



Review

Individual variation by self-organisation

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Abstract

In this paper, we show that differences in dominance and spatial centrality of individuals in a group may arise through self-organisation. Our instrument is a model, called DomWorld, that represents two traits that are often found in animals, namely grouping and competing.

In this model individual differences grow under the following conditions: (1) when the intensity of aggression increases and grouping becomes denser, (2) when the degree of sexual dimorphism in fighting power increases. In this case the differences among females compared to males grow too, (3) when, upon encountering another individual, the tendency to attack is ‘obligate’ and not conditional, namely ‘sensitive to risks’.

Results resemble phenomena described for societies of primates, mice, birds and pigs.

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1. Introduction

Even among individuals of a single population, and of the same sex and size, there may be consistent differences in their behaviour towards a specific environmental stimulus (Wilson 1998; Sih et al. in press). Such individual differences may take the form of polymorphisms or quantitative individual variation. They may result from genetic, environmental or ontogenetic factors, as well as the interaction of these factors [1]. Here, we mainly look at cases of phenotypic plasticity. In particular we study short-term changes in dominance (due to the winner/loser effect) in response to the (social) environment [2,3]. Our approach is unusual, because we study cases where dominance may result in, and be caused by, patterns at the level of the group that arise by self-organisation. With self-organisation we mean that interactions among lower level units lead to unexpected patterns at a higher level see e.g. [4,5]. This we will demonstrate with the help of a so-called 'bottom-up' procedure: a model in which units (individuals) interact with their environment by reacting only to stimuli from their nearby environment. When in this model complex patterns develop, these patterns become intelligible in a way that cannot be achieved when they are studied from the 'top-down'. In a 'top-down approach' the usual, reverse method is followed, in which rules of the behaviour of animals are inferred from observations in nature. We may illustrate the 'bottom-up' procedure with an eco-evolutionary model of the origination of high diversity of toxicity and corresponding immunity in the bacterium *Escherichia coli* [6]. Bacteria may carry 'colicin'-plasmids that produce one of many types of toxins and/or corresponding immunity. Both toxicity and immunity come at a cost to the bacterium. High diversity of toxins and immunity in a population arises in the model in two ways. Either in the form of a homogeneous population of bacteria in which each bacterium has a high number of immunity genes but produces only few toxics (named 'hyper-immunity' mode), or in the form of a heterogeneous population that is spatially structured into patches of different bacteria each producing a low number of toxins and corresponding immunities

(so-called 'multi-toxicity'). In case of 'hyper-immunity', all bacteria are protected against a great number of the same toxins. However, if the number of immunity genes becomes too high and thus, immunity is too costly, bacteria lose some of these genes, and the 'multi-toxicity' mode arises by spatial self-organisation. Here, bacteria are toxic and immune for only a few substances that differ between patches. Within such a patch bacteria are identical and thus, protected; there is a kind of 'cooperation' within a patch. At the boundary of a patch it borders on a patch of different bacteria, and here, bacteria may kill each other. Whereas, in case of 'hyper-immunity' a new bacterium, if it contains more toxins than the rest, may take over the complete population, 'multi-toxicity' prevents a complete take-over. New bacteria (with different immune and toxicity genes) can only take over part of the population, because they are out-competed elsewhere. Thus, despite its small number of immunity-genes per bacterium, the 'multi-toxicity' mode seems better protected against invasion.

The aim of the present paper is to give other examples of self-organised individual differences: namely the differentiation of competitive power (or dominance rank) among individuals that strive to group. After this, we give a survey of factors that influence such differentiation.

We take dominance as our objective, because it is a general and important aspect of social behaviour. It is general, because in many species, a dominance hierarchy is observed in which certain individuals in conflicts consistently are superior to others in conflicts [7]. It is important, because dominance has great influence on many other aspects of behaviour, e.g. grooming and the formation of coalitions among primates [8,9], on the reproductive success in group-living animals [10–12] and on behavioural activities (such as foraging and the care for offspring) among social insects [13].

Whereas, some argue that dominance is (genetically) inherited [14], in many animal species (from insects to humans) it has been shown that the acquisition of a dominance position is (at least partly) due to the so-called winner/loser effect; this implies that the effect of victory and defeat is self-reinforcing: in other words, after being

defeated the chance to lose again is increased and, vice versa, after a victory the chance to win again is increased too [15,16]. This has been demonstrated experimentally in many species; In these experiments, two individuals were matched in size and brought together in a fight. The winner (or loser) of this contest was matched to a new opponent (of the same size) again [17].

In this paper, we study the consequences of this winner/loser effect among initially completely identical individuals in a model, which we call DomWorld. This model we have provided with the essentials of sociality. It is an artificial ‘world’ in which the actions of the agents are confined to grouping and competing, and in which the effects of winning and losing an interaction are self-reinforcing. The model generates artificial ‘societies’ that resemble the societies of real primates [18]. The resemblance is particularly clear with species of the genus *Macaques* in which two kinds of competitive regime are distinguished: egalitarian and despotic [10]. This similarity shows that DomWorld can be used for the development of ideas about differences in behaviour between individual animals in nature.

Our model shows that the degree of hierarchical differentiation (i.e. the extent to which individuals differ in competitive power) depends on certain characteristics that are found also in real animals: e.g. intensity of aggression (biting versus slapping), density of grouping, attack strategy (which may be risk-sensitive, ambiguity-reducing or obligate), sexual dimorphism and sexual attraction. These factors are usually considered to be both genetically encoded and environmentally influenced.

Obviously, the model does not represent real animals, but merely reflects the process of grouping and competition and its effect on a two-dimensional environment. The results of this model may serve as a theoretical background for the study of dominance-related differences among real individuals.

2. Methods

2.1. The model, DomWorld

There are three basic elements to our model: it is a ‘world’ with its interacting agents, it is visualised in a practical way and it contains as it were observers who collect and analyse data of what happens in the ‘world’ (cf. the ‘recorders’ and ‘reporters’ of [19]). The space of the world is made continuous, in the sense that agents are able to move in all directions [20]. Agents have an angle of vision of 120° and their maximum perception distance (MaxView) is 50 units. Activities of agents are regulated by a timing regime. Here, a random regime is combined with a biologically plausible timing regime (see also [21]) in which 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 ‘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 [22]). Agents group and perform dominance interactions according to a set of rules described below (Fig. 1).

2.2. Grouping rules

Usually, two opposing tendencies affecting group-structure are supposed to exist: on the one hand animals are believed to be attracted to one another because living in a group has advantages (such as increased safety); on the other, grouping implies competition for resources, and this drives individuals apart e.g. [23].

In DomWorld this is represented by two sets of rules graphically displayed in Fig. 1 see [18]. The resources about which the agents compete are not specified.

1. If an agent observes another within a critical distance, its ‘personal space’ (= PerSpace of 2 units), 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, if not, it makes a 180° turn and flees away two units under a small random angle.
2. If nobody is observed in PerSpace, but an agent notices others at a greater distance, still within NearView (of 24 units), 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 the other sex over one unit distance when they observe it in NearView (see ‘attraction’ in Fig. 1).
3. If its nearest neighbours are outside NearView, but within its maximum range of vision (= MaxView of 50 units), the agent moves one unit towards them.
4. If an agent does not notice other agents within MaxView, it looks around for them by turning a SearchAngle of 90 degrees at random to the right or left.

2.3. Dominance interactions

In models of self-organised hierarchies winner and loser effects that are of fixed size have been implemented [16] and of a size that depends on the dominance position of the opponents [24]. If the higher-ranking opponent is victorious, as expected, the change in dominance is small. If, however, the lower-ranking one of the pair unexpectedly defeats the other the dominance values of both partners are changed by a larger amount. We have chosen for the latter representation because it is more natural.

Therefore, dominance interactions between agents are modelled after Hogeweg and Hesper [24] and [18], as follows: Each agent has a variable that is called ‘Dom’ (=dominance, representing the capacity to win an

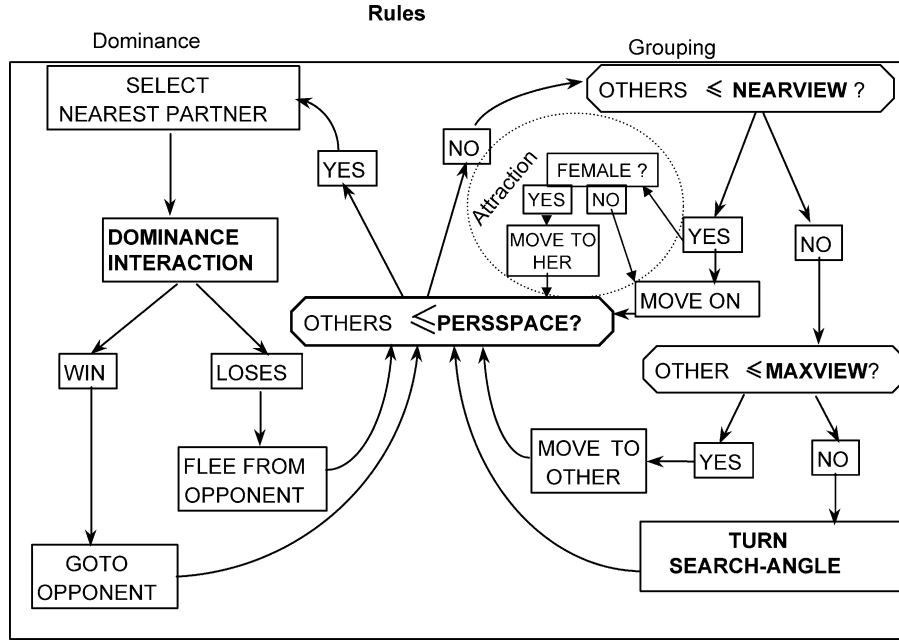


Fig. 1. Flow chart for the behavioural rules of the individuals. Encircled part is the rule for attraction to females. This rule is only operative in male agents during sexual attraction. The terms PersSpace, NearView, MaxView and SearchAngle are described under Grouping Rules.

interaction). After meeting one another in their PerSpace (4 units distance), 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. This is in line with experimental studies [17,25] and is implemented as follows: Upon meeting another agent and observing its Dom-value, an agent may foresee it will win or lose on the basis of a ‘mental’ battle, which follows the rules of a dominance interaction as described below. If ego loses the mental interaction, it will refrain from action and move away two steps (thus displaying ‘non-aggressive’ proximity). If it wins the mental battle, it will start an ‘actual’ dominance interaction.

If an actual dominance interaction takes place, then agents display their Dom-value and observe that of the other. Subsequent winning and losing is determined by chance and by values of Dom as follows:

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

Here w_i is the outcome of a dominance interaction initiated by agent i (1=winning, 0=losing). In other words, if the relative dominance value of agent i is greater than a random number (drawn from a uniform distribution), then agent i wins, else it loses. Thus, the probability of winning is greater for whoever is higher in rank, and this is proportional to the Dom-value relative to that of its partner.

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

the loser:

$$\begin{aligned} DOM_i &:= DOM_i \left(w_i - \frac{DOM_i}{DOM_i + DOM_j} \right) \\ &\quad * \text{STEPDOM} \quad DOM_j \\ &:= DOM_j \left(w_i - \frac{DOM_i}{DOM_i + DOM_j} \right) * \text{STEPDOM} \end{aligned} \quad (2)$$

The change in Dom-values is multiplied by a scaling or stepping factor, so-called StepDom, which varies between 0 and 1 and represents intensity of aggression. High values imply a great change in Dom-value when updating it, and thus indicate that single interactions may strongly influence the future outcome of conflicts. Conversely, low StepDom-values represent low impact. 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 pre-defined Fleeing-Distance of 2 units.

2.4. The sexes and sexual attraction

In the model, the artificial ‘sexes’ differ in their competitive ability and in the presence or lack of attraction to the opposite sex. In line with descriptions of primates [26], 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, indicated by the scaling factor of 1.0 and 0.8 for males and females, respectively). Note that the intensity of an interaction depends on the StepDom value of the initiator of the fight. Unless otherwise stated, reflecting the physiologically superior fighting ability of males, artificial males start with a higher ability to win than artificial females (InitDomMales=32, InitDomFemales=16), but all individuals of the same sex start with the same ability. By keeping individuals of the same sex completely identical at the start of a run, we make sure that there are no genetic differences among individuals of the same sex in a group.

As regards sexual attraction, 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. We study females that are attractive synchronously and asynchronously, in which case a different female is attractive in each subsequent interval (with interval lengths of 5, 13 and 52 time units) [27].

2.5. 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, the degree of rank-differentiation, its stability and the overlap between the dominance-hierarchies of Males and Females and the spatial structure are measured as follows.

Rank differentiation is measured by the coefficient of variation (standard deviation divided by the mean) of Dom-values [28]. For each run the average value is calculated over the stable period from time-unit 200 to 260 (one time unit lasts x activations, whereby x equals 20* the number of individuals). Higher values indicate larger rank distances among entities.

The degree of dominance of females over males is estimated as the sum of the number of males dominated by each female separately and reflected in the Mann–Whitney U -statistic [29]. At the start of each run, each female is subordinate to all males, and therefore at the beginning of the run U -values are zero. Since during run-time some females may become dominant over (some or all) males, U -values later on may become positive.

The degree to which dominants occupy the centre is measured by means of the Kendall rank correlation between

the dominance value and the average distance of ego to others. This is based on the notion that individuals in the centre have a shorter average distance to others than individuals at the periphery. Thus, stronger centrality of higher-ranking entities is reflected in a larger negative correlation between rank and average distance to others.

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.

2.6. Experimental set-up and data-collection

Here, the same parameter setting is used as in former studies [20,30]. The present study is confined to a population of ten agents including five females and five males.

Several conditions, such as intensity of aggression, degrees of sexual dimorphism and sexual attraction, are compared. For each one of these conditions 50 runs are conducted.

3. Results and discussion

3.1. Intensity of aggression and spatial structure

Species of the primate genus *Macaca* differ in intensity of aggression. In some species aggression is of a low intensity (mild), restricted to slapping and menacing; in others, such as long-tailed macaques, biting occurs and aggression may be intense. When in our model DomWorld, we increase the intensity of aggression from mild to intense, a cascade of effects results. Higher intensity of aggression accelerates the development of individual differences in dominance (Fig. 2A). Consequently, low-ranking individuals develop into constant losers: they flee from all others and so, the group spreads out (which in its turn reduces the frequency of aggression). At the same time, a spatial structure develops with dominants in the centre and subordinates at the periphery; besides, all individuals are close to those with a similar dominance value (Fig. 2B). This spatial structure in turn strengthens the hierarchy, because individuals, when mainly interacting with those that are close by, interact usually with agents of similar dominance. Thus, if a dominance reversal takes place as the result of an interaction, it is only a minor one because the opponents were similar in dominance before their fight. Therefore, the spatial structure stabilises the hierarchy. In this way, the hierarchy and the spatial structure are mutually reinforcing each other. In other words, at a high intensity of aggression, the gradient of the hierarchy is steep, and individual differences are great.

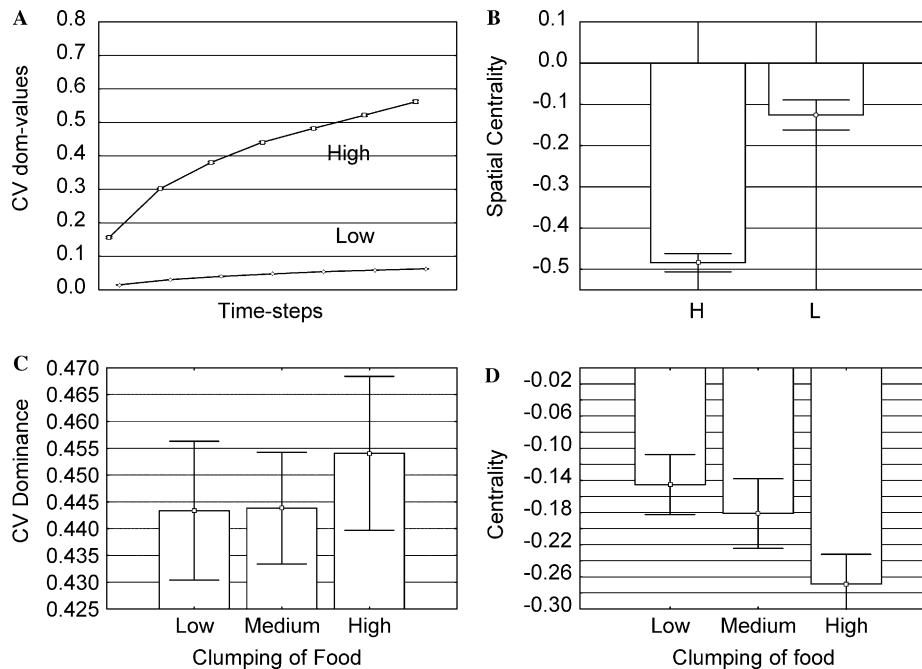


Fig. 2. Effects of intensity of aggression (A,B) and of distribution of food (C,D) on hierarchical differentiation and spatial centrality of dominants. Intensity of aggression and (A) coefficient of variation of dominance, (B) spatial structure. Three degrees of clumping of food and (C) coefficient of variation of dominance and (D) spatial structure.

Also, individuals are spread out further and their location depends on their dominance position.

3.1.1. Discussion

The differences between an artificial society with an intensity of aggression that is high and another one in which it is low, resemble in all respects the differences between the societies of an egalitarian species and of a despotic one among real animals, especially the genus of macaques [18,31–35]. Some aspects, such as spatial structure, have in primates not yet been studied systematically, but they have been observed in other animals (in insects, fish, and birds, for a review see [36]). It has been suggested that in ants spatial structure functions as a mechanism for the division of tasks [37,38]. It appears that at the periphery individuals are inclined to collect food, whereas individuals in the centre tend to care for the young. Therefore, it seems likely that differences in dominance, spatial location and performance of tasks are interdependent.

3.2. Distribution of food, cohesion of grouping and spatial structure

In the model differences similar to those between societies with a low and a high intensity of aggression ('egalitarian' and 'despotic' societies) can also be created by experiments with group cohesion at a relatively high intensity of aggression. In real animals, group cohesion is thought to be related to predator pressure and food

distribution. Group-density or -cohesion can be varied in DomWorld in two ways. In the first place directly, by changing the angle over which individuals turn to look for others when they happen to have lost their group. In this case, increasing the so-called SearchAngle in the model enables individuals to find back their group sooner, and therefore, the group becomes more compact [30]. In the second place, group cohesion is influenced by the degree to which food is clumped [27]. For this, food sources (with exponential regrowth) were added to the model and the behaviour of individuals was extended with hunger (due to energy loss) and feeding behaviour. A higher degree of clumping of food appears to lead to greater individual differences in dominance, and a clearer spatial segregation of individuals of different dominance values (Fig. 2c and d).

3.2.1. Discussion

Van Schaik and co-authors [23,39] suggest that, when competition within primate groups and between groups is great, a despotic society with a clear differentiation in the hierarchy develops. However, according to Matsumura [40] no competition between groups is needed for this. In the model, competition within groups also suffices for a despotic system to develop.

3.3. Inter-sexual dominance and the type of society

Many groups of animals consist of individuals of both sexes. In primates, males are usually larger and stronger

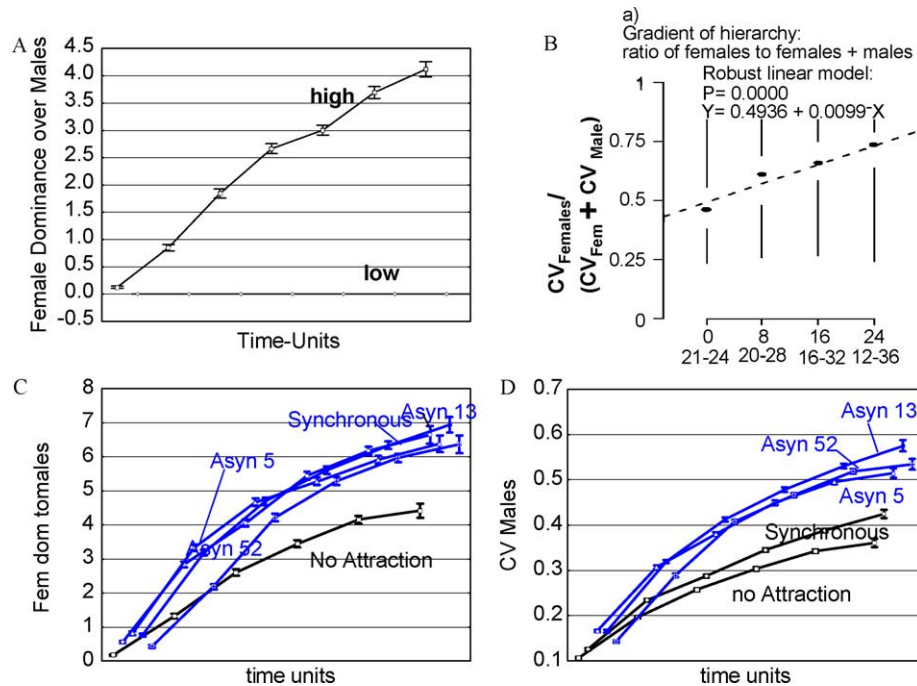


Fig. 3. Female dominance and (relative) hierarchical differentiation of both sexes. (A) Intensity of aggression and the degree of female dominance over males measured by the Mann–Whitney U value (average and SE). (B) Relative degree of differentiation of the hierarchy for different degrees of sexual dimorphism at a high intensity of attack (points represent median value, vertical lines are quartile above and below it). Social relations during sexual attraction. (C) female dominance (average and SE). (D) Differentiation of the hierarchy among males (average and SE).

than females and, due to their muscular structure their aggression is more intense. In the model we implement males with a higher initial dominance value and a greater intensity of aggression. When we increase the intensity of aggression to a high degree, it appears that at this high intensity female dominance over males is also increased. In other words, intense aggression reduces the initial difference in dominance between the sexes whereas mild aggression does not (Fig. 3A). This happens, because at a high intensity the hierarchy differentiates strongly which causes some males to sink very low in dominance (below high-ranking females) and some females to rise very high (above low-ranking males). At a low intensity, however, nothing much happens and females that started out being lower than males, simply remain so. In other words, female dominance over males appears to be greater at a high intensity than at a low one [18].

3.3.1. Discussion

This agrees with observations in the real world: Ref. [33] reports that female dominance over maturing sub-adult males in fiercely aggressive despotic females is greater than in mildly aggressive, egalitarian females. However, his explanation is different. He assumes that increased female dominance may arise from the fact that coalitions among females against (sub-adult) males are stronger in a despotic than in an egalitarian species. In DomWorld, however, the cause is different and far simpler.

3.4. Sexual dimorphism and individual differences per sex

In some species there is a strong sexual dimorphism in body size, males being much larger than females. Due to this and their intense aggression, we may expect individual differences in dominance among such males to be greater than among their females and therefore, that in this type of society males are more despotic among themselves than females.

Unexpectedly, the model produces exactly the opposite result: the gradient of the hierarchy is weaker among males (and therefore, males are more egalitarian) than among the females [41]. This holds for all parameters (high and low intensity of aggression both species-specific and sex-specific). This weaker differentiation is unexpected in males, because in the model, their aggression is more intense than that of females. It is, however, a consequence of the higher initial dominance of the males: if we give the sexes the same initial dominance value, the hierarchy of the males does actually develop more strongly than that of the females. Thus, although high intensity of aggression of the males increases the gradient of their hierarchy, the development of the hierarchical gradient is slowed down by their high initial dominance, because a single act of victory or defeat has less effect on a high dominance value than on a low one. Thus, if we increase the degree of sexual dimorphism in the model, the differentiation of the hierarchy of females becomes relatively stronger (compared to that of both sexes summed, see Fig. 3B).

3.4.1. Discussion

These results resemble the sex difference that has been observed for Barbary macaques. Whereas, we would expect male Barbary macaques to show greater individual differences in their dominance than females (because of their larger body size), their individual differences appear to be relatively smaller and their male-society more egalitarian than that of the females! This is exactly so in our model.

Whereas, on the basis of their findings of Barbary macaques, Preuschoft and co-authors [42] question the value of the classification into egalitarian and despotic types as a species-specific trait in general, the results of our model point to the opposite conclusion: First, in real animals the degree of sexual dimorphism is species-specific. Second, in the model the degree of hierarchical differentiation differs between the sexes in a similar way as in Barbary macaques. Therefore, in real animals the strong degree of individual variation in dominance among females compared to males is, it appears, species-specific [41].

3.5. Sexual attraction

In the model we may also add attraction between the sexes. In primates females are fertilisable either at the same time or not. If we introduce these two possibilities in our model, the result is that sexual attraction towards females increases the similarity in dominance between the sexes (Fig. 3C). In other words, female dominance increases whether the cycle of females cycle is synchronous or not. However, in the case that females are attractive at different times, the differentiation of the male hierarchy also increases strongly (Fig. 3D). These results come about as follows.

If single females are attractive in turn (for an arbitrary duration of 5, 13 or 52 time steps), many males cluster around a single female. Consequently, the frequency of male–male interactions is markedly increased, but the frequency of interaction between the sexes and among females remains similar to that when females are not attractive to males. Due to the higher frequency of interactions among males, the male hierarchy differentiates more strongly than without such attraction (Fig. 3D) and this causes some males to become subordinate to some females [27]. On the other hand, if females are attractive at the same time, the number of interactions between the sexes increases. Therefore, low-ranking females have more opportunities (though it is unexpected) to beat higher-ranking males. When this happens, the dominance-value of females increases by a greater degree than if, as expected, females defeat individuals of lower rank than themselves.

Note that at a low intensity of aggression, female dominance does not increase when males are attracted to them. Female dominance over males remains almost nil, because due to their low intensity of aggression and low initial dominance value they have hardly any chance to beat a male [43].

Further, the model shows that at a high intensity, during periods of sexual attraction, males approach females with less aggression than at other times [27]. This results because, during sexual attraction, female dominance over males increases and, therefore, the risks for males in attacking females increases also. This restrains male aggression to females, but it looks like a positive increase of male ‘tolerance’ to females.

3.5.1. Discussion

The increase of male ‘tolerance’ is of interest, because a similar increase is observed in chimpanzees and is explained as ‘exchange of friendship for sex’ [44]. However, so far there is no evidence that male services to females lead to an increased number of matings with, and offspring born to, these females [45,46]. Therefore, in line with the suggestions of the model, male ‘tolerance’ may be directly beneficial to the male chimpanzees, because this protects them against a defeat inflicted by females.

As for ‘sexual preference’ in our model, agents are not built to prefer certain partners above others. Yet, spatial proximity to females may differ depending on the spatial social structure. If at a high intensity of aggression all female agents are attractive at the same time, artificial males will be more often near to females of similar dominance. This is due to spatial-social structuring. At a low intensity, however, spatial structuring is weak and therefore, males will be close to a greater diversity of female-partners. If, however, single females are attractive one at a time, the highest-ranking males are likely to be near the attractive females (both, in high and low intensity of aggression). Note that in societies of real macaques synchronisation of tumescence overrules the effects of hierarchical differentiation: unexpectedly, male dominance has a stronger effect on the frequency of mating in egalitarian than in despotic species, because females are tumescent in turn in egalitarian species, but simultaneously in despotic ones [47].

3.6. Different attack strategies (‘personality styles’)

Different types, styles or strategies of aggression may be distinguished. Whereas, some individuals attack only if an opponent is clearly seen to be inferior [48], others attack always (compare the short latency of attack in mice and birds, [49,50]).

These strategies are implemented in DomWorld as, ‘risk-sensitive’ and ‘obligate’ attack [51]. It appears that they differ in the degree in which individuals vary in dominance. Differentiation of dominance values appears to be greater when attacking is obligate than when it is risk-sensitive due to the higher frequency of attack [51]. This has nothing to do with the intensity of aggression (Fig. 4A).

Consequently, also in mixed groups in which there is an equal number of individuals of both types of strategies, obligate attackers rise very high and descend very low in the hierarchy (resulting in a bi-modal distribution of dominance

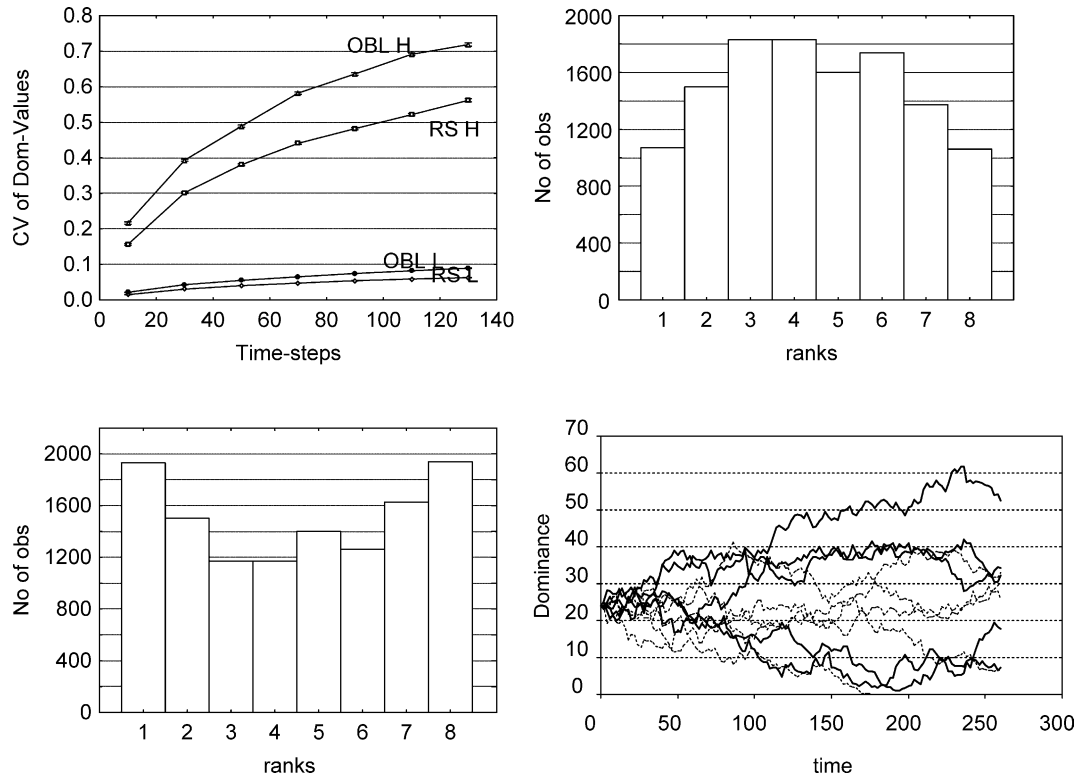


Fig. 4. Hierarchical characteristics in groups with a single strategy of attack and in mixed groups. Pure groups with a single attack strategy: (A) hierarchical differentiation for each strategy of attack and two intensities of aggression. Mixed groups with an equal number of both strategies of attack: Distribution of dominance values of individuals with (B) obligate attack and (C) risk-sensitive attack strategy. (D) Dominance development in a single run of a mixed group (fat lines: obligate attackers, thin lines: risk-sensitive).

values, Fig. 4B), whereas risk-sensitive attack leads to less variation, a uni-modal distribution of values (Fig. 4C) and therefore to more intermediate dominance positions (Fig. 4D). Further, among individuals built to use risk-sensitive attacks, the average dominance is slightly higher than among individuals that attack always (obligatorily). This is due to their more ‘intelligent’ attack-strategy, because agents that are sensitive to risks will attack especially when the risk to lose a fight is small.

3.6.1. Discussion

Different strategies of attack in the model (obligate and risk-sensitive) produce results that resemble the ‘coping styles’ or ‘personality styles’ known as ‘bold’ and ‘cautious’ (also known as fast-explorers and slow-explorers, respectively), which are found in, for instance, mice, birds and pigs [52]. We will discuss explanations generated by the model for three studies, two of which concern great tits and one on sticklebacks.

First, these results resemble the distribution of dominance among slow and fast attackers in mixed groups of great tits [49]. Here too, fast attackers end very high up in the dominance hierarchy or descend very low.

This is explained, however, by the assumption that the high and low ranking individuals were in different stages of moulting. Further, the distribution of dominance of

slow-explorers was approximately normal and clearly uni-modal and the average dominance was somewhat above the average. This success of the slow and ‘cautious’ ones is, however, not explained as suggested by our model, but attributed to their tendency to attack from a familiar territory and their faster recovery from defeats. Since DomWorld produces similar results for groups of individuals that attack obligatorily and risk-sensitively, this implies that the differentiation of dominance values in these birds can also entirely be explained by their different strategies of attack: there is no need to add causes based on different stages of moulting, or on familiar territory or faster recovery. Thus, the model produces a far simpler explanation for the distribution of dominance values in these groups of great tits.

Second the model provides us with a parsimonious alternative explanation for the associations between dominance behavior and exploratory style in great tits found by [53]. This association appears to differ among individuals that own a territory and those that do not; whereas among territory owners fast-explorers were dominant over slow ones, they were subordinate to them among those without a territory. To explain this the authors use a context-specific argument in which they need an additional trait, namely speed of recovery from defeat [54]. They argue that particularly among those individuals without a territory,

fast-explorers have more difficulty to recover from defeat than slow-ones and thus, they become low in rank, whereas territory-owners do not suffer this setback and, thus, become high in rank. Thus, the dominance position of individuals depends on the context (namely, the possession of a territory). However, so far, this has not been shown empirically, because single individuals have not been studied under the both conditions (regarding territorium-ownership). Therefore, a simpler explanation, in line with our model, may apply. As is usual in a process-oriented explanation, we start from existing dominance relationships and suppose that these decisively influence who will obtain a territory (instead of the other way around). We assume that, because territories are limited in numbers, the higher-ranking individuals (say the top half of them) will acquire them, whereas individuals in the lower part of the hierarchy are unable to get one. Due to the bi-modal distribution of dominance values among fast-explorers, and the uni-modal distribution of slow-explorers, the most extreme dominance positions in the colony will be occupied by fast-ones and the slow-explorers are located in the middle of the hierarchy. Thus, among individuals in the top half of the hierarchy (thus, among territory-owners) fast-explorers will rank above slow-explorers, whereas in the bottom half of the hierarchy, namely among those individuals without a territory, the reverse holds (Fig. 4d). Note that in this explanation the personality style of an individual is not context-dependent (fast-explorers and slow-ones keep their dominance position, whether or not they were able to obtain a territory).

The third example concerns the positive association between boldness towards predators and aggression to conspecifics in wild-caught sticklebacks from two environments. The correlation appears to occur among the animals from one environment but not among individuals caught in the other environment [55]. Bell et al. suggest that the environments differ in predator pressure. With the help of our model we explain this difference through a kind of ‘environmental’ shaping of personalities through a spatial-social structure that may build among fish if predators are present but not if they are absent. Suppose that in the environment with high predator pressure, shoaling is stronger. This implies that individuals perform dominance interactions more often (such as in sticklebacks, [56,57]). Thus, a spatial-social structure may form with dominants in the centre and subordinates at the periphery [51]. As a consequence of this structure, individuals of different dominance may get different experiences: the lower ranking individuals, because they are at the periphery of the group, run more often the risk of meeting predators than the dominants (in the center). Therefore, they will be more careful with predators than high ranking ones are. Such a correlation does not develop among individuals that came from an environment in which predators were absent because in that case, shoaling and spatial-structure are weak.

4. Evolutionary considerations

As regards considerations of evolution, our model points to the fact that experience (the winner/loser effect) and self-organisation result in groups that are spatially heterogeneous and groups that may differ in degree of hierarchical differentiation. Natural selection may operate on these differences. As regards the spatial heterogeneity, in several of the models mentioned above, dominant individuals end up in the centre and subordinates at the periphery. Since all agents are genetically identical and it depends on chance which of them becomes dominant, dominance is not genetically inherited. In primates, however, dominance of offspring is regarded as culturally inherited due to support in fights by the mother. This means that offspring of high-ranking mothers are of high rank too. When over evolutionary time, dominants are exposed to selection pressures in the group centre that differ from those of the subordinates at the periphery, they may develop genetic qualities that differ from those of the subordinates [58]. In this way, chance effects of winning and losing may have genetic consequences via dominance and the change of the (social) environment.

Further, among groups that differ in their hierarchical gradient stronger hierarchical differentiation (through either strong cohesion or high intensity of aggression) may be favoured by group-selection. This may come about in two ways, through selective group survival and through competition between groups. First, in periods when food is scarce, groups with a steeper hierarchy will survive more easily, because, though others perish, at least the individuals with the highest rank will get enough food to survive and reproduce (compare Ref. [59]). Second, in conflicts between groups, the competitive power of high-ranking males will be greater in a despotic than in an egalitarian system (due to the strong differentiation of the hierarchy in despotic societies). It follows that despotic groups survive egalitarian ones, but only if mainly the highest-ranking males take part in these fights (as is the case in primates). In these two ways, marked individual variation in dominance (strong hierarchical differentiation) may be favoured by selection between groups (Wantia and Hemelrijk, in prep).

5. Conclusion

Our model represents a selection of aspects, namely dominance processes, grouping, sexual attraction, spatial structure, distribution of food, and their immediate consequences for behaviour. We hope that our examples of self-organisation of individual variation in dominance and behaviour and their resemblance to the behaviour of real animals, have shown that models based on self-organisation are a useful tool for the study of animal behaviour. They show us the consequences of interactions among individuals themselves and between individuals and their physical

environment. This is helpful, because the human mind on its own tends to reason in terms of individual traits rather than of environmental effects.

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