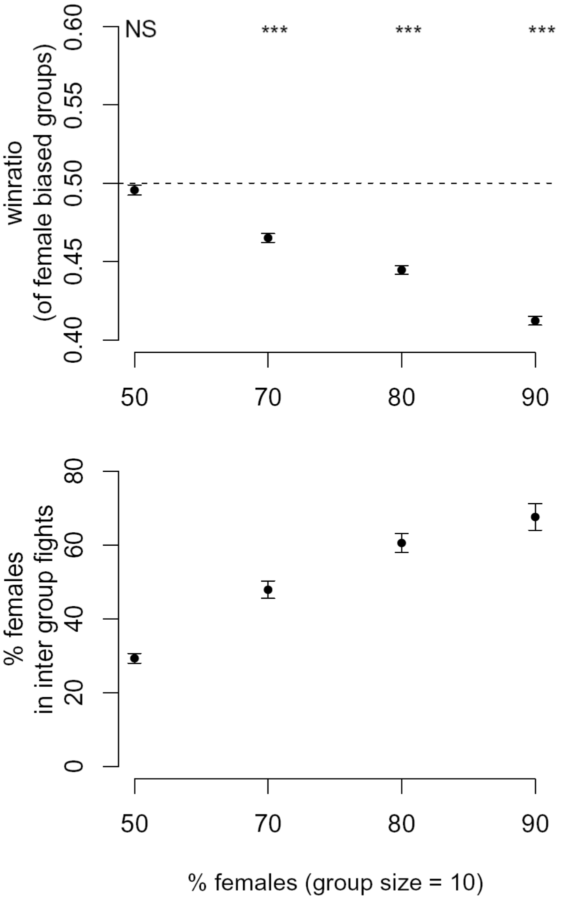

Figure 6, *Top: Dyadic Fights. Winratio of groups with a female-biased sex ratio against groups with an equal sex ratio. The dashed line indicates the winratio by chance. Significance of the* X^2 *Goodness of fit test: *** =* $p < 0.001$*, NS = not significant. Bottom: The percentage of fights carried out by females of groups with a female-biased sex ratio against members of groups with an equal sex ratio.*

In real primates, the sex ratio may vary per group. Therefore, it is of interest to study what happens if we adjust the sex ratio in favour of egalitarian groups by reducing its percentage of females, for instance, from 70 % to 50 % females in extremely egalitarian groups (EE) and to 60 % in egalitarian ones (E), and from 80 % to 70 % in mildly despotic groups (D). As expected, their performance improves. The improvement is most expressed if coalitions consist of individuals similar in rank to the top ranking one (Figure 8): In this case, males are always sufficiently similar to join these coalitions, since the hierarchy in egalitarian groups is only weakly differentiated. Thus, having more males directly increases the success of egalitarian groups in competition with despotic ones.

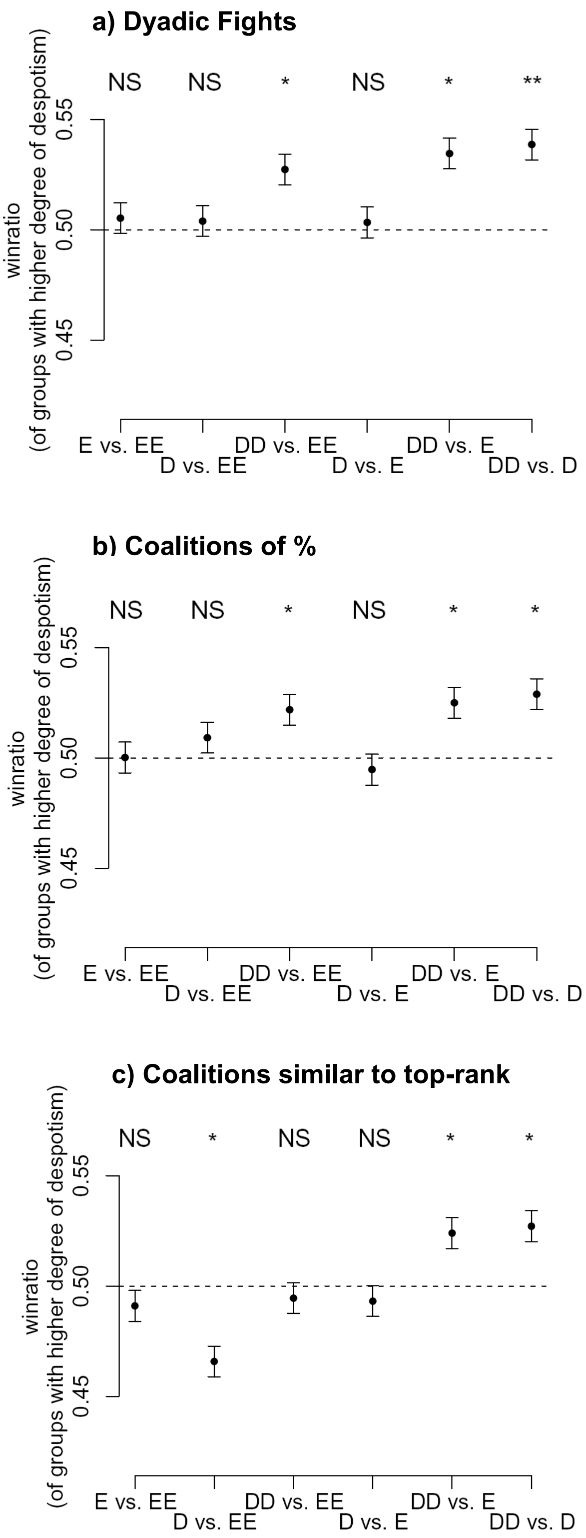

Figure 7: *Winratio of groups with more despotic characteristics against those that are more egalitarian. For degrees of despotism, EE to DD, see table 1 b. The dashed line indicates the winratio by chance. Significance of the X^2 Goodness of fit test: ** = p < 0.01, * = p < 0.05, NS = not significant.*

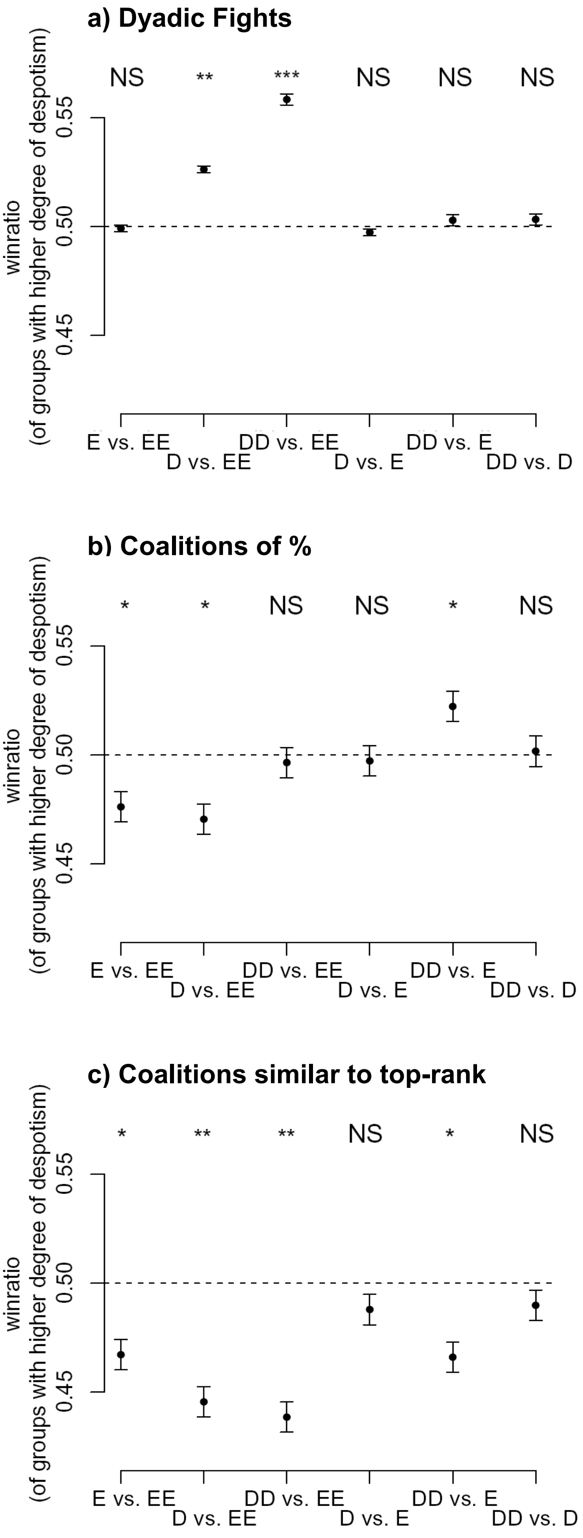

Figure 8: *Winratio of groups with more despotic characteristics. For degrees of despotism, EE to DD, see table 1 b, but the percentage of females in egalitarian groups has been increased to 50 % for EE, 60 % for E, 70 % for D, 80 % for DD. The dashed line indicates the winratio by chance. Significance of the X^2 Goodness of fit test: *** = p < 0.001, ** = p < 0.01, * = p < 0.05, NS = not significant.*

Discussion

In our model, dominance style and group composition appear to greatly influence the success of a group in fights with other groups. Regarding dominance style, we find that under most conditions, fights are won by groups with more despotic characteristics, because they have a few very strong individuals. In line with this result is the finding that the despotic rhesus macaque has displaced the egalitarian assamese macaque in Nepal (Wada, 2005). Our results contradict, however, the socio-ecological model of van Schaik (1989), which supposes that egalitarianism emerges through strong competition between groups (meaning frequent and/or intense clashes), as follows: When communally defending their territory, all group-members should benefit equally and therefore, differences in dominance should be small. On the other hand, large differences in dominance (*i.e.* despotism) should result if competition between groups is low, and competition within groups is strong. Although this socio-ecological model is supported by many studies (Sterck *et al.*, 1997), it is challenged by findings in macaques, where inter-group fights were found to be rare among groups of egalitarian macaques, but severe in fights between groups of despotic species (Matsumura, 1998; 1999).

Further, regarding group composition, our model suggests that performance is also influenced by variation of the sex ratio in groups of real primates: A coalition of few males with many females cannot persist against a coalition of many males, because females are on average too weak to beat males. This is in accordance with the situation in primates, where males are often larger than females (Smith & Cheverud, 2002). Consequently, it has been suggested that females accept powerful males in a group as ‘hired guns’, so that these strong males defend the group (Wrangham, 1980; Fashing, 2001; Cooper *et al.*, 2004). Additionally, if fights consist of dyads, in the real world the risks of fighting would be distributed on many shoulders if there are many males that take turns in the duels, while a male from a single-male group, for instance, would have to bear these risks almost by itself, being the strongest fighter of the group.

In addition to dominance style and sex ratio, our model suggests a third factor that may influence the outcome of inter-group fights, namely the way in which inter-group encounters are carried out (dyads or coalitions, Figures 7 & 8). This factor appeared to have a strong effect in the model; however, it has not yet been considered in fieldwork, which may explain the discrepancy between the socio-ecological model and the macaque data. Future field studies are needed to illuminate the relevance of the specifics of fighting behaviour in real primates.

In sum, these results indicate that the success of a group in inter-group encounters cannot be easily related to one trait, such as its size or its dominance style. Rather, the performance of a group is determined by a combination of factors. Two examples may illustrate this. First, if in the model inter-group fights are carried out as coalitions, a large group with many females may lose from a small group with many males. Second, if coalitions consist of individuals similar to the top ranking one, a large despotic group may be defeated by a small egalitarian one. Since only few individuals of the despotic group are sufficiently similar to the top ranking one to join the coalition, their coalition will be smaller and weaker than the one of the egalitarian group. Indeed, in the model the success of a group can be predicted by one trait, such as its size, only if all other parameters are similar (*i.e.* intensity and frequency of aggression per agent, sex ratio, and the way they fight, data not shown).

These results crucially depend on the assumption that inter-group fights are carried out mainly by high ranking individuals. This is widely supported by findings in real primates (Cheney, 1987; Perry, 1996; Kitchen *et al.*, 2004; Cooper *et al.*, 2004; Majolo *et al.*, 2005). However, our model does of course not represent the complexity of real primates. For simplicity, we omit, for instance, migration between groups, kin relations, and the fact that the probability of winning depends on the location of a group relative to their home range (*e.g.*

Kitchen *et al.*, 2004). Yet, these factors do not contribute to revealing underlying processes of inter group fights. Therefore we did not consider these phenomena here.

Since in the model some groups on average lose (such as egalitarian groups under most conditions), one may speculate about their evolutionary consequences. We find that our model is in accordance with a recent hypothesis regarding the evolution of dominance style in real macaques, which suggests that from the common ancestor of macaques that was moderately egalitarian, evolution proceeded in two directions: Mainly towards despotism (mild and extreme), but also towards extreme egalitarianism (Thierry *et al.*, 2000). However, while in the model it is obvious how under most conditions despotism within groups contributes to the success in inter-group contests, the question remains how an extremely egalitarian species could evolve from a moderately egalitarian one. Our model suggests that extremely egalitarian groups could beat egalitarian ones if they have a higher percentage of males (Figure 8). As well, one may imagine that different groups adopt different fighting 'strategies': if extremely egalitarian groups form coalitions of individuals similar to the top ranking ones, all males participate, because the differentiation of the dominance is weak. Thus, they could beat egalitarian groups with coalitions of a fixed, small proportion of males. In addition, in real primates there may be energetic advantages to mild aggression. Likewise, regarding the question why not all egalitarian species have been displaced by despotic ones, egalitarian species may remain if their coalitions are larger than those of despotic ones. Still, in the model the superiority of despotism under most conditions seems overwhelming; in this context, it is noteworthy that in real primates, all extremely egalitarian macaque species live on Sulawesi Island in the absence of any despotic species. Thus, these extremely egalitarian species could also have survived due to their isolation from the mainland, which prevented intrusion of more despotic species (Abegg & Thierry, 2002).

During the evolution of dominance style, selection could target multiple levels. First, there is individual selection within groups. Second, competition within groups may also lead to selection at the level of the group. This has been suggested by Ulbrich *et al.* (1996) on the basis of models for, and experiments with, social spiders. In times of food scarcity, in egalitarian colonies of spiders no one will receive enough food for reproduction and the group becomes extinct. In despotic colonies, however, a few strong individuals can monopolise all food. Therefore, they are the only ones that survive and reproduce. Thus, there will be group-selection for despotism, and we may imagine that this also may occur in primates. For instance, the finding that among vervet monkeys, under extreme drought only the highest ranking females managed to drink and many low ranking individuals died (Wrangham, 1981), may be interpreted as a hint for this. Finally, there could be selection between entire groups, since competition between groups may result in the extinction of certain groups.

In general, lacking more detailed field observations, a process oriented model such as ours may provide a starting point that inspires future field work, which in turn will allow a refinement of the model. The aim of our model is to highlight proximate mechanisms, and the development of new hypotheses that may not come to mind when we think in a less mechanistic, purely adaptive framework. The hypothesis we deliver here is that the success of despotic groups in competition against egalitarian ones depends, among other things, on the interaction details of inter-group fights (dyadic or in coalitions). Our results show that we need empirical data on real primates to establish the relation between the success of a group, its sex ratio, its degree of despotism, and details of the interaction process of inter-group fights, such as the number of participants involved, position in the hierarchy of the participants, their sex, and their way of fighting (*e.g.*, whether in coalitions or dyads).

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8) General discussion

Part I of this thesis deals with female dominance, where it occurs, and how the degree of female dominance may be influenced. In part II, the relation of social organisation within groups (different compositions of personality types, dominance style) and the success of group in competition between groups is investigated. In the following, the new findings are summarised and discussed more generally. As well, critique points of the models that have been raised frequently are addressed, and finally a short outlook regarding future work and extensions of the models is given.

Female dominance

Although some or all females may dominate males in several primate species, female dominance as a phenomenon in social organisations has not been studied systematically (except for a few lemur species). However, in analysing empirical data on female dominance in primates for the first time, it turns out that it occurs in many different species to various degrees (Chapter 2). Model results suggest that influences on the degree of female dominance are manifold. In Chapter 3, a number of unexpected causes are presented, such as food distribution, sexual attraction, and group cohesion: All of these affect which and how often individuals meet, which in turn influences the development of the hierarchy via winner-loser effects. Chapter 4, in turn, focuses on the consequences of winner-loser effects and inter- versus intra-sexual interactions. It appears that the degree of female dominance may be influenced not only directly by inter-sexual interactions, but also indirectly via the proportion of males in the group. In addition, from the model a new method emerged for estimating what role inter-sexual fights, and hence, winner-loser effects, play in the development of intra-sexual hierarchies in real primates. When applied to eight species of the genus *Macaca*, it appears that self-reinforcing winner-loser effects are effective in inter-sexual encounters, but not as much as those in intra-sexual fights.

The finding that the degree of female dominance relates to the proportion of males in a group inspired an analysis of female dominance in empirical data of 22 primate species (chapter 5). Here a positive correlation between female dominance and the proportion of males is confirmed. Surprisingly, this correlation is independent of the degree of sexual dimorphism.

In sum, the findings presented in Part I suggest that the degree of female dominance is not an entirely species-specific trait. This is supported by empirical data, which document large variation in the degree of female dominance even between different groups of the same species (see chapter 2). Rather, the interactions among individuals also influence the degree of female dominance.

As demonstrated in Chapter 4, the degree to which females dominate males is positively correlated to the proportion of males in the model. Whereas in the empirical results (chapter 5) it was already shown that this correlation arises because a high proportion of males leads to more fights with a high intensity, these correlations were not yet investigated in the model. Here it is shown that indeed, also as in the model, the degree of female dominance is significantly positively correlated with the proportion of all fights that involve males, with the proportion of all fights among males, and with the proportion of inter-sexual fights (Table 1). This arises since many interactions with males cause large changes in dominance values in both sexes, and thus a strong differentiation of intra-sexual hierarchies. This, in turn, increases the chance that some high ranking females may dominate some low ranking males. As a result, DomWorld offers a proximate, mechanistic explanation for the degree of female dominance.

Correlation of:	with:	Tau	p
FemDom	% fights involving males	0.148	< 0.0001
FemDom	% fights among males	0.157	< 0.0001
FemDom	% inter-sexual fights	0.136	< 0.0001

Table 1: *Correlations of the degree of female dominance and the proportion of all fights that involve males, the proportion of all fights among males, and the proportion of inter-sexual fights. n = 40 runs * 9 sex ratios = 360.*

This mechanistic model-approach is a new alternative to previous explanations that interpreted female dominance mainly in an evolutionary framework. It has been argued that in lemurs, females are dominant to secure feeding priority, and thus to meeting the increased demand of energy that females require for gestation (Jolly, 1984; Young *et al.*, 1990) and lactation (Jolly, 1984; Richard & Nicoll, 1987; Sauther, 1993). However, later studies did not find evidence for exceptionally high reproductive investment in lemurs (Kappeler, 1996), so it remains unresolved why in lemurs the degree of female dominance is higher than in other primates. Another hypothesis is that female dominance could be regarded as a kind of paternal investment in monogamous species (Jolly, 1998): Males grant feeding priority to females, and from their improved conditions in turn the offspring profits. Yet, this explanation cannot account for the occurrence of female dominance in species that are not monogamous.

Other researchers use similar arguments to question the existence of female dominance altogether, stating that females are not really dominant, but only seem to be dominant over males (*e.g.* Stanford, 1998; Pochron *et al.*, 2005; reviewed for bonobos by Parish & de Waal, 2000): Males supposedly concede feeding priority to females in exchange for mating, so that males permit females to act dominantly as a kind of exchange mechanism.

However, all of the explanations mentioned concern cases where either female dominance is complete (*i.e.*, that all females are dominant over all males), or where ‘female dominance’ is equated with ‘feeding priority’. This seems to be a too narrow perception of female dominance, since even in lemur species the degree of female dominance may vary (chapter 2), and in numerous species female dominance occurs to a lesser degree (chapter 2). The explanations mentioned fail to cover this phenomenon in these species altogether. Female dominance may manifest in other ways than feeding priority, such as control of mating opportunities (reviewed for bonobos by Parish & de Waal, 2000), or rejection of undesired attempts of coerced copulations (Smuts & Smuts, 1993). Therefore, none of the above explanations is satisfactory for lemurs, and even less so for the understanding of female dominance as a phenomenon in many social societies.

Thus, the new, proximate model explanation is more general and parsimonious than previous ones: some females become dominant over some males due to chance and winner-loser effects. Still, DomWorld does not solve the puzzle of complete female dominance in lemurs, either. In the model experiments, females are maximally co-dominant with males (in the absence of initial differences in dominance values), but never completely. More field data, in particular of non-lemur primates, will be necessary to refine the model on the one hand, and to understand the contribution of winner-loser effects of the degree of female dominance in real primates on the other hand.

Sensitivity analysis

Reviewers have often questioned the robustness of the models DomWorld and GroupWorld. Several unpublished experiments have shown that the results are robust. For example in DomWorld, after an initial phase where hierarchies are weakly developed and rank reversals are frequent, stable hierarchies develop (from about period 200 onwards, Hemelrijk & Gygax 2004). Data were collected usually in the stable phase, from period 200 to 260. Now a frequently mentioned concern is that if the model would run for a longer time, would the dominance values of the individuals not keep diversifying, so that egalitarian societies would turn despotic over time? As it appears, this is not the case. Once a stable hierarchy is established, the degree of diversification remains constant (see examples over 800 periods, Figure 1).

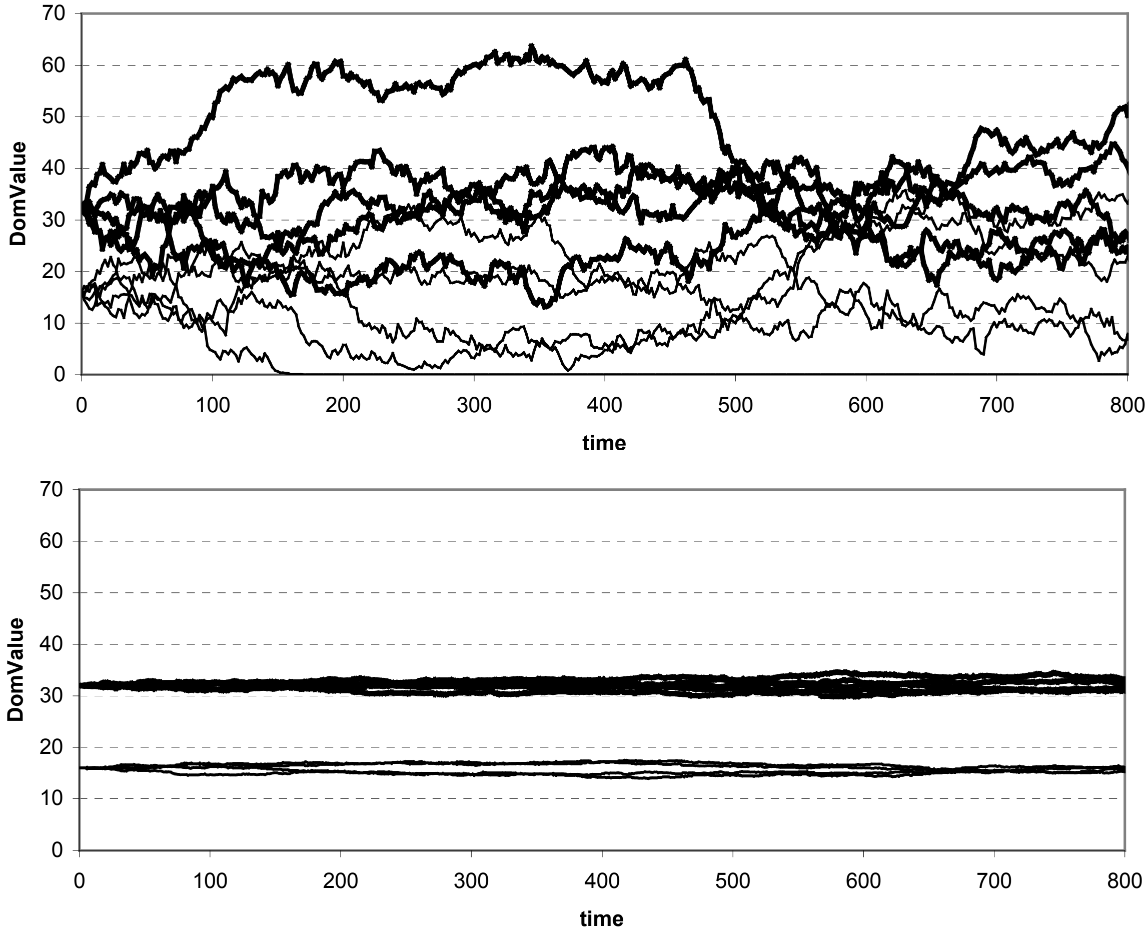

Figure 1: *Development of the hierarchy at a high intensity of aggression (StepDom = 1, above) and at a low intensity (StepDom = 0.1, below).* ▬ *= 'males',*— *= 'females'.*

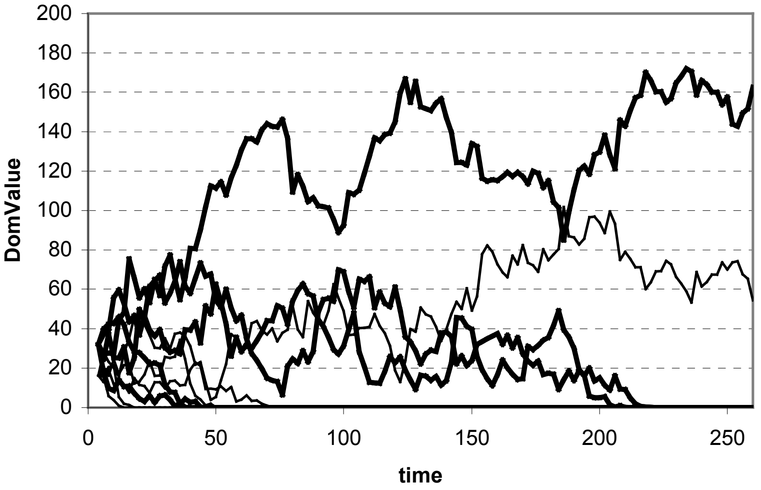

Figure 2: *Development of the hierarchy at a very high intensity of aggression (StepDom = 2.15). Note that a female has the second-highest rank.* ▬ *= 'males',* — *= 'females'.*

As regards the intensity of aggression, StepDom-Values in the range from 0.001 to 2.15 have been examined. Low values of StepDom result in little differentiation of the hierarchy; if StepDom is very low (0.01 or smaller), DomValues hardly change at all. We used a value of 0.1 as a lower limit for egalitarian groups. If StepDom-values are very large (such as 1.5 or larger, Figure 2), DomValues differentiate so quickly that one or two 'super-agents' emerge that defeat all others. This seems unrealistic for real primate groups; therefore, the maximal value for StepDom was set to 1 in the model. Note, though, that even in these extreme hierarchies sometimes females may become dominant over some males (Figure 2).

GroupWorld uses the same fighting algorithm as DomWorld, and therefore, the same values for StepDom. However, in GroupWorld, phases of fights within groups alternate with phases of fights between groups. Parameter settings of GroupWorld take into account the finding that in real primates fights between groups are relatively rare (macaques: between 0.3 and 0.64 per day, Cooper, 2004): Experiments in this thesis were run with 500 fights within groups that are followed by 50 fights between groups (or one clash of coalitions, chapter 7). Previous preliminary results had shown, however, that as long as the number of fights within groups greatly exceeds the number of fights between groups, results remain unchanged also for other frequencies of encounters within or between groups (Figure 3).

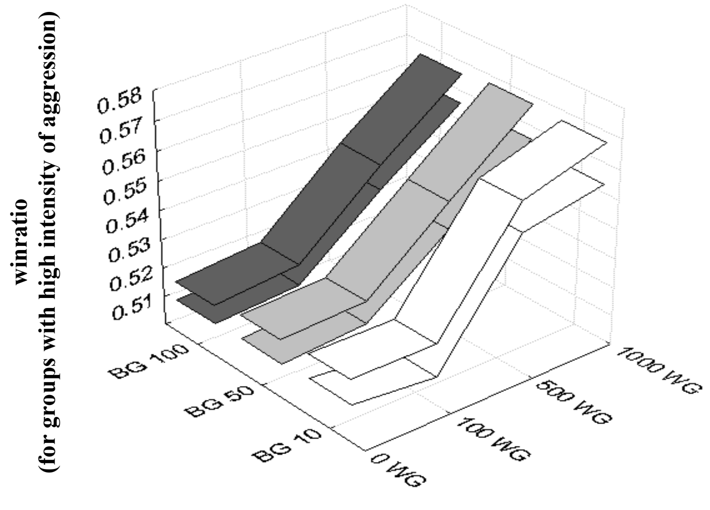

Figure 3: *Standard error of the winratio of groups with a higher intensity of aggression (StepDom = 1) over a group with a low intensity (StepDom = 0.1) for various numbers of fights within groups (WG) and between groups (BG).*

In sum, both models appear to be robust to parameter changes. This indicates that the results of the model are consequences of the described mechanisms, and not of random fluctuations.

General aspects of the models

Even though both DomWorld and GroupWorld are simple and highly abstracted models, the modelled groups exhibit complex patterns that are similar to that of real animals (female dominance, personality types, *etc.*). Common to all findings is that they illustrate the contribution of winner-loser effects to the social organisation of groups. For example, due to the self-reinforcing effects of winning and losing, females may become dominant over males in the model even though males start with higher initial dominance values. The strong development of the hierarchy in despotic groups is a consequence of the fact that due to the high intensity of aggression, a fight may cause large changes in dominance, which means that winner-loser effects are stronger in despotic societies. Thus, winner-loser effects may have far reaching influences in the model that even stretch to the performance of a group in inter-group encounters.

Winner-loser effects have also been demonstrated in a great number of real animals (Hsu *et al.*, 2006), and it seems promising to consider these self-reinforcing effects when interpreting the results of future experimental studies of social organisation.

Of course, both models are a simplification of the real world. Not only are the virtual individuals much simpler than real animals, but also the group level lacks natural complexity. For example, in the model, groups cannot hide or avoid other groups, like in the real world, and every encounter of groups includes at least a few acts of fighting. We omitted coalition formation within groups, which often occurs in primates and other species (Harcourt & de Waal, 1992), as well as kin relations (Sherman *et al.*, 1997; Mateo, 2002). Also, we ignored migration although in many primate species males leave their natal group to join other groups, or to live in male associations, which results in female biased sex ratios in many groups (Pusey & Packer, 1987). In order to keep the model simple, these aspects are not included here. To avoid confining it to a specific species, or a small range of species by making too many narrow, species-specific assumptions. Thus, although DomWorld and GroupWorld are strongly inspired by studies on primates, and in particular on macaques, the aim of this thesis is to identify generic mechanisms that could apply also to other primates, or group living animals in general. This is exemplified in this thesis in the case where two model-derived hypotheses concerning female dominance over males and the importance of inter-sexual winner-loser effects could be directly tested and confirmed with empirical data (chapters 4 & 5). Such mutual feedback between experimental data and model underlines the value of individual oriented models as a contemporary heuristic, and may greatly contribute to augment the acceptance of models by a broad range of researchers.

Outlook and future work

Carrying the results of the model GroupWorld a bit further, one may imagine that individuals or groups that constantly lose will have a lower reproductive success than others, so that traits that cause a bad performance of individuals or groups may in the long run be selected against, and eventually may go extinct. Due to time constraints, however, it was not possible to include evolution in the model. This would require to implement resources, an algorithm of their distribution and how they translate to offspring, inheritance and mutation of traits, and death, among other things. These extensions would have to be preceded by extensive literature research. Still, such an endeavour seems worthwhile. The most eminent tasks would probably be to test in a new evolutionary model whether evolution of dominance style could indeed proceed into two directions. This was suggested by Thierry *et al.* (2000) for the case of macaques, which is supported by our model (chapter 7).

Selection in such an evolutionary model, and possibly in nature, could target multiple levels, as may be speculated from the results in part II. However, while in the case of personality types selection would favour different traits at different levels (individual selection for cautiousness, group selection for boldness, chapter 6), despotism may under most conditions be selected for within as well as between groups (chapter 7).

If selection at both levels favours the same trait, as is the case with despotism under most conditions, one may argue that there is no need to apply group selection arguments, since despotism could evolve by individual selection alone. However, the coexistence of personality types due to performance in different contexts cannot be accounted to individual selection only. Thus, group selection may work on more traits than previously thought. So far, in primates it has only been suggested to play a role in the evolution of altruism, for instance in the case of alarm calls and coalition formation (Bradley, 1999).

9) Nederlandse Samenvatting

Onderzoeksvragen

In dit proefschrift onderzoek ik hoe winnaar-verliezerseffecten kunnen bijdragen aan hiërarchievorming en de sociale organisatie van groepen. Winnaar-verliezerseffecten zijn verantwoordelijk voor het feit dat de rang van een individu in een groep vaak niet gecorreleerd is met een bepaalde eigenschap zoals leeftijd of lichaamsgrootte. De kans op winst in een conflict is daarentegen vaak afhankelijk van eerdere gevechtservaring die het individu heeft opgedaan: Winnen vergroot de kans op wederom winnen, en verliezen vergroot de kans om in de volgende confrontatie het onderspit te delven. Dit winnaar-verliezerseffect is waargenomen in vele diersoorten in evenzovele taxa. Aangezien het winnaar-verliezerseffect in echte dieren moeilijk te quantificeren is, en omdat het doel van dit proefschrift het bestuderen van algemene mechanismen en niet zozeer van bepaalde diersoorten is, bestudeer ik het winnaar-verliezerseffect, en daaruit voortvloeiende consequenties, in dit proefschrift met gebruik van twee modellen.

Dit proefschrift heeft twee hoofdonderwerpen: Ten eerste, wijdt deel I zich toe aan de study van hoe winnaar-verliezerseffecten wel bijdragen aan de emergentie van vrouwelijke dominantie in enkele soorten, maar juist niet in andere. Hoewel voor vrouwtjes dominantie over mannetjes belangrijke voordelen kan hebben is vrouwelijke dominantie nooit op systematische wijze bestudeerd, behalve in enkele soorten lemuren op Madagascar. Voor het onderzoek in deel I wordt DomWorld gebruikt.

Ten tweede, eerder onderzoek met DomWorld heeft aangetoond hoe een enkele individuele eigenschap, zoals de intensiteit van aggressie of de aanvalsstrategie, de sociale organisatie van de gehele groep beïnvloedt. Groepen echte dieren interacteren echter meestal met naburige groepen. In deel II wordt de invloed van de sociale organisatie binnen groepen en de prestaties in competitie tussen groepen onderzocht met behulp van het multi-groep model GroupWorld.

De modellen

Computermodellen, met name individu-georiënteerde, worden heden ten dage steeds meer gezien als een nieuwe heuristiek om complexe sociale systemen te onderzoeken, bij voorbeeld de hiërarchievorming in sociale insecten of primaten. Een voorbeeld van een dergelijk model is DomWorld. In DomWorld worden individuën gesimuleerd als onafhankelijke agents die sich verplaatsen en interacteren in een twee-dimensionale virtuele ruimte. Elk individu heeft een dominantiewaarde die zijn gevechtssterkte aangeeft, en die toeneemt na overwinningen en afneemt na verliezen. Het blijkt dat door dit winnaars-verliezerseffect dominantiehiërarchiën ontstaan die op de lange termijn stabiel zijn. Dit simplistische, procesgeoriënteerde model is geënt op bevindingen in makaken, en heeft reeds geleid tot nieuwe inzichten en op minimale aannamen gebaseerde verklaringen, in een reeks onderzoeken naar primaten en andere diersoorten.

Het nieuwe model ‘GroupWorld’ is afgeleid van Domworld, en simuleert meerdere groepen met verschillende parameterinstellingen die competitie met elkaar voeren, waarbij wordt onderzocht welke soort groepen het meeste wint.

De hoodstukken

In hoofdstuk 2 wordt voor de eerste keer gequantificeerd in welke mate vrouwtjes dominant zijn over mannetjes d.m. van analyse van data uit de beschikbare literatuur over dominantie interacties in primaten. Hiernaast wordt een nieuwe en praktische maat voor de mate van vrouwelijke dominantie gepresenteerd.

Hoofdstuk 3 laat zien hoe enkele onverwachte oorzaken, zoals voedeldistributie, sexuele aantrekking en cohesie van de groep, de mate van vrouwelijke dominantie kunnen beïnvloeden door middel van zelfversterkende effecten. De voornaamste ontdekking is dat er sterke vrouwelijke dominantie is als de ontwikkeling van de dominantiehiërarchie sterk is, aangezien dit enkele sterke vrouwtjes in staat stelt enkele zwakke mannetjes in rang voorbij te streven.

Voorts behandelen rapporten over dominantie in in groepen levende dieren meestal slechts een geslacht. Het is echter de vraag of het correct is de hiërarchën van de geslachten gescheiden van elkaar te behandelen, aangezien hiërarchiën ontstaan door zelfversterkende winnaars-verliezerseffecten, en deze treden in beide geslachten op. In hoofdstuk 4 wordt het belang van inter-sexuele effecten in het model onderzocht door de winnaar-verliezerseffecten aan en uit te schakelen voor inter-sexuele conflicten. Het meest opvallende resultaat is dat inter-sexuele conflicten de vrouwelijke dominantie versterken. Hiernaast wordt een methode om het belang van inter-sexuele gevechten in echte primaten te schatten zowel voorgesteld als getest. Bij toepassing van de methode op acht soorten in het genus *Macaca* blijkt dat zelfversterkende effecten belangrijk zijn in inter-sexuele onflicten, maar niet zo belangrijk als in intra-sexuele conflicten. Tenslotte wordt getoond dat in het model de mate van vrouwelijke dominantie verband houdt met het percentage mannetjes in de groep.

Dit resultaat was de inspiratie voor een analyse van de beschikbare empirische data over 22 primaatsoorten (hoofdstuk 5). We bevestigen dat de in het model gevonden positieve correlatie tussen vrouwelijke dominantie en percentage mannetjes in een groep ook in de empirische data bestaat.

Hoofdstuk 6 gaat verder op enkele eerdere onderzoeken in DomWorld naar persoonlijkheidstypes, namelijk vermetele en voorzichtige persoonlijkheden. Deze onderzoeken lieten zien hoe het persoonlijkheidstype de sociale organisatie binnen de groep beïnvloedt: vermetele individuën eindigen in de meest extreme posities in de rangorde (hoog zowel als laag), en de voorzichtigen krijgen de middenrangen. Het blijkt echter in echte dieren onduidelijk hoe het mogelijk is dat verschillende persoonlijkheidstypen in één groep voor kunnen komen. Voor andere soorten werd gesuggereerd dat verschillende persoonlijkheidstypen in verschillende contexts beter presteren, maar in primaten lijkt het dat het voorzichtige type altijd in het voordeel is. We gebruiken daarom het model om de prestaties van persoonlijkheden in competitie binnen en tussen groepen te onderzoeken; deze verschillende contexts zijn tot nu toe niet experimenteel onderzocht, hoewel ze zeer belangrijk zijn voor primaten. De modelresultaten tonen aan dat de prestaties van de verschillende persoonlijkheidstypen inderdaad per context verschillen: voorzichtige individuën verslaan gemiddeld de vermetelen binnen de groep, maar in conflicten tussen groepen winnen de vermetelen het. Op deze wijze zouden de verschillende typen naast elkaar kunnen leven door selectiedruk op verschillende niveaus (individueel en groep).

In hoofdstuk 7 wordt onderzocht hoe de dominantiestijl en het aantal mannetjes in de groep het resultaat van gevechten tussen groepen kan beïnvloeden. Het blijkt dat onder de meeste omstandigheden de groepen met despotische eigenschappen het winnen van meer egalitaire groepen, en dat egalitaire groepen het slechts onder zeer weinig omstandigheden winnen. Deze resultaten contrasteren sterk met het socio-ecologisch model, dat aanneemt dat de meer egalitarische groepen de competitie met despotische groepen winnen. De resultaten worden echter ondersteund door bevindingen in echte makaken. Hiernaast suggereert het model dat vanuit een mild egalitarische voorouder, de dominantiestijlen wellicht in twee richtingen geëvolueerd zijn zowel in de meer despotische als de meer egalitaire richting. Dit is recentelijk voorgesteld voor makaken.

Conclusies

Uiteindelijk, als we de lessen geleerd in het model toepassen op echte dieren, kan het zijn dat vrouwelijke dominantie niet een geheel sort-specifieke eigenschap van echte primaten is, maar dat het ook afhangt van omgevingsvariabelen als de voedseldistributie (hoofdstuk 3), groepssamenstelling (hoofdstukken 4 & 5) en gevechten tussen groepen. Hoewel de invalshoek voor de modellen en de bespreking van de model resultaten vooral die van de primaten is, was een van de voornaamste doelen van dit werk het aanwijzen van algemene mechanismen, en het inspireren van nieuwe hypothesen. Dit ziet men het best in het geval waarin twee uit het model afgeleide hypothesen, aangaande vrouwelijke dominantie over mannetjes en het belang van inter-sexuele winnaars-verliezerseffecten direct getest en bevestigd konden worden met behulp van empirische data (hoofdstukken 4 & 5). Hiernaast is het, aangezien winnaars-verliezerseffecten zijn waargenomen in vele diersoorten, zeer wel mogelijk dat de resultaten van het model relevant zouden kunnen zijn voor een groot aantal soorten naast primaten.

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