

Evolutionary fundamentals of social inequality, dominance and cooperation

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Evolutionary Fundamentals of
Social Inequality, Dominance and Cooperation

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I. Introduction

There are two fundamentally distinct, yet complementary approaches to explaining social behavior. The first approach is explaining in terms of behaviour physiology. An example of this type of explanation would be: People tend to be aggressive, if they are frustrated. Another example: The level of aggressiveness correlates to some extent with the testosterone level in blood, therefore some individuals may be more aggressive than others because of the increased testosterone level.

In general, explanations of this type want to identify the psychophysiological mechanism which produces the behaviour in question, and to explain, how it works.

The second approach is explaining in terms of behavioral ecology. An example of this type of explanation would be: People tend to exhibit a certain level of aggressiveness while competing for some valued resource. This level must not be too high, otherwise there is too high a risk to get injured, but if it is too low, one will lose the fight and be deprived of the resource.

Explanations of this second type want to identify the cost-benefit rationale behind observable behaviour: why and in which respect does a certain behaviour add to the fitness of the agents involved?

The overall framework of behavioral ecology is the evolutionary perspective. The Costs and Benefits of a behavior are measured in terms of the increment it yields to the evolutionary success of the agents. This increment depends on the physical and social environment in which the behavior takes place.

There is an important difference in how evolutionary selection works:

How well adapted most physiological and many psychological traits are in a certain environment does not depend on the frequency of these traits in the population as a whole. In contrast to this frequency-independent selection, we have a frequency-dependent selection of traits, as soon as we turn to strategies of interaction with other members of the population. How well adapted certain strategies of mating, contest, communication, and so forth, are depends on the relative frequency of alternative strategies in the population. Thus, a frequency-dependent selection does not aim for evolutionary optimization, but for evolutionary stability. Formally, this

concept has been defined by Maynard Smith as follows (Maynard Smith and Price, 1973): We assume a finite or an infinite population of agents that can choose (by mutation, individual learning, socialization, etc.) among an infinite or finite set of pure or mixed strategy alternatives. Let V_{ij} stand for the evolutionary value of strategy i played against strategy j (the relative survival chances of an individual playing strategy i against an individual playing strategy j). If the population plays strategy z (which can be a mixed as well as a pure strategy), z is said to be an Evolutionarily Stable Strategy (ESS), if one of the following two conditions holds

$$V_{zz} > V_{pz} \quad (1)$$

or

$$V_{zz} = V_{pz} \quad \text{and} \quad V_{zp} > V_{pp} \quad (2)$$

for all alternative strategies p different from z , which are rare in the population. Thus evolutionary stability of strategy z means that a population playing z cannot be invaded by a rare mutant p . The difference to the classical notion of evolutionary rationality as the result of an optimizing process becomes clear by noticing that neither (1a) nor (1b) preclude the possibility of

$$V_{zz} < V_{pp} \quad (3)$$

That means evolutionary stability may be suboptimal, measured against what could be accomplished with the present means under the condition that mutations and disturbances of group composition did not occur.

Stability may be polymorphic. Conventional functionalism has taught us always to single out one behavior pattern in a population as normal, rational, in accordance with the norms and cultural patterns, and to label all alternative behavior as deviant, as pathologies, or as an evidence for the malfunctioning of a society's socializing agencies. Now we have to accustom ourselves, that a mixture of alternative behavior patterns may be a

stable thing, and that the alternative patterns may be as well adapted and as rational as the others. A simple model for a polymorphic equilibrium of alternative behavior patterns is Maynard Smith's Hawk and Dove game (Maynard Smith and Price 1973):

Let Hawks be those members of a population which fight in contests until victory or severe injury, and let Doves be those members, who engage only in ritual contests but retreat when attacked earnestly. Clearly in a population of Doves a Hawk is king. Hawk wins all contests, and therefore the Hawkish habit - by whatever mechanism - will spread. In a population of Hawks Dove, however, with its injury-avoiding strategy will on the average do better than the average Hawk, and will therefore be able to invade the Hawk population, as Hawk was able to invade a Dove population. The resulting polymorphic equilibrium is stable, even under extreme environment conditions: even if all resources abound, a small pool of Hawks will remain, and even in the most frugal environment you do not have to fight for every resource but may get it sometimes by luck, therefore also the Doves will not die out.

In a more sophisticated version of this game Maynard Smith and Price had three more strategies compete with each other:

Bully: attacks as long as not attacked, but retreats when attacked;

Retaliator: plays the ritual contest strategy against other players playing the ritual contest strategy, but attacks attackers;

Prober-Retaliator: like Retaliator, but attacks with small probability non-attackers. If in these cases no counterattack occurs, he continues attacking, otherwise he returns to the ritual contest strategy.

In this game, several polymorphic equilibria are possible. Prober-Retaliator and Retaliator are the predominant strategies, while the other strategies are maintained at a low frequency. The proportion between the two main strategies depends on the initial frequency of Dove, because probing is advantageous only against Dove.

Maynard Smith and Price interpret these results as a convincing demonstration of the evolutionary superiority of "limited war" strategies in

comparison to "all-out-war" strategies like Hawk. We will come back to the results of this game later.

In this paper I wish to sketch some ideas about the evolutionary fundamentals of social inequality among humans, and consequently of hierarchy and democracy in human societies.

I will group these ideas in three sections. First, I want to deal with social inequality in the access to scarce resources. This is the broadest and oldest dimension of social inequality. Human populations share this dimension with all socially living species. Second, I want to turn to social inequality with respect to social power. This concept does not mean inequally distributed fighting capacity. Rather it means the inequality in the giving and taking of orders.

The chance of finding obedience for given orders is in general not based on the threat of physical force alone; equally important are the threat of being expelled from the community, or the threat of losing respect and status within the community, or the threat of being excluded from spiritual goods.

If fully developed in this sense, social power is exclusively human. In both dimensions, the dynamics work towards extreme inequality, confining the larger part of society to a life on bare subsistence level.

The social potential of the human species, however, entails despotism and democracy. Therefore in the third section I will sketch the forces in human populations which work against this extreme inequality. The basic mechanism behind these forces is the ubiquitous emergence of coalitions of commoners against the powerful and the rich. The coalitions become possible through the division of labor and the growth of specialized technical skill among all parts of society.

II. Unequal distribution of scarce resources:

The exponential growth equation and the logistic growth equation are among the cornerstones of classical population biology, on which all predator-prey and all interspecies competition models rest. The exponential growth equation

$$\dot{N}(t) = rN(t) \quad (4)$$

is a preferred example of how a certain behavior on the individual level - reproducing at constant rate r - results in a certain dynamics on the population level - exponential growth (see fig. 1).

The logistic growth model in continuous time, as given by

$$\dot{N}(t) = rN(t)((K - N(t))/K) \quad (5)$$

and in discrete time by

$$N_{t+1} = N_t (1 + r(1 - N_t/K)) \quad (6)$$

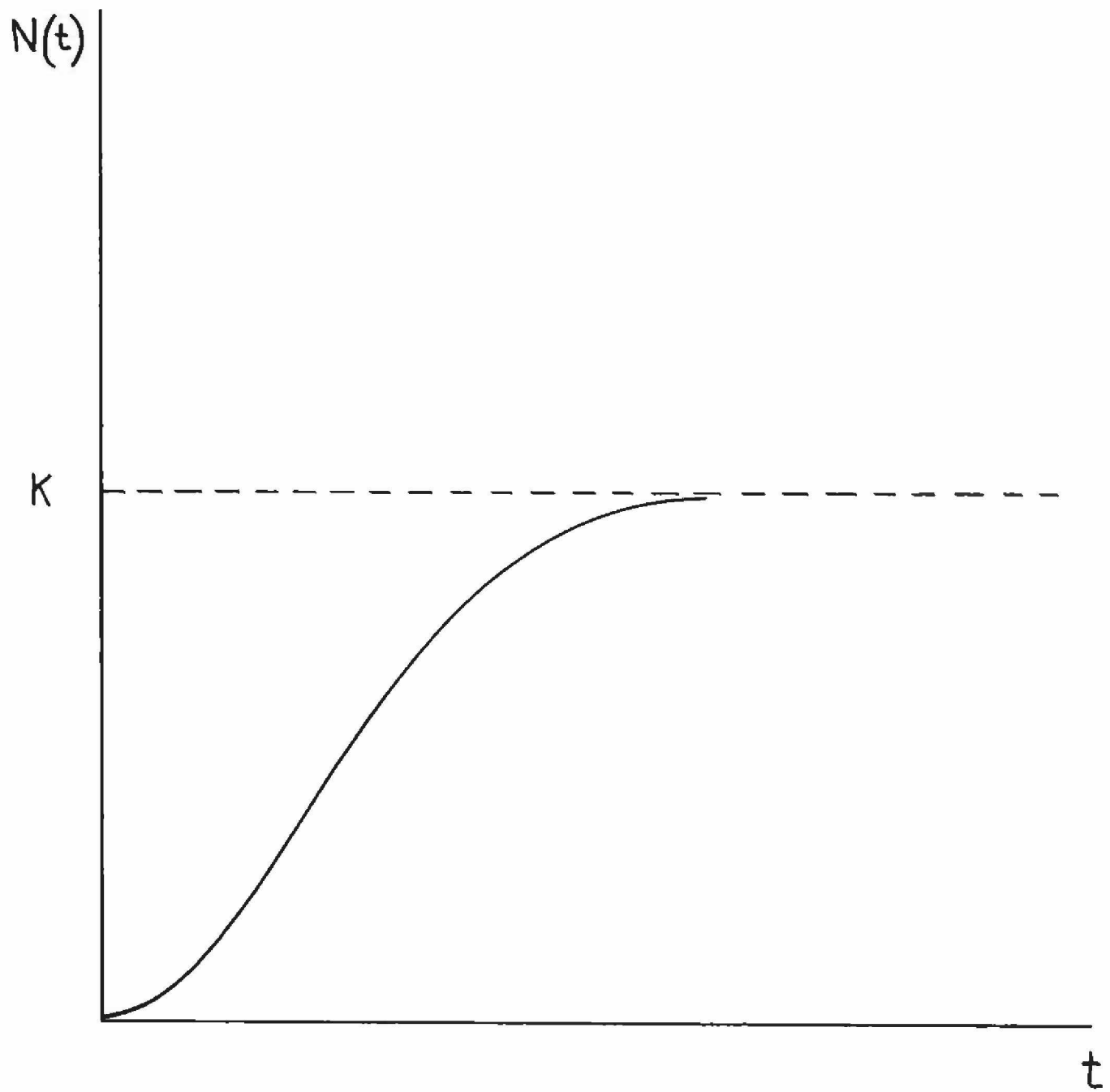
furthermore assumes that in linear dependence of the occupation of a given habitat the individual reproduction rate is subject to a reduction down to the point of zero growth, once the population $N(t)$ has reached the carrying capacity K .

In contrast to the exponential growth equation, which has only one - unstable - equilibrium, namely the origin, the system modelled by the logistic growth equation has an additional equilibrium in $N = K$, and this equilibrium is asymptotically stable: From any point in its neighborhood the system will tend to approach this equilibrium.

The core idea of this logistic growth model is that the state of the population is reflected in the reduced growth rates on the individual level, whether we take this linear reduction literally for every individual member of the population, or if we have here in mind only the average member.

This reasoning is inherent in all applications of the logistic growth equation - for example the distinction of r - versus K - selection. If a species typically lives in volatile environments, with populations far below the carrying capacity, evolution selects for producing as much offspring as possible, with little investment per individual offspring, this is r -selection.

fig. 1



The logistic growth function

If a species, however, lives in stable environments, with populations close to or at the carrying capacity, evolution is said to select for producing only small numbers of offspring, but with large investment per individual offspring, this a K-selection.

This conclusion from the observed dynamics of population - bound growth - to the behavior on the individual level is by no means convincing. In fact if we start with two additional, sensible assumptions on the individual level from the very onset on, we shall come to quite different results. These additional assumptions are simply:

- a) the use of resources by any individual is subject to stochastic fluctuations;
- b) the access to resources varies among individuals. We can express differential access by different rank.

Then we can derive the following simple growth model. The amount of resources used by an individual is a function of the population size in absolute numbers N , the amount of resources V and the individuals' rank x (high rank corresponding to low values of x). Every individual can use resources up to a maximum amount a .

The function $y(N,V,X)$ can be specified as having the following four properties.

- 1.) y is an increasing function of V , with $\sum_{x=1}^N y \leq V$
- 2.) If the distribution of resources is either completely inegalitarian in the sense that some members of the population take all resources then y is independent of N . If the distribution is not completely inegalitarian, then y is a decreasing function of N , once $N \geq V/a$.
- 3.) y is by definition of x a non-increasing function of x . If the distribution of resources is completely egalitarian, then $\partial y / \partial x = 0$.

4.) In a very general way we can assume stochastic effects on individual resource intake to be binominally distributed. We regard a time unit short enough that within this time unit, with constant probability p , at most one resource unit can be taken by an individual. The number of all resource units consumed by an individual during his lifetime is then binomially distributed with the mean $\bar{y} = np$ if his life has lasted n time units, and the variance $s^2 = np(1-p)$. The coefficient of variation therefore is $s/\bar{y} = \sqrt{(1-p)/(np)}$

This coefficient is a decreasing function of p , which explains, why a resource shortage comes along with an increase in individual resource usage variation. The more scarcely population is supplied with resources, the less unequal these resources are distributed. Therefore, we can justify as a fourth property of the function $y(N,V,x)$, that the absolute amount of its first derivative with respect to x should be an increasing function of N and a decreasing function of V .

We cannot further specify $y(N,V,x)$, but, as we shall see, even from these four properties we can get quite a bit of mileage. We just compare the two extreme cases of completely egalitarian and of completely plutocratic types of resources partitioning.

Let L be the number of individuals who get resources at all, and therefore $(N-L)$ the number of individuals who get nothing.

In both cases as long as $V/a > N$ we have

$$y(x,V,N) = a \quad (7)$$

In the egalitarian case we have : $L = N$, thus if $N > V/a$ then in the egalitarian case we have

$$y(x,V,N) = V/N \quad (8)$$

In the plutocratic case we have $L = V/a$ individuals, each of whom take an amount a of resources, while the other $(N-L)$ individuals get nothing. Therefore here we have:

$$y(x,V,N) = a, \text{ for } x \leq L$$

and

(9)

$$y(x,V,N) = 0 \text{ for } x > L$$

We want to study the population dynamics for these two extreme cases. We assume an asexually reproducing population with non-overlapping generations. Conveniently we chose the unit of time such that it equals the span of a generation. We furthermore assume the amount of resources V to be constant - a simplification which will have no effect on the qualitative results of our analysis, as long as V remains independent of N .

An individual consumes $y(x,V,N)$ amount of resources, and uses m of them for its own maintenance throughout his life, while $(y-m)$ resources are used for producing offspring with efficiency h . If an individual receives $y < m$ resources, it does not survive to reproduce; if it manages to get hold of $y > m$, it will produce $h(y-m)$ offsprings. The efficiency factor h has the dimension: number of offspring per number of resource units. We do not take explicit precautions against the occurrence of non integer-valued offspring, since this would only complicate the formulas unnecessarily.

The general equation of population growth in discrete time model is

$$N_{t+1} = \max \left\{ 0, h \sum_{x=0}^L (y(x,V,N_t) - m) \right\} \quad (10)$$

An analytical solution shows for the egalitarian case

$$N_{t+1} = h N_t (a-m) \quad \text{for } N_t \leq V/a$$

and

(11)

$$N_{t+1} = h (V - mN_t) \quad \text{for } N_t > V/a$$

Obviously a necessary condition for $\bar{N} = 0$ to be an unstable equilibrium of this equation, i.e. a necessary condition for population growth of this equation is that

$$h(a-m) > 1 \quad (12)$$

the growth factor has to be outside the unit circle for small values of N_t . If this inequality holds, the system has a non-trivial equilibrium, at

$$\bar{N} = hV/(1 + hm) \quad (13)$$

This equilibrium is asymptotically stable for values of N_t in a neighborhood of \bar{N} , if $(N_{t+1} - \bar{N})/(N_t - \bar{N}) < 1$, which is the case if

$$m < 1/h \quad (14)$$

In fact, then \bar{N} is globally stable, i.e. there is no other stable equilibrium in the system.

Clearly the maximum value of N_t is $N_{t,max} = V/m$ with $N_{t+1,max} < N_{t,max}$. Therefore the system has an upper bound.

The point is that inequality (14) is hardly ever fulfilled in any population where members die after some time (i.e. are not virtually immortal). Inequality (14) states that population stability in the egalitarian case is possible only if the investment in producing one offspring is higher than the investment put into oneself throughout life - a condition which certainly is not fulfilled even for large vertebrates with few children.

The model can easily be extended in order to cover overlapping generations as well, and thus this statement seems to be a fairly fundamental one for all growth phenomena in populations. The other extreme case, the one of complete plutocracy, is even more easily analyzed. For $N_t < V/a$ the situation is the same as for the egalitarian case, for $N_t > V/a$ the population dynamics is simply

$$N_{t+1} = hV(1-m/a) \quad (15)$$

which reflects the fact, that N_{t+1} is independent of N_t , instead depends on constant parameters for all t and is therefore a globally stable non-trivial equilibrium of the system.

Ironically, in the plutocratic equilibrium as defined by eq (15) the population is larger than in the egalitarian equilibrium as defined by eq (13):

$$\bar{N}_{\text{egal}} < \bar{N}_{\text{pluto}} \quad (16)$$

as long as inequality (11) holds, which is fulfilled once any growth from small values of N_t onwards is possible at all.

We can conclude from all this that a plutocratic distribution of resources may be stable, while a egalitarian distribution of resources in general is not. At the same time the plutocratic non-trivial equilibrium is higher than the alternative non-trivial egalitarian equilibrium.

I do not want to finish this section of my paper without mentioning the name of Adam Lomnicki, who in a paper of 1980, published in a rather obscure Scandinavian journal, has laid down the core ideas of the argument above.

In behavioral ecology group size for large, socially living mammals is a function of the resource location type, of predator pressure and of the degree of despotism in the group. The first two factors do not pose special problems in our context here. Clearly, in the absence of predators or any dangerous competitors, small groups feed more efficiently on scarce resources than large ones, and this the more the more thinly and the more evenly resources are distributed in space.

On the other hand, with high predator pressure large groups will provide their members greater survival chances than small ones, since large groups can earlier detect and warn of predators, in the presence of many prey predators are more easily disturbed, and will in any case not be able to capture many prey at the same time. At last in a large troop, there may even be a chance of active defense. The observation of hunting chimpanzees, for

example, has shown that while a single small monkey, say a macaque, once captured by a chimpanzee usually is lost, while a troop of macaques quite often by attacking and biting the chimpanzee, is able to salvage their captured fellow.

The optimal group size then is just where the two fitness functions of group size - the decreasing fitness from foraging opportunities and the increasing fitness from protection against predators are equal. The fact that all old-world primates who live monogameously, i.e. in the smallest group possible, live in areas where no large predators notably large cats occur, and where man has not begun to hunt these primates before some decades ago, is seen as a forceful confirmation of this theory (Alexander, 1974, van Schaik 1983, van Schaik and von Hooff 1983). Interesting for the purpose of this paper is the degree of despotism within the group or the effect on group size exercised by the third factor.

When is despotism within the group about to develop, and what are its consequences on group size and composition? In a simple but instructive model Alexander (1974) and Vehrencamp (1983) have considered the cost of leaving the group as the ultimate determinant for the degree of despotism, which can be maintained in the group. Egalitarian societies' net benefits are distributed equally, while in despotic societies these net benefits disproportionately accrue to a few members. Obviously such exploitation finds its limits by the options the exploited members have outside the group.

Within the framework of the Alexander and Vehrencamp model we can analytically obtain an interesting result, to which Alexander and Vehrencamp pay no attention.

The assumptions of the model are: In each group there is one manipulator or one compact subgroup of manipulators, which can freely appropriate resources from the rest of the group. The manipulators will do so to the limit set either by the minimal supply an individual needs to live on in the group (and to produce surplus resources for the sake of the manipulators) or by the option to leave this group and to survive outside. For simplicity, we

assume that this lower limit of supply is the same for all members of the group.

Let N be the number of individuals in the group (manipulators, or despots, as we call them from now on, and subordinate subjects).

Let $W(N)$ be the accumulated resources provided by and to the group. In the beginning, the marginal output must be increasing in order to make group life versus solitary life an attractive option at all. On the other hand, marginal output can not increase forever, beyond some group size it must decrease. Thus, this function may conveniently be conceived as a convex-concave, i.e. S-shaped function (see fig.2).

Let $W_{\min}(N)$ be the accumulated minimal resources to be supplied to the group, which are necessary for the subsistence of all group members. Since the individuals make all the resources available in the first place, before they can be redistributed, $W_{\min}(N)$ in fact is a production function or input function and therefore has to be conceived at least as a non decreasing function. A concave-convex (inverted S-shaped) non-decreasing input function (see fig.3) may be most realistic (marginal input first declines, than rises again), but we will consider linear input functions as well. Both, output function and input function are given, and cannot be modified by members of the group.

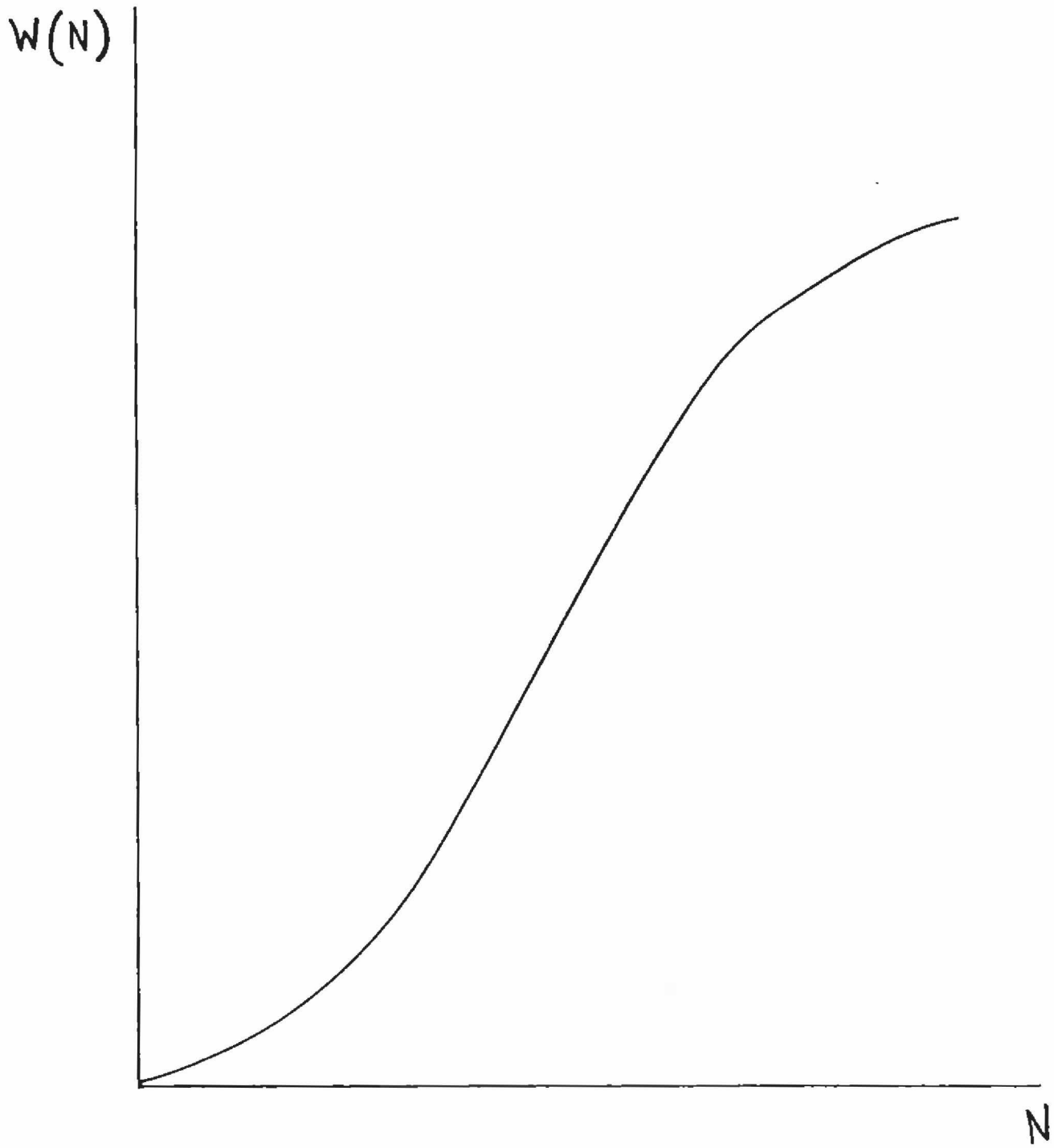
Now let us compare the two extreme modes of resource distribution. In the egalitarian mode all resources are distributed evenly, and therefore the optimal group size is the one which maximizes the uniform surplus output per capita, namely the function:

$$(W(N) - W_{\min}(N)) / N \quad (17)$$

the first order conditions for a maximum are, after a little algebraic manipulation:

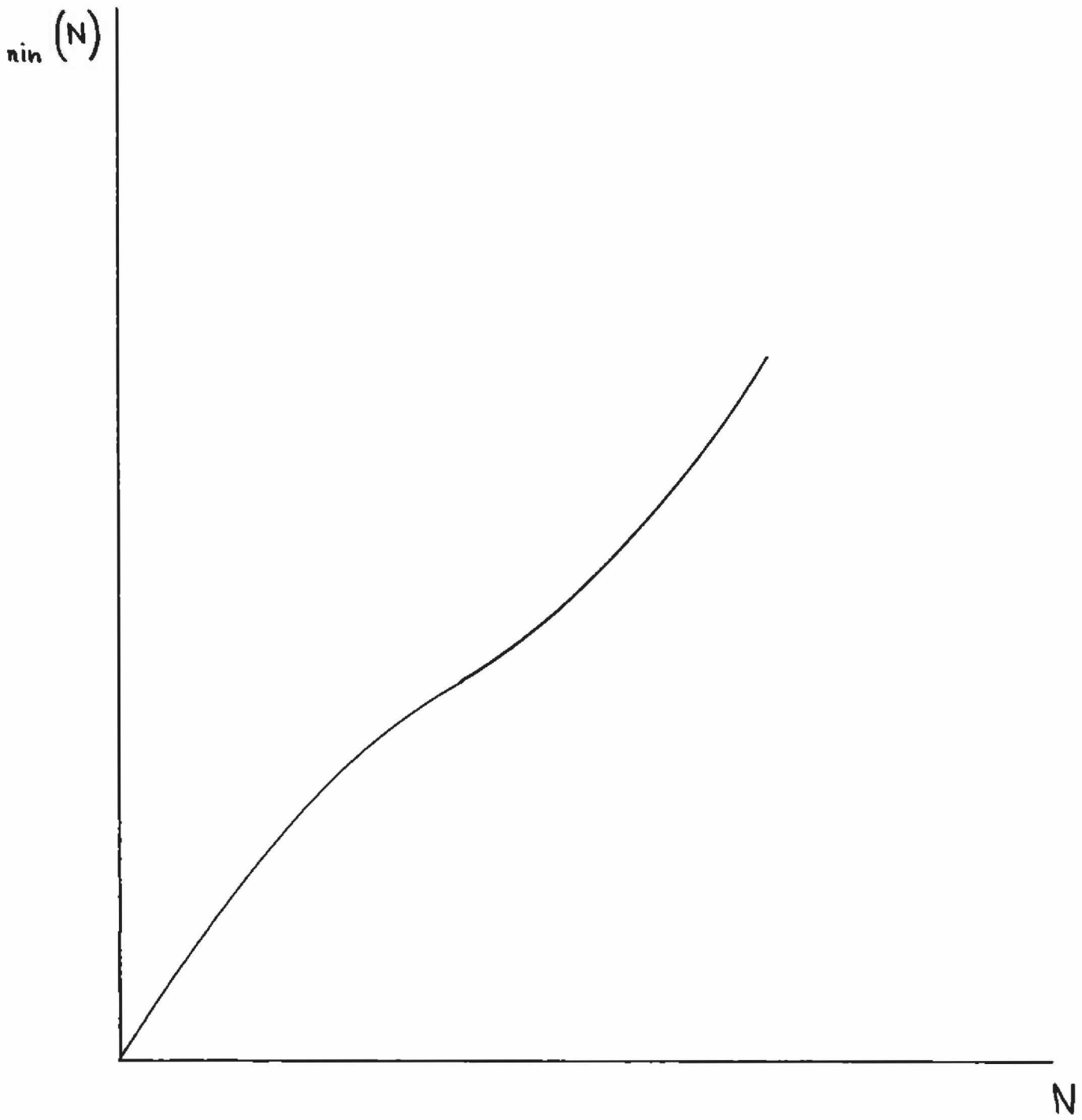
$$\dot{W}(N) - \dot{W}_{\min}(N) = (W(N) - W_{\min}(N)) / N \quad (18)$$

fig. 2



convex-concave output function

fig. 3



concave-convex input function

This means, the group size N which maximizes the egalitarian surplus output per capita, is the one where the egalitarian surplus output per capita equals the marginal total surplus output.

The despot or the despotic subgroup faces a different maximization problem. They want to maximize the accumulated surplus output which they subsequently will appropriate:

$$W(N) - W_{\min}(N) \quad (19)$$

the first order conditions for a maximum are:

$$\dot{W}(N) - \dot{W}_{\min}(N) = 0 \quad (20)$$

This means, the group size N which maximizes the despots' surplus output is the one where the marginal total surplus output and therefore also the marginal surplus output per capita is zero.

Given the general properties of the output and the input-function - notwithstanding whether we consider a concave-convex, or a linear input function - the group size \bar{N}_{desp} which maximizes the despots' surplus output is necessarily larger than the group size \bar{N}_{egal} which maximizes the egalitarian groups' surplus per capita (see fig. 4):

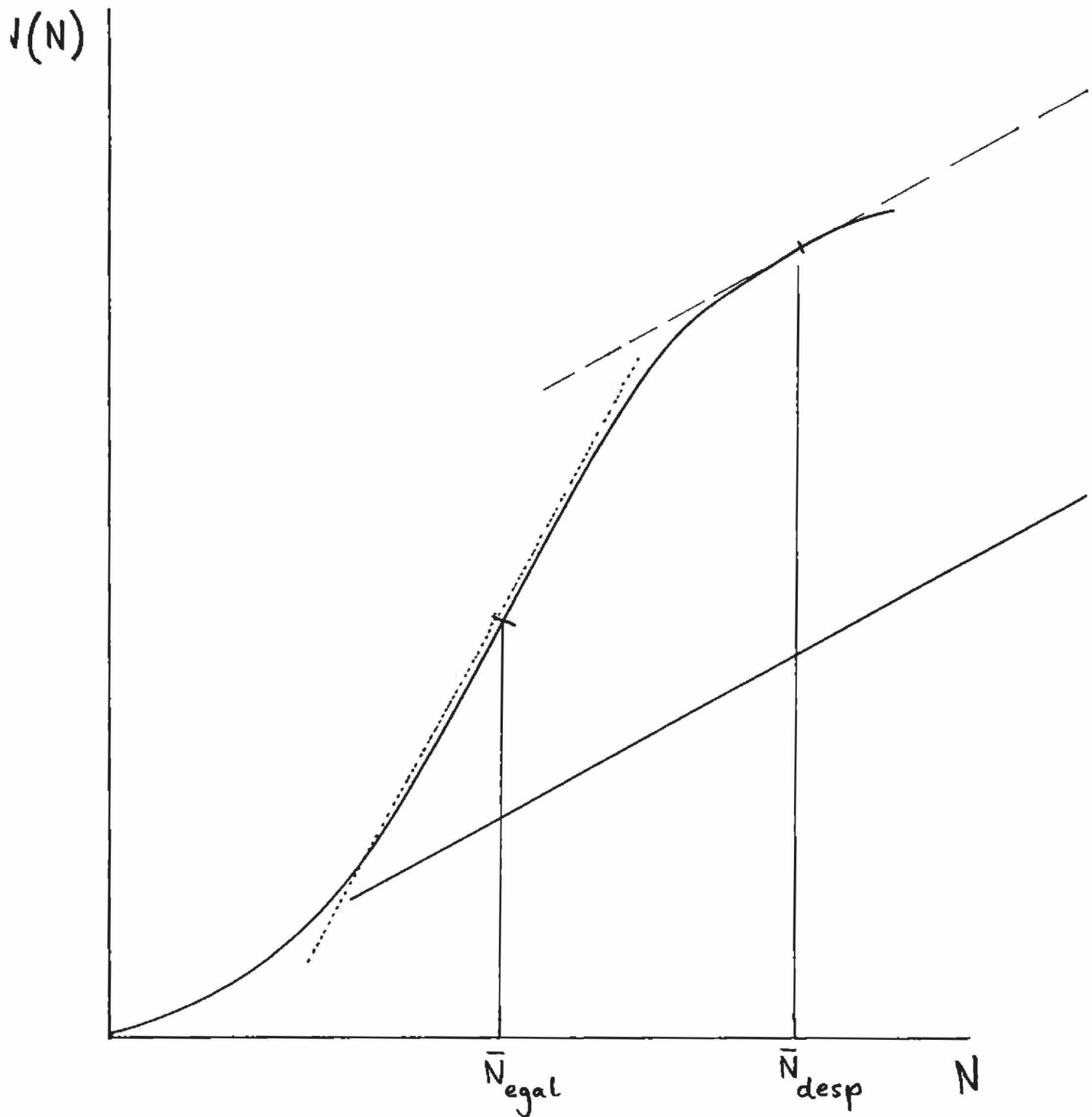
$$\bar{N}_{\text{egal}} < \bar{N}_{\text{desp}} \quad (21)$$

Consequently the total output in absolute terms of an optimal group under a despotic regime is larger than an egalitarian regime.

This is the surprising result we get from the Alexander/Vehrencamp model, that under a despotic regime, optimal group size is larger than under an egalitarian one. This is a striking parallel to the result from the general population dynamics model in the previous section, that evolutionarily stable group size is larger under a plutocratic regime than under an egalitarian one:

$$\bar{N}_{\text{egal}} < \bar{N}_{\text{pluto}} \quad (16)$$

fig. 4



convex-concave output function
and linear input function
with egalitarian and despotic
optima

By integrating the Alexander/Vehrencamp model, which is a rational choice model of optimal group size, into models population dynamics, we may obtain a profound intellectual access to the expansionism inherent in any markedly non-egalitarian social groupings from families up to whole nations: The more despotic their domestic regime is, the more they tend to expand and the more they tend to use up their natural environment.

III. Unequal distribution of social power:

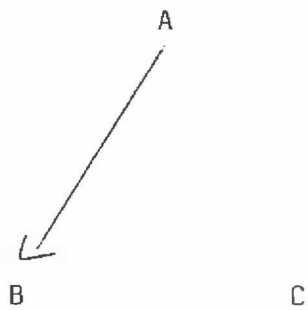
From the extended Hawk-Dove game - see the introductory section - we know the evolutionary superiority of "limited war" strategies over "all-out-war" strategies. In the preceding section we saw how unstable any egalitarian distribution of scarce resources is. An unequal distribution of scarce resources, on the other hand, may lead to unequal fighting prowess. But even less well endowed, and therefore weaker members of a group of animals have, under certain circumstances, a greater-than-zero chance of defeating a stronger member.

Therefore, the lower the level of the actually applied physical force is in a conflict, the better for the contestants, as long as the outcome in a "limited-war" conflict does not deviate totally from the one in an "all-out-war" conflict, to which the contestants still could take refuge..

Because of this joint interest of all potential contestants, evolution has favored "limited-war" strategies, which are, in the ultimate consequence, "symbolical-conflict" strategies. This is why dominance hierarchies are so widespread among socially living species.

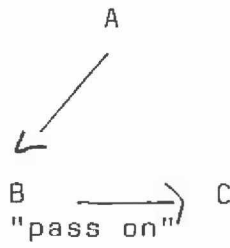
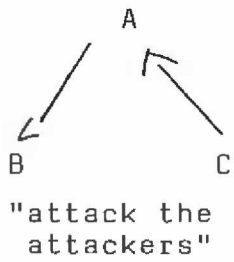
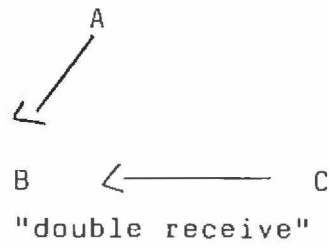
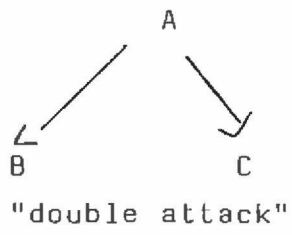
Only during the first encounters, when a dominance relation between two individuals has not been determined yet, there may be an enhanced level of overt aggressiveness. As soon as it is established who is stronger, future conflicts can be solved by symbolic means: The dominant displays his interest and his undiminished readiness to fight it out, if necessary, and the subdominant, remembering the outcome of the first and aware of the probable outcome of any future fight, gives in as long as this giving in leaves him with the same chance of using the resource, discounted by the expected cost of injury, which a fighting out would have left him with.

Fig. 5



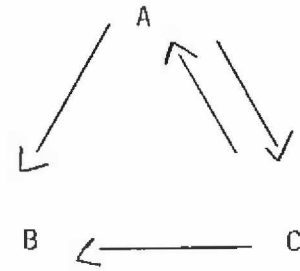
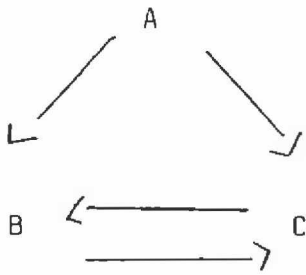
The arrow indicates that a successful attack has established a dyadic dominance relation between A and B.

Fig. 6



The four possibilities how in a second attack a triadic dominance relation can be established.

Fig. 7



After "double attack" and "double receive" the triadic dominance system is already linear.

The advantageous function an established dominance order system has for all its members, does not explain, however, how its evolution has been possible. Dominance order systems can fulfil this function only if they are "linear", or weakly transitive: if A dominates B, and B C, then also A C. Non-linear dominance ordering systems obviously do not have this pacifying effect. Linear dominance ordering systems can be observed in many human groups and in many other social species (Appleby 1983). Schjelderup-Ebbe (1922), working with fowl, found that in groups up to 10 individuals the dominance ordering was strictly transitive. It is not satisfactory to explain this fact by the difference in physical fighting prowess alone since these differences predetermine the outcome of actual fights only with a certain probability, not with certainty.

A Gedanken-experiment may demonstrate this: In a group of N individuals there are N! different strictly transitive orderings. At the same time there are $N(N-1)/2$ different dyadic relations among the members of this group. Since each dyadic relation in a dominance ordering can be in two states (A dominates B, B dominates A), there are $2^{N(N-1)/2}$ different dominance orderings in the group. If we make the - unrealistic - assumption, that the state of all dyadic relations is completely random, then the probability of a transitive dominance ordering is given by

$$\frac{N!}{2^{N(N-1)/2}} \quad (22)$$

Some numerical values for (22)

group size	proportion of transitive dominance orderings
n = 3	.75
n = 4	.375
n = 5	.117
n = 6	.022
n = 7	.002
n = 8	.00015
n = 9	.000005
n = 10	.0000001

If we assume that there is a weakly transitive ordering of individual fighting capacity in dependence of the unequal resource distribution - a quite questionable assumption - and that this ordering of fighting capacity translates into high probabilities for an analogous outcome of a fight, we still get a increasingly large probability of non-transitive dominance orderings with increased group size. Therefore linear dominance orderings cannot be explained as simple manifestations different fighting capabilities among the members of a group.

The key to the understanding of linear dominance hierarchies has to be searched for in the individual conflict strategies applied in the dyadic conflicts by which a dominance system is step-by-step established.

A very promising approach to such transitivity producing conflict strategies can be found in Ivan Chase's (Chase 1985) investigations. Working with fowl he found that dominance systems in general were formed by successive integration of individuals into triadic or tetradic dominance orderings. As for the emergence of triadic and tetradic dominance orderings the following could be observed: Three fowl, unknown to each other, are brought together. Let A have successfully attacked B. Thus one dyadic dominance ordering has been established (fig. 5).

There are now four possibilities, how in the next step a triadic dominance ordering could determine the status of C (fig. 6).

The first two types of attacks ("double receive" and "double attack"), if successful, guarantee a linear dominance system in the triad, notwithstanding the outcome of the last dyadic conflict, which is still open (fig. 7):

The other two types ("attack the attacker", and "pass on") do not share this property.

Chase observed that the chances of success are very high for "double attack" or "double receive", either because A, the winner of the first fight, self-assertive and aroused, in most cases has an easy game with the bystanding C, or because the defeated B has not the resilience to withstand C's attack, which immediately follows the humiliation in the first attack.

Chase found that in groups of three individuals, unknown to each other, 91 % and in groups of four individuals, unknown to each other, 87 % of all second attacks after the first dyadic dominance relation has been established, were either "double receive" or "double attack".

Barchas/Mendoza (1985), working with macaques, could replicate Chase's results.

We can interpret these findings as a support of the postulate that we have to look for evolutionarily stable strategies on the individual level, which actively produce linear dominance hierarchies. In order to be evolutionarily stable, these strategies must contribute more to the individual fitness than all alternatives. These strategies will follow some general rules, as

- produce linear dominance orderings;
- try to dominate as many conspecifics as possible;
- once established, accept subdominance.

In all species with dominance systems, dominant rank allows for exploitation of subdominants.

The human species has added a new dimension to exploitation (at least among vertebrates): rather than just robbing someone you have him work for you. You do not confine yourself to what the exploited has collected for his own consumption, you have him planfully produce things which you desire. The dominance system thereby acquires a new quality. It serves not only to deprive other individuals access to scarce resources, now it serves to turn other individuals into tools for the production of additional resources.

This requires considerably enhanced cognitive and communicative capabilities.

A dominance relation is not the only mean of coordinating productive work of several individuals. Equally important is cooperation among individuals which do not dominate each other. It is an empirical question whether the

process of production-by-division-of-labor in early human societies was organized along dominance relations or by cooperation in this sense. But in any case, dominance systems can be used to coordinate the joint production work of several individuals and to exploit the subdominant individuals among the process.

One more important development is to be mentioned. Once the groups (societies) become larger, there will be workers who produce goods and services which are useful by themselves, and there will be workers who maintain the coordination and the - inegalitarian - distribution of the produced goods and services. For the latter type of workers Max Weber has coined the expression "Erzwingungsstab" ("enforcement staff") (Weber, 1956, 17f.).

Here we can recall a result of section II of this paper, namely that on the same resource base a larger population can be maintained, if its internal structure is despotic, than a population with a egalitarian internal structure.

If we assume equal technology, then a despotic society will not only be larger, but be able to translate its superior size into superior power, and thus outcompete rival societies, which are not completely despotic. The crucial condition, of course, is: equal technology. This brings us to the last main section of this paper.

IV. Counterforces against unequal distribution of resources and power

We may begin our last section by raising the question why is it then, that human societies (and many non-human societies as well) are not organized in the most despotic manner? The answer is: the tendency towards despotism is mitigated by the evolution of cooperation, mainly based on reciprocity selection.

Cooperation within a group, which means collective efforts for the achievement of a common good, is the very core of human sociality, and is

marked by two characteristics. First, if successful, it makes everyone in the group better off than if left with the alternative individualistic solution to a particular problem. Secondly, it is exploitable: from a purely individualistic cost-benefit viewpoint, the best choice is the one which allows you to enjoy the fruits of the collective effort without having contributed properly to its cost: while the worst choice is the one which leaves you alone with the costs for what is collectively enjoyed thereafter, because then you have spent more than would have been necessary for an individualistic solution for you alone. If we denote with V_{ij} the value of the behavior i in an encounter with behavior j , and if we denote cooperative behavior with c and non-cooperative behavior with n , then we can express these two characteristics by the following inequalities:

$$V_{nc} > V_{cc} > V_{nn} > V_{cn} \quad (23)$$

The problem is: how could cooperation have evolved in the first place, if evolutionary success depends on the relative individual advantage of a trait over competing traits?

From (23) three basic properties of the cooperation problem can be derived:

- (i) V_{cc} is Pareto-optimal, and V_{nn} is not;
- (ii) V_{nn} is a strongly stable equilibrium, and V_{cc} is not;
- (iii) non-cooperation is a dominant strategy, and no mixed equilibrium is possible.

Pareto-optimality is obviously no point in a constant-sum game; thus, a social dilemma or cooperation game in its most simplified form is a symmetrical 2x2 non-constant = bimatrix game, where all strongly stable equilibria are Pareto-deficient. Strong stability of an equilibrium means that any unilateral deviation makes you strictly worse off. Generality requires symmetry of payoffs, because from an evolutionary perspective, the cooperation problem within a population or a species as a whole must be the same for all members competing for survival and growth. Besides, any assumed asymmetry of chances for survival and growth can be justified only with

additional reasoning: why and to what extent should players be subject to different payoff conditions?

Focusing on social dilemmas with dominant strategies as models for the cooperation problem has been criticized for being too restrictive (e.g. Liebrand, 1983). Considering social dilemmas with nondominant strategies, however, seems to be rather questionable.

All non-cooperative symmetrical 2x2 non-constant = bimatrix games without a dominant strategy have at least one Pareto-optimal equilibrium (for a proof, see Mueller, 1987). It is difficult to see how games with at least one Pareto-optimal Nash-equilibrium could serve as models for the cooperation problem. Therefore the equilibrium strategy must be a dominant strategy. These properties - symmetrical 2x2 non-constant = bimatrix game; all strongly stable equilibria Pareto-deficient; the equilibrium strategy a dominant strategy - uniquely define the classical 2x2 Prisoner's Dilemma, which, therefore, can still be regarded as the best model for the cooperation problem (Boyd 1988).

In the elementary cooperation game, as represented by the symmetrical PD game, no other evolutionarily strategy exists but the noncooperative strategy.

There are two main mechanisms by which in individual selection (we disregard in this paper any group-selection approaches) the evolution of cooperation is possible: kin-selection and reciprocal-selection.

The kin-selection-model is based on the notion of extended fitness: behavior which benefits Alter at Ego's expense may still be advantageous to Ego, if the ration between the loss in Ego's individual fitness and the gain in Alter's individual fitness is smaller than the degree of relatedness r between Ego and Alter, measured in the relative quantity of games Ego and Alter share:

$$r > C_E / G_A \quad (24)$$

where C_E is the cost to Ego, and G_A the gain to Alter. Of course this concept cannot be properly defined without taking into account the genetical variance in the population, i.e. the average relatedness among two randomly selected individuals.

Kinship selection of cooperativeness without doubt is a strong evolutionary force also in human populations. We only have to consider the importance of family ties in politics and business in all societies. Nevertheless Kin-selection cannot be the only force behind the evolution of human cooperativeness.

In all developed cultures political associations are no more identical with clans and family associations. This is highlighted in an extreme manner in political associations of which the members are committed to celibacy - like the monastic orders, which can be found in many cultures.

It is the quintessence of bureaucratic organisations that they demand cooperation among its members, independent from all private sympathies and interests, and therefore: independent from all family loyalties.

The widespread occurrence of matrilinear family systems, in which the wealth of a man is inherited by his sisters' children, and not by his own children, is another argument in favor of additional selection forces for the evolution of cooperativeness in human societies.

The most important of these additional selection forces is reciprocity selection of cooperativeness: reciprocity of cooperation and non-cooperation between potential partners over an extended period of time.

Kinship selection requires only minimal cognitive capabilities: it is sufficient to make all my close relatives to preferred recipients of acts which accrue certain costs for me, but are even more beneficial to them. They will behave analogously toward me.

Reciprocity selection requires disproportionately more developed cognitive abilities: I have to be capable of identifying and recognize every single

potential cooperation partner. I have to be able to keep in mind his past actions towards me, and my own past action towards him. I have to have good empathic capabilities: what was the cost and the benefit my action had for him? Has he realized the cost and benefits of his past actions for me?

Reciprocity based cooperation (mostly as coalitions-of-two) occurs among primates (Packer 1977) and carnivores (Packer and Pusey 1982), but has been evolving among humans in an incomparably more sophisticated form. This is the basis for all the complex forms of division of labor, of barter, and of power, which distinguished the human sociality from the sociality of all other species. It should be mentioned, that reciprocity selection and kinship-selection of cooperativeness are not antagonistic forces. On the contrary, one may expect, that among kinspeople reciprocity based cooperativeness had particularly good evolutionary chances (Rothstein and Pierotti 1988).

During the last decade there were many theoretical as well as empirical studies of reciprocal cooperation (Axelrod 1981, 1984; Axelrod and Hamilton 1981, Brown et al. 1982; Friedman 1977; Grofman and Pool 1977; Smale 1980; Kreps et al. 1982, Moore 1984). I can only sketch the most general conclusions one can draw from these studies.

(1) The game has to be played for more than one round of moves, since in the PD game no equilibrium distinct from the Nash equilibrium - constant noncooperation - is possible if the total number k of rounds is determined before the game and made known to the players (Luce and Raiffa, 1957). Therefore, we have to conceive of an iterated game with an indefinite number of rounds. The overall evolutionary value of the competing strategies has to be computed by a "discounting" approach (Friedman, 1977; Axelrod and Hamilton, 1981). In its standard interpretation, discounting simply means that a payoff in the future is valued less than the same payoff now, and that we can express this devaluation by a constant discount on the payoff of every future move. Thus a sequence of identical moves, resulting in the total payoff $V_{ij}(\text{total})$ to the player playing strategy i against strategy j , would yield the total payoff expressed in present value

$$V_{ij}(\text{total}) = V_{ij} + wV_{ij} + w^2V_{ij} + w^3V_{ij} + \dots \quad 0 < w < 1 \quad (25)$$

w being the constant discount factor, or according to the formula for the geometric series,

$$V_{ij}(\text{total}) = \sum_{k=0}^{\infty} w^k V_{ij} = V_{ij}/(1-w) \quad (26)$$

The greater w, the greater is the expected length of the total interaction sequence that can be calculated according to

$$E_{(\text{Length})} = 1/(1-w) \quad (27)$$

if we assumed the first move to occur with certainty. Thus, by selecting different values for w, we can model social encounters of different duration, which in whole populations of players can be thought of as an indicator of social cohesion in the population. We can define that the higher the expected number of social encounters with a given interaction partner, the greater the social cohesion.

(2) Introducing the idea of iterated games unfolds its full impact only if we simultaneously introduce reactive or learning strategies. A reactive strategy can be formalized through an updating function that defines A's probability of choosing an alternative in move k as a function of the outcome of round k-1, k-2, ...

Since A's previous moves were also a function of previous outcomes, A's k-th move can completely be described as a function of B's previous moves and both parties' initial moves. The advantage of reacting strategies is that they, for example, can play cooperatively with cooperative partners, and noncooperatively with noncooperative partners.

(3) But even the best reactive strategy cannot defeat an ALL DETECT strategy in pairwise encounters. Therefore Axelrod introduced a third extension of the PD game, the idea of a population game, where the probability of random pairwise encounters between different individual strategies reflects the

relative proportions of these strategies in the population. The total expected value of a strategy in a population is then the weighted average of the expected values of this strategy when played against the other strategies present in this population.

A critique of these ideas can be found in Mueller 1987.

With regard to our subject - social inequality in resources and power - we can state the conditions under which cooperative coordination of individual activities has an evolutionary advantage over hierarchical coordination. Cooperation, to state this explicitly, does not require partners which are equally endowed or equally powerful in all aspects.

Cooperation can evolve among unequal partners, where has to be equality among them is that each has to be able of enforcing sanctions (punitive moves) against all others (not necessarily at the same time). On the other hand, the potential for cooperation is the bigger, the greater the synergetic effects of division-of-labor are, which means: the greater the additional benefits to be reaped by moving from non-cooperation to Pareto-optimal cooperation, the greater the potential that cooperation can evolve, provided that the necessary cognitive and ecological prerequisites, as mentioned above, are existent.

Ultimately the options of cooperation in human societies are provided by the level of technology and by the level of instrumental social reasoning. These options are at the same time options against the power of dominance hierarchies.

The subdominants, endowed with ever more specialized skills, and therefore more and more difficult to replace, and better equipped to do substantial harm as well as to give substantial support to the interest of the dominant, are able to secure themselves access to desired resources above the subsistence level. The crucial mechanism, by which this is accomplished is the creation of coalitions against the dominant members on the top echelons of the social hierarchies.

This Hegelian dialectics of master and slave - the master rules by force, but the slave educates himself in his work, and finally by superior skill

and knowledge is able to topple the master, underlies the Marxist ideas on the dialectics of technical progress, class struggle and social evolution. I readily acknowledge my indebtedness to this intellectual heritage; as the more these ideas find new support by modern behavioral ecology.

The more the members of a group or a society are held together in a cobweb of mutual long-term cooperation loyalties, the more easily dominance systems can be disposed of, since this cobweb has not less a pacifying potential.

It is, however, in contrast to Marxist theory, not technology in a narrow sense alone, but also instrumental social skills, which drive social evolution.

On a very elementary level the role of these instrumental social skills for building coalitions of the subdominant against dominants has been studied by de Waal and Luttrell (1988). Studying mechanisms of reciprocity in rhesus monkeys, in stumptail monkeys and in chimpanzees, they discovered that reciprocity has two dimensions, which seem to represent subsequent stages of evolution.

The older is beneficial reciprocity: if A does something good to B, B will do something good to A in the future. If dominant A, however, does something harmful to subdominant B, B will not reciprocate in kind. Such partial reciprocity goes well with the strict dominance hierarchies in rhesus monkeys and stumptail monkeys. Chimpanzees, however displayed both dimensions: they reciprocated against harmful as well as against beneficial actions. Quite exciting was, how the problem of the dominance relation was overcome, if a subdominant had to square a bill with a dominant individual. The subdominant waited until the dominant was engaged in a conflict with a third party, and then intervened on behalf of this opponent, against the dominant. Thus in quite an effective way low ranking individuals could influence the distribution of rank and the balance of power among the top members of the hierarchy.

From such ethological studies we may obtain important insights into the issue of the evolution of social norm systems. A promising new topic in evolutionary game theory are models of the evolution of metanorms of cooperativeness in population games (Axelrod 1986). Norms of cooperativeness (punish anyone, who does not reciprocate your cooperativeness) are quite

effectively stabilized in such games by metanorms of cooperativeness (punish anyone, whom you see not reciprocating a third individual's cooperativeness).

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