

Self-Organization and Natural Selection in the Evolution of Complex Despotic Societies

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Abstract. Differences between related species are usually explained as separate adaptations produced by individual selection. I discuss in this paper how related species, which differ in many respects, may evolve by a combination of individual selection, self-organization, and group-selection, requiring an evolutionary adaptation of only a single trait. In line with the supposed evolution of despotic species of macaques, we take as a starting point an ancestral species that is egalitarian and mildly aggressive. We suppose it to live in an environment with abundant food and we put the case that, if food becomes scarce and more clumped, natural selection at the level of the individual will favor individuals with a more intense aggression (implying, for instance, biting and fierce fighting).

Using an individual-centered model, called DomWorld, I show what happens when the intensity of aggression increases. In DomWorld, group life is represented by artificial individuals that live in a homogeneous world. Individuals are extremely simple: all they do is flock together and, upon meeting one another, they may perform dominance interactions in which the effects of winning and losing are self-reinforcing. When the intensity of aggression in the model is increased, a complex feedback between the hierarchy and spatial structure results; *via* self-organization, this feedback causes the egalitarian society to change into a despotic one. The many differences between the two types of artificial society closely correspond to those between despotic and egalitarian macaques in the real world. Given that, in the model, the organization changes as a

side effect of the change of one single trait proper to an egalitarian society, in the real world a despotic society may also have arisen as a side effect of the mutation of a single trait of an egalitarian species.

If groups with different intensities of aggression evolve in this way, they will also have different gradients of hierarchy. When food is scarce, groups with the steepest hierarchy may have the best chance to survive, because at least a small number of individuals in such a group may succeed in producing offspring, whereas in egalitarian societies every individual is at risk of being insufficiently fed to reproduce. Therefore, intrademic group selection (selection within an interbreeding group) may have contributed to the evolution of despotic societies.

Introduction

The assumption that evolution occurs through a single evolutionary process is no longer tenable (*e.g.*, see Plotkin and Odling-Smee, 1981), and multiple-level selection theories have slowly become more accepted (*e.g.*, Hogeweg, 1994; Maynard Smith and Szathmary, 1995; Mitteldorf and Wilson, 2000). Multiple-level selection processes may include some, or all, of the following factors: the multi-level character of biological systems and natural selection operating on them (Lewontin, 1970; Hogeweg, 1994; Sober and Wilson, 1998), self-organization and its consequences for evolution (Boerlijst and Hogeweg, 1991), and nonlinear genotype-phenotype mappings (Kauffman, 1993; Huynen and Hogeweg, 1994; Kauffman, 1995).

Within this framework of multiple-level selection theories, I present in this paper an example of the way in which a certain type of society may evolve. In studies of animal behavior, a distinction is usually made between two types of societies—egalitarian and despotic. In her studies of birds, Vehrencamp (1983) distinguishes between these two on the

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This paper was originally presented at a workshop titled *The Limits to Self-Organization in Biological Systems*. The workshop, which was held at the J. Erik Jonsson Center of the National Academy of Sciences, Woods Hole, Massachusetts, from 11–13 May 2001, was sponsored by the Center for Advanced Studies in the Space Life Sciences at the Marine Biological Laboratory, and funded by the National Aeronautics and Space Administration under Cooperative Agreement NCC 2–896.

basis of reproductive success. In egalitarian societies, the reproductive success of all female group members is more or less the same, whereas in despotic ones there is a great variation in the reproductive success of individual females. When the terms egalitarian and despotic are used for other taxa, such as primates, these terms denote their so-called dominance style rather than their reproductive success (Hand, 1986). Dominance style depends on the gradient of the hierarchy (van Schaik, 1989): despotism signifies that the dominance hierarchy is steep (which means that there is a great difference in the success in fighting between individuals); egalitarianism implies that the hierarchy is weakly developed. Furthermore, in primates, particularly of the genus macaques, these societies differ in a number of other characteristics: in despotic societies aggression is more unidirectional, social behavior is correlated more strongly with dominance, grouping is less cohesive (de Waal and Luttrell, 1989; Thierry, 1990), mate choice is more selective, and male migration is more frequent (Caldecott, 1986). Whereas each of these differences between related species is usually explained as a separate adaptation shaped by individual selection, I propose to show in this paper how a despotic species may evolve from an egalitarian one by a combination of individual selection, self-organization, and group-selection, involving an evolutionary adaptation in one single trait only.

How individual selection and self-organization may operate, I will explain with the help of an individual-centered model of a group-living species, called "DomWorld" (Hemelrijk, 1999a,b, 2000). How group selection may favor the survival of groups with the steepest hierarchy above groups with weaker gradients of the hierarchy, I will explain with the help of an ecological model at an evolutionary time-scale designed by Ulbrich *et al.* (1996).

The Model DomWorld (Dominance World)

A summary of DomWorld may suffice (for a more complete description, see Hemelrijk (1999b, 2000)). The model is based on only a small number of essentials of social life. It represents a homogeneous virtual world inhabited by agents that are provided with only two tendencies: to group (right half of Fig. 1) and to perform dominance interactions (left part of Fig. 1). Why agents actually do group (whether this is 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.

When an individual is activated and it does not see another agent close by (within its personal space, see PersSpace in Fig. 1), then grouping rules come into effect. It starts looking for others at greater and greater distances (Near View = 24 and Max View = 50 units). If even then no one else is in sight, it turns over a SearchAngle (Fig. 1)

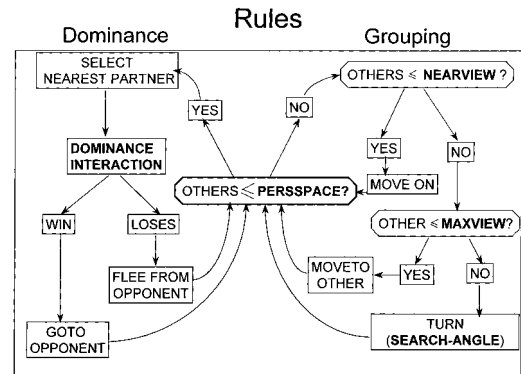


Figure 1. Flow chart for the behavioral rules of agents.

in order to rejoin its group. In this way individuals tend to remain in a group.

If, however, an agent sees another agent close by, within its personal space ($PersSpace = 2$ or 4), a dominance interaction takes place. The likelihood that an agent initiates an aggressive interaction increases with its chance to defeat its opponent (Hemelrijk, 2000). The agent's capacity to be victorious (reflected in its dominance value) depends on chance, on its current dominance value (which initially is the same for all individuals), and on the self-reinforcing effect of the outcome (winning a fight increases the probability of winning the next one and losing decreases it). This is known as the "winner and loser" effect and has been empirically established in many animal species (*e.g.*, see Chase, 1985). After victory, the dominance value of the victorious agent increases and that of its defeated opponent is reduced by the same amount. When, unexpectedly, an agent defeats a higher ranking opponent, the dominance values of both opponents are changed by a greater amount than when an agent conquers, as expected, a lower ranking opponent (this result conforms to detailed behavioral studies on bumblebees by Honk and Hogeweg, 1981). In this way the model allows for rank reversals. After a fight, the winner chases the opponent, and the defeated agent flees.

Groups usually consist of 8 to 10 individuals. The behavior of the agents is analyzed by means of behavioral units and statistical methods similar to those used for observing real animals.

Natural Selection and Self-Organization

Group life of primates (including macaques) is generally supposed to have evolved as a protection against predators (van Schaik and van Hooft, 1983; van Schaik, 1989). Egalitarian primate societies, at least those of macaques, are thought to precede despotic ones evolutionarily (Matsumura, 1999; Thierry *et al.*, 2000). Correspondingly, let us suppose that a group-living egalitarian species lives in an environment in which food is abundant, and therefore its competition is low and its aggression mild (consisting of, for instance, threats and

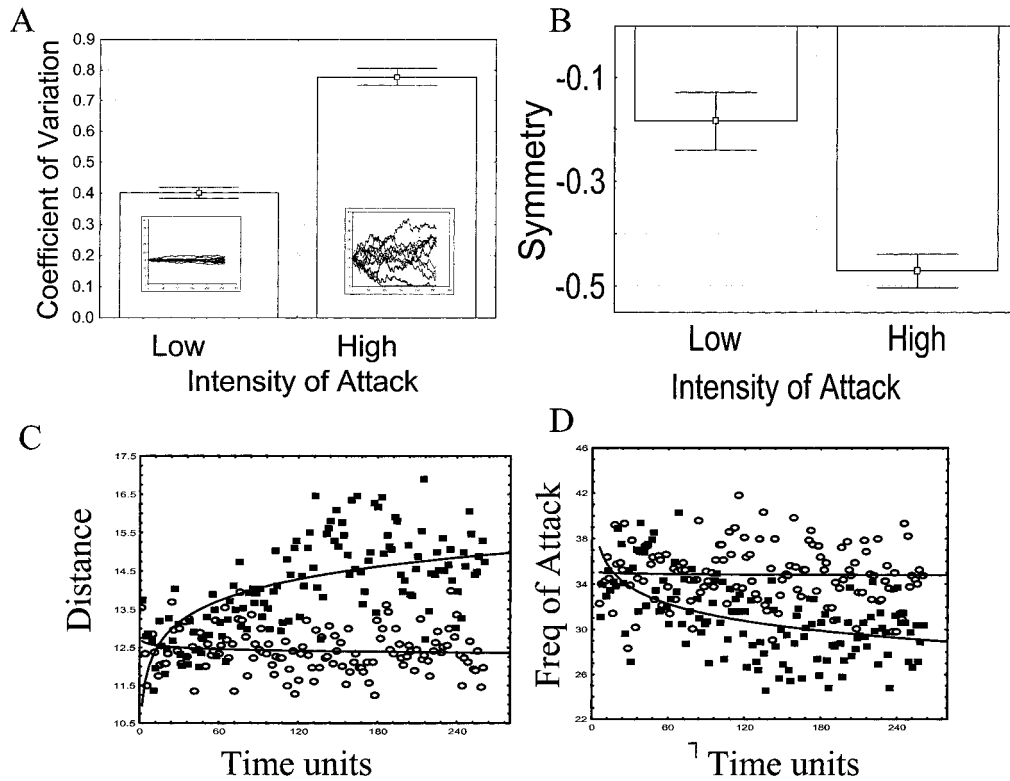


Figure 2. Effects of different intensities of aggression. (A) Gradient of the hierarchy as measured by the coefficient of variation of dominance values. (B) Symmetry of aggression measured as a τ_{KR} -correlation between an actor- and receiver-matrix of aggression. (C) Average distance among all individuals over time. (D) Average frequency of aggression over time. Open circles: low intensity of aggression, closed boxes: high intensity of aggression.

slapping). Now suppose that some populations of this species are forced to invade an environment with resources that are more clumped and where food is scarce: what do we expect to happen? Natural selection then favors individuals gifted with more intense aggression (manifesting itself, for example, by biting), because they are more able to get hold of the food. In the course of evolutionary time, a population with higher intensity of aggression may thus evolve. What are the consequences of such increasing intensity of aggression if applied to a model that simply reflects grouping and competition, such as DomWorld (Hemelrijk, 1999b)? First, at a high intensity of aggression, the hierarchy is steep (as measured by the high value of the coefficient of variation of the dominance values, see Fig. 2A), because each interaction is fiercer and therefore has a greater impact. Simultaneously, we see that aggression is less symmetrical (Fig. 2B): the correlation between aggression directed against and received from certain partners measured by a τ_{KR} -correlation between the actor- and receiver-matrix of aggression (see Hemelrijk, 1990a, b) is more negative. Symmetry of aggression decreases, because, if the hierarchy is steep, it is a greater risk for low-ranking individuals to attack higher ranking agents (and less risky the other way around). Perhaps unexpectedly, the average distance among individuals

is larger, because groups spread out over time more at a high intensity of aggression than at a low one (Fig. 2C and (1) in Fig. 3) due to the increasing steepness of the hierarchy, which turns some individuals into permanent losers that flee from everyone else. As a consequence, the encounter frequency diminishes and thus aggression declines (Fig. 2D and (2) in Fig. 3). (This decrease of aggression is also observed in real

High Intensity of Attack

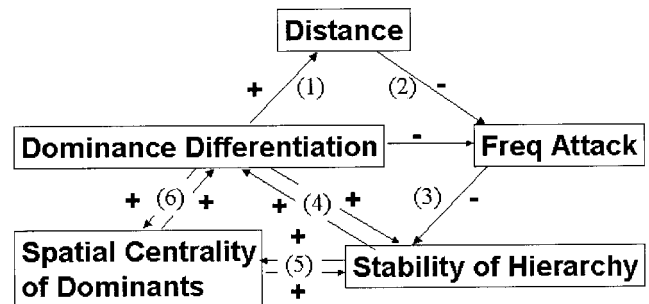


Figure 3. Summary of spatial-social structuring among artificial individuals (for explanation see text).

animals when unfamiliar individuals are put in a group together, but the decline of aggression has so far never been attributed to a widening of the group.) A consequence of the decline of aggression is that the hierarchy becomes more stable ((3) in Fig. 3). Further, because low-ranking individuals flee from everyone else, they end up at the periphery of the group; this automatically leaves the dominants in the center ((5) in Fig. 3). This spatial structure develops in spite of a total lack of any preference of the individuals to be in the center. Yet such a preference (a so-called centripetal instinct) is assumed in the “selfish herd” theory by Hamilton (1971). It is supposed to have been evolved because individuals are better protected in the center, where they are shielded on all sides from possible predators. However, the model shows that even without such a centripetal instinct, whenever the hierarchy is steep, we must expect a spatial structure with dominants in the center.

Spatial centrality, in turn, stabilizes the hierarchy and supports its differentiation ((5) and (6) in Fig. 3). This arises because the spatial structure causes individuals to be close to partners of similar dominance rank: therefore, if incidentally a dominance-reversal occurs, it is usually between individuals that are similar in dominance, and thus the extent to which dominance values are changed is only a minor one. In this way, the spatial structure strengthens the hierarchy ((5) and (6) in Fig. 3). This becomes evident when we eliminate spatial centrality. We can do this by decreasing the SearchAngle. If the SearchAngle for returning to the group is made smaller, so that individuals return more slowly and the group therefore spreads out more and more, no spatial structure develops. In this case (for the same number of dominance interactions), the hierarchy becomes weaker (*i.e.*, dominance values differentiate less) than in cohesive groups (Hemelrijk, 1999a). The steeper hierarchy in cohesive groups is thus partly due to a feedback reinforcement of the hierarchical development under the influence of spatial structure.

We may also include the sexes in the model; for instance, by making two classes of individuals that differ in initial dominance value and intensity of aggression (both are made higher for “males” than for “females”). Unexpectedly, it turns out that at a high intensity of aggression, female dominance over males is greater than at a low one. This arises because a stronger differentiation of the hierarchy causes some females to reach high dominance and some males to become very low in rank. Consequently, some females become dominant over some males. This is of interest, because in comparative studies between egalitarian macaques (with mild aggression) and despotic ones (with fierce aggression), Thierry (1990) notes that despotic adult females remain dominant over fast-growing adolescents longer than females in egalitarian species do (which is in accordance with DomWorld). He attributes this to a stronger coalitionary tendency among kin-related individuals in despotic species than in egalitarian ones. DomWorld, however, shows that greater female dominance may also arise as a

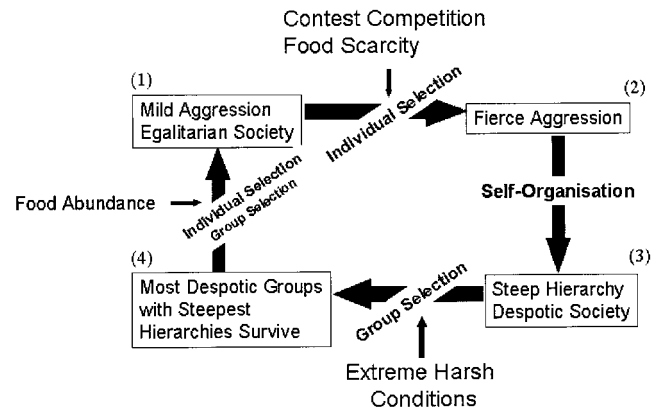


Figure 4. Sketch of the evolution of a despotic society. (1) Food is abundant, aggression is mild, society is egalitarian. (2) Food is scarce: aggression has become intense *via* individual selection. (3) Grouping and fierce aggression have led to a steep dominance hierarchy *via* self-organization due to social-spatial structuring. (4) Food availability has decreased even further and only the most despotic societies survive.

direct consequence of a steeper hierarchy. Further, at a high intensity of aggression the lowest ranking males in the model are of a lower rank than they are at a low intensity. It is known that in real primates, the lowest males migrate to other groups; supposing migration were possible in the model, we would surely expect a higher frequency of migration for a higher intensity of aggression. This indeed is exactly what Caldecott (1986) describes for real macaques, where migration is higher among despotic than among egalitarian species.

In general, it appears that all differences between egalitarian and despotic societies in DomWorld resemble those found between real groups of egalitarian and despotic macaques as far as they have actually been measured. Since, in the model, such differences (those regarding cohesion, bidirectionality of aggression, and correlations of behavior with dominance, see Hemelrijk, 1999b) arise from a change in one trait only (intensity of aggression), we may take it that also in the real world a single mutation (in the form of an increase of intensity of aggression due to food shortage) may have caused an egalitarian ancestor to beget a fledgling species that is in many characteristics despotic. Thus individual selection on intensity of aggression may lead, *via* self-organization, to a switch from an egalitarian to a despotic society (Fig. 4).

Group Selection

Suppose that in this way groups have evolved with high intensity of aggression, and suppose there is a certain variation among groups in their average intensity of aggression and therefore in the gradient of their hierarchy. Then, what do we expect to happen if environmental conditions worsen even more? In that case group selection may further increase despotism in a way similar to that shown in a model study of social spiders by Ulbrich *et al.* (1996). Their individual-based

model represents, among other things, colony survival, reproductive behavior, the kind of competition for food (“contest” or “scramble” competition), and feeding behavior. If food is clumped, it leads to contest competition, whereby dominants get more than subordinates; if it is scattered and unpredictable, everyone gets about the same (so-called scramble competition, see Nicholson, 1967). Results show that during levels of food scarcity, colonies where there is contest competition survive longer than colonies in which competition is of the scrambling type. This is a consequence of the steeper dominance hierarchy and, therefore, greater variety in body-size of members, which allows a small number of dominant individuals to eat all the food so that at least some of the females are sufficiently nourished to reach reproductive age. In this way, because some individuals in more intensely despotic groups are likely to survive and reproduce, the group itself may survive (although the number of its members decreases during periods of diminished food availability). In contrast, in groups with a weaker hierarchy, food will be distributed more evenly and no single individual may reach reproductive success (see also Rypstra, 1993). Thus, severe shortage of food in clumped patches may result in group selection in favor of the most despotic societies ((3) to (4) in Fig. 4).

Note that in macaques, adult males usually migrate from their natal group to other groups. Therefore, the degree of despotism in macaques is defined on the basis of the dominance hierarchy among the females. Also, the survival and extinction of “the group” implies the core group of females only, because they are the resident sex. Among such female resident core-groups, we may expect that when food is scarce, group selection will lead to better survival of those groups that have a steeper hierarchy (in accordance with the findings in social spiders).

Discussion

Changing only one trait—intensity of aggression—in the model leads to a great number of phenotypic differences at the level of the individual and of the group. Thus, by changing the intensity of aggression in DomWorld, as suggested by the hypothesis for egalitarian and despotic macaques (McKenna, 1979; Thierry, 1985a, b, 1990), we may switch from an egalitarian society to a despotic one. Intensity of aggression is not the only variable, however, that can produce such a cascade of effects. If we increase cohesion under one and the same level of intensity of aggression (which must lie somewhere between medium and high values), the society becomes more despotic in all its characteristics (Hemelrijk, 1999a). The question of whether stronger cohesion of groups is also accompanied by greater despotism in real primates must be studied empirically.

Thus, the model shows how self-organization causes non-linearity in the connection between the behavioral rules and the observed behavior (which respectively correspond to the ge-

notype and the phenotype). These results of DomWorld may also be relevant to results of a selection experiment with fish by Ruzzante and Doyle (1991, 1993). After two generations of selection for speed of growth, an increase in growth speed among fish fed on clumped food (leading to intense competition) was accompanied by three effects: a decrease in aggressiveness, an increase in density of schooling, and an increase in social tolerance. According to the authors, selection for fast growth results in a high threshold for aggression, and this threshold also genetically influences the other two features of social behavior—cohesion and social tolerance. These findings resemble those from DomWorld; but in DomWorld only the intensity of aggression is changed “genetically,” and all other changes of social behavior are mere side effects. Such parsimonious explanations may be relevant to many species of despotic animals that have been studied and possibly even to plants, where a kind of despotism is also described (for a study on a hemiparasite, see Prati *et al.*, 1997).

Groups with different degrees of intensity of aggression may be liable to group selection similar to that suggested for spiders by Ulbrich *et al.* (1996). Group selection has always been a controversial issue. The only studies in which any evidence has been produced (Bradley, 1999) concern invertebrates (namely, a species of virus, social spider, and ant). However, designating group selection as a useful explanation for behavior of (non-human) primates is usually avoided (Bradley, 1999). Yet, primates utter alarm calls that, though they are at the expense of the fitness of the individual that uses them, may serve to protect group members (both kin and non-kin). When alarm-calls are more beneficial for the group than they are costly for the individual, they will evolve by group selection, as explained by differential selection among groups for the same trait—so-called intrademic group selection (Wilson, 2001). Computer models show how such an intrademic group selection favors altruistic traits, particularly under harsh conditions (Mitteldorf and Wilson, 2000; Pepper and Smuts, 2000).

Similarly, I suggest that group selection may operate on a non-altruistic trait, namely intensity of aggression, in primate societies in which there is sharp contest competition for food (during harsh conditions). Such stronger competition leads to a more asymmetrical distribution of food intake, and by guaranteeing that at least some individuals of a group reproduce, aids group survival (of the core group of the resident sex).

Note that in the other transition, from despotic societies to egalitarian ones (see Fig. 4), progressively milder aggression would be favored by selection on the level of the individual and the group, because less energy is wasted on conflicts. In this case, selection at the level of the group and the individual will be weak, and self-organization will not be operative. Thus, a different number of processes are at work depending on the direction of the transition between egalitarian and despotic societies.

The different ways in which selection may act (namely, on self-organized patterns, and on the level of the individual

and the group) illustrate how we may envision a multiple-level selection theory for the creation of a despotic society. Although, for the sake of clarity in the sketch I have given above, I have made individual selection, self-organization, and group selection function one after the other, in reality they operate mostly simultaneously in different proportions (Lewontin, 1970).

Acknowledgments

I thank Rolf Pfeifer and Bob Martin for continuous support. I am grateful to Scott Camazine for inviting me to the workshop on "The Limits to Self-organization in Biological Systems," and to Bernard Schmidt and Jens Krause for making me aware of similarities between DomWorld and plant and fish communities. This work is partly supported by a grant from the A. H. Schultz foundation.

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