Species Survival and Evolutionary Stability in Sustainable Habitats[*]
– The Concept of Ecological Stability –

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Abstract

Whoever exists belongs to a species, which did not become extinct, has a (geno-)type, which should be well adjusted, and lives in a habitat which has been sustainable for a long time. To capture the first aspect we allow for interspecies competition and analyze the conditions for species survival. The second aspect refers to success in intraspecies competition of (geno-)types as in evolutionary biology and game theory. Survival in inter- and intraspecies competition together with sustainability define ecological stability, a concept which we illustrate by an example of solitary and social grazers who compete for food supply and who are endangered by the same predators. Although our approach is inspired by empirical evidence, no systematic attempt is made to apply it to some specific ecology.

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1. Introduction

Having survived means

(i) to belong to a species which has not (yet) become extinct,

(ii) that one's genetic program is well adjusted to the habitat (including the population composition of one's own species), in which one lives, and

(iii) that the habitat is used by all its inhabitants in a sustainable way.

Requirement (i) is what we mean by species survival. Condition (ii) refers to the familiar idea of evolutionarily stable strategies and its variations (e.g. Maynard Smith and Price, 1973, and Maynard Smith, 1982). Of course, the two processes of species and strategy selection can be only well defined for a given, possibly stochastic habitat which must be sustainable (see Ostrom et al., 1997, for sustainability of human habitats) since strategy selection, but also species selection may need a long time to converge. The concept of ecological stability requires that the geno-types or strategies of all existing species are evolutionarily stable, that no other species can enter the habitat and thereby endanger the existing species, and that all existing species together make use of the habitat which does not question its future existence.

What can such a – more general – concept explain? In our view, many existing species – among them many primate species, especially those like chimpanzees or bonoboes which are closely related to mankind, but also less developed species like birds (e.g. the great tit, see Aumann, 1987, as well as Regelmann and Curio, 1986) – display a lot of cooperative behavior, e.g. by collectively watching out for predators, by collectively fighting against predators etc. A further impressive example are (non-related) bats who engage in cooperative insurance against starvation by allowing non-successful hunters to drink the blood of the more successful hunters. If one just requires evolutionary stability, e.g. in the sense that

no mutant strategy is a better reply against the actual species behavior, it often seems that a "mutant", who more or less openly is shirking, could do better.

What one should clearly distinguish here is mutation in the sense of adopting another strategy by a given species and behavioral changes due to exchanging species. So, for instance, solitary animals cannot just behave more cooperatively since this requires a social group which does not exist for solitary animals. Similarly, shirking from cooperation in a socially living species can only mean to be less involved in cooperative behavior and not to change to solitary life. Male lions, for instance, are often rather inactive during the hunt, but they may be non-substitutable when actually trying to throw down large prey, e.g. a buffalo, or when defending a catch against other predators, e.g. hyaenas. Here a strategy change as studied in evolutionary biology or game theory could mean to become more or less active in collective hunting.

If shirking is observable, it can be easily punished by assigning lower ranks (and thereby lower reproductive success) in the pecking order. Thus for a given species of socially living animals cooperation can be stabilized by evolutionary stability of strategies, i.e. by intraspecies competition of strategies. More dramatic deviations from cooperative behavior, e.g. by refraining from any kind of cooperation, seems for most socially living species no alternative since they will end most surely in starvation. A solitary lion will, for instance, hardly be successful in hunting. Such changes in behavior will thus have to explained by substituting species, i.e. by interspecies competition to which we refer as species survival.

This does not exclude that a similar species exists which only differs in the social structuring of the species population. So our main example involves solitary grazers and social grazers which we assume to be rather similar except for their social structuring. They nevertheless belong to different species, i.e. the strategies of solitary grazers are non-feasible for social grazers and vice versa which, however, does not exclude that they may have similar implications.

The main purpose of our example is to illustrate the possibility that only the rather cooperatively behaving social grazers survive species selection. We thus

explain cooperative behavior not by strategy selection, but simply by showing that the evolutionarily stable strategies of solitary and social grazers may, in a given habitat, result in higher fitness of social grazers as compared to solitary ones.

In the following section 2 we first define the concept of ecological stability which we then illustrate by our example of solitary and social grazers. Like in evolutionary biology and game theory stability conditions can be either static or dynamic. In our Conclusions we are summarize our discussion of ecological stability and compare this concept to other ways of explaining cooperation.

2. Ecological Stability

When defining the concept of ecological stability we rely on the notation of Table II.1. Here the set A of species a is assumed to include all possible species, the existing and the non-existing ones. For each species $a \in A$ the possible set of behaviors is S^a. Clearly, knowing S^a for a non-existing species is often difficult. In case of extinct, but formerly existing species it is nevertheless possible – all dinosaurs could not fly and we know which were vegetarian and which were carniverous.

We do not necessarily want to defend our definition of a habitat H by its components N^a, i.e. the population distributions over strategies in S^a for all $a \in A$, as well as by its other characteristics φ, as the most natural one. But it seems well suited for defining the concept of ecological stability.

That the number N^a of animals of species $a \in A$ is bounded (from above) probably needs no justification. Clearly, the upper bound $\overline{N}^a$ for N^a will depend on H, i.e. on how the habitat is inhabited and on its other characteristics φ.

The lower bound $\underline{N}^a$ for N^a can be justified in several ways. Many species, especially the sexually reproducing ones, require a minimal population size to prevent

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inbreeding and/or to guarantee sufficient chances for mating. Also catastrophic, e.g. climatic events, species specific epedemies, short time overpopulation of predators can endanger a species $a \in A$ if its population size is too small. This lower bound $\underline{N}^a$ for N^a will often depend on H as it is true for the upper bound $\overline{N}^a$.

A	set of different species a
$S^a = \left\{ s_1^a, ..., s_{m(a)}^a \right\}$	set of strategies/(geno-)types of species $a \in A$
$N^a = \left(n_1^a, ..., n_{m(a)}^a \right)$	population distribution of species $a \in A$
φ	other (than the inhabitation) characteristics of habitat
$H = \left((N^a)_{a \in A} ; \varphi \right)$	habitat
$\mathcal{H}(\varphi)$	set of sustainable habitats H for a specific φ
$N^a = \sum_{i=1}^{m(a)} n_i^a$	number of animals of species $a \in A$
$\overline{N}^a(H)$	upper bound for N^a depending on H
$\underline{N}^a(H)$	lower bound for N^a depending on H where $\overline{N}^a(H) > \underline{N}^a(H)$ for all $H \in \mathcal{H}$, $a \in A$
$\widehat{n}^a(s_i^a; H)$	fitness/expected number of offspring for species $a \in A$ when using strategy s_i^a in habitat H

Table II.1: Notation of section 2

The fitness function $\widehat{n}^a(\cdot)$ for all species $a \in A$ is a familiar concept in evolutionary biology and evolutionary game theory. The interpretation of $\widehat{n}^a(s_i^a; H)$ is that in habitat H – which includes also the population distribution N^a over S^a – the strategy s_i^a yields the expected number $\widehat{n}_i^a$ of offspring, i.e. if one neglects stochastic events, the new habitat H will have $\widehat{n}_i^a$ animals of species a who rely on strategy $s_i^a \in S^a$.

With the help of this notation we now proceed to define the concept of ecological stability. We first adapt the concept of evolutionarily stable strategies to our

framework. For a given habitat H and a given species $a \in A$ the population distribution N^a is **evolutionarily stable** if

$$(ES.1) \quad \widehat{n}^a \left(s_i^a; H \right) = \max_{s^a \in S^a} \widehat{n}^a \left(s^a; H \right) \text{ or } n_i^a = 0$$

and if for all s_l^a satisfying (ES.1)

$$(ES.2) \quad \widehat{n}^a \left(s_i^a; \widetilde{H} \right) > \widehat{n}^a \left(s_l^a; \widetilde{H} \right) \text{ if } \widetilde{n}_i^a < n_i^a \text{ and } \widetilde{n}_l^a > n_l^a,$$

where $\widetilde{H}$ differs from H at most in the components n_i^a and n_l^a, respectively $\widetilde{n}_i^a$ and $\widetilde{n}_l^a$.

Such static conditions for evolutionary stability will, of course, make sense only if they capture the requirements for dynamic stability for certain classes of evolutionary dynamics, e.g. for the well-known replicator dynamics (see Hammerstein and Selten, 1994, as well as Weibull, 1995, for surveys). In our context such dynamics could be of the form

$$\widehat{n}_{t+1}^a \left(s_i^a; H_t \right)$$

where $\widehat{n}_{t+1}^a$ is the expected number of animals of species a relying on s_i^a in period $t + 1$ and H_t the habitat in the preceding period t. Such evolutionary dynamic can, of course, be stochastic, e.g. in the form of probabilities

$$q_{t+1}^a \left(n_{t+1}^a \left(s_i^a; H_t \right) \right)$$

for observing $n_{t+1}^a \left(s_i^a; H_t \right)$ animals of species a relying on s_i^a in period $t + 1$. For such a dynamic (Markov-) process the dynamic analogue of the static evolutionary stability conditions (ES.1) and (ES.2) would simply require that N^a is a stationary solution of the dynamic process and an at least local attractor, i.e. when starting in some open neighborhood of N^a the process will converge to N^a over time.

In the following it will be assumed that for all existing species $a \in A$ the distribution N^a over S^a is evolutionarily stable. If this is true, a habitat H is said to be evolutionarily stable.

An evolutionarily stable habitat H is said to satisfy **species survival** if for all species $a \in A$

(SS)   either $\overline{N}^a(H) \geq N^a \geq \underline{N}^a(H)$ or $N^a = 0$.

Similar to evolutionary stability also species survival can be given a dynamic stability formulation. If

$$N = (N^a)_{a \in A}$$

is the vector of numbers N^a of animals of all species, the inhabitation dynamics could be described as

$$N_{t+1}(N_t)$$

when one assumes that the second component φ of the habitat $H = (N; \varphi)$ does not change over time. A habitat $H = (N; \varphi)$ or its inhabitation vector N would then satisfy species survival if N is a stationary solution of the dynamic process $N_{t+1}(N_t)$ and an at least local attractor. Again there are obvious ways to generalize such conditions to stochastic (Markov-) processes

$$q_{t+1}(N_{t+1}(N_t))$$

specifying for all N_{t+1} the probability of reaching the inhabitation vector N_{t+1} after N_t.

If an evolutionarily stable habitat H satisfies the species survival condition (SS) for all $a \in A$ it is **ecologically stable** if the condition

(SH) $H \in \mathcal{H}(\varphi)$

that the habitat H is **sustainable** holds. The explicit meaning of (SH) will often be in restrictions for the numbers of inhabitants. One probably does not have to justify that sustainability will usually require upper bounds for the numbers N^a of existing species with $N^a > 0$. It may, however, also require lower bounds for these numbers $N^a > 0$. A large grassland habitat may, for instance, need a sufficient number of grazers to prevent it from becoming a large forest.

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Species survival limits the number of animals of a certain species $a \in A$ since this must be in proportion to the living conditions. It also means that only those species $a \in A$ (continue to) exist for which the minimal size requirement is met. Clearly, a habitat must be sustainable for the sometimes long time spans of genetical evolution (intraspecies competition of strategies) and possibly also of species selection (interspecies competition).

What is missing yet is the **model of interspecies competition**. In our view, this is most easily accomplished via the functions $\overline{N}^a(H)$. Imagine, for instance, two grazer species $\underline{a}$ and $\overline{a} \in A$ that rely on the same food supply. In such a case the characteristics φ of the habitat might define an upper bound

$$N^{\underline{a}} + N^{\overline{a}} \leq \overline{N}^{\underline{a}+\overline{a}}(\varphi)$$

only for the sum of grazers $\underline{a}$ and $\overline{a} \in A$. One thus can use the familiar concept of expected numbers of offspring, i.e. the fitness functions $\widehat{n}^{\underline{a}}(\cdot)$ and $\widehat{n}^{\overline{a}}(\cdot)$, to determine whether both species survive, i.e.

$$N^{\underline{a}} \geq \underline{N}^{\underline{a}}(H),\ N^{\overline{a}} \geq \underline{N}^{\overline{a}}(H),\ N^{\underline{a}} + N^{\overline{a}} \leq \overline{N}^{a+b}(\varphi)$$

$$\text{and } \widehat{n}^{\underline{a}}(s_i^{\underline{a}}; H) = \widehat{n}^{\overline{a}}\left(s_j^{\overline{a}}; H\right)\ \text{whenever } n_i^{\underline{a}}, n_j^{\overline{a}} > 0,$$

or just one, i.e. after a process with

$$\widehat{n}^{\underline{a}}(\cdot) > \widehat{n}^{\overline{a}}(\cdot)\ \text{ or }\ \widehat{n}^{\overline{a}}(\cdot) > \widehat{n}^{\underline{a}}(\cdot)$$

species $\overline{a}$, respectively $\underline{a}$ finally reaches $\widehat{n}^{\overline{a}}(\cdot) < \underline{N}^{\overline{a}}$, respectively $\widehat{n}^{\underline{a}}(\cdot) < \underline{N}^{\underline{a}}$ and thus becomes extinct.

Other two species $\widetilde{a}$ and $\widehat{a}$ in A may, however, rely on different food supply of the habitat H. Let $\widetilde{a}$ be, for instance, the prey species which is main diet of the predator species $\widehat{a} \in A$. Clearly, the upper bound $\overline{N}^{\widehat{a}}$ will then mainly depend on the component $N^{\widetilde{a}}$ of H in the sense that $\overline{N}^{\widehat{a}}$ will increase when $N^{\widetilde{a}}$ becomes larger. Thus whenever trying to model interspecies competition, i.e. when asking which species $a \in A$ finally satisfy the first alternative $\overline{N}^a(H) \geq N^a \geq \underline{N}^a(H)$ of species survival (SS), the model will crucially depend on the specific nature of the competing species.

Nevertheless the general nature of interspecies competition seems to be determined by the dynamics of the numbers N^a and $\underline{N}^a(H)$ of the different species a in A. The species $a \in A$ which first falls short of its minimum threshold $\underline{N}^a(H)$ will be first in becoming extinct (one will usually assume that N^a decreases over the whole range $0 < N^a < \underline{N}^a(H)$ according to the interpretation of $\underline{N}^a(H)$). As a consequence initial conditions will often be crucial when determining which species will continue to exist and which species become extinct. We view this **path dependence** of species survival as an advantage rather than a weakness. Two similar habitats may very well be differently inhabited simply because the initially existing species were different.

Up till now our discussion of interspecies competition has focussed on how species may become extinct. It may, however, be necessary to outline also how new species might arrive. One easy way is migration of new species from neighbouring habitats. The Galapagos Islands are a striking example for a habitat without neighbouring habitats and for interspecies competition with a therefore much smaller set A of species. An immigrant species $a \in A$ will often have to adopt, of course, a different strategy $s_i^a \in S^a$ in its new habitat. This again illustrates how important it is to differentiate between behavioral differences due to different strategy selection and those which are due to differences in species characteristics and how the familiar concepts of intraspecies competition or evolutionary biology and game theory, may be also useful when modelling and analyzing interspecies competition.

3. An example: Solitary versus social grazers

To describe the habitat of our example we rely on the same notation as in the previous section (Table II.1). To keep things as simple as possible let

$$A = \{\underline{a}, \overline{a}, \tilde{a}\}$$

with the following interpretation:

$\underline{a}$ the solitary grazers

$\overline{a}$ the social grazers

$\widetilde{a}$ the only predator species

It seems reasonable to assume that $N^{\underline{a}}$ and $N^{\overline{a}}$ are subjected to a joint upper bound of the form

$$N^{\underline{a}} + N^{\overline{a}} \leq \overline{N}^{\underline{a}+\overline{a}}\left(\varphi\right)$$

whereas

$$\overline{N}^{\widetilde{a}}\left(H\right) = N^{\underline{a}} + N^{\overline{a}}.$$

Thus the total number $N^{\underline{a}} + N^{\overline{a}}$ of grazers in the habitat is limited by the other characteristics φ of the habitat H whereas for the predator species $\widetilde{a} \in A$, which lives on both species of grazers, the upper bound $\overline{N}^{a}\left(H\right)$ is the total number $N^{\underline{a}} + N^{\overline{a}}$ of prey.

Let $w\left(N^{\underline{a}}\right)$ denote the probability by which an animal of species $\underline{a} \in A$, whose total number is $N^{\underline{a}}$, is spotted by a predator. For social grazers $\overline{a} \in A$ this probability will also depend on the herd size $h^{\overline{a}}$ so that $w\left(N^{\overline{a}}, h^{\overline{a}}\right)$ is the corresponding probability for social grazers. Clearly, one should have

$$w\left(N^{\underline{a}}\right) < w\left(N^{\overline{a}}, h^{\overline{a}}\right) \text{ for } N^{\underline{a}} = N^{\overline{a}} \text{ and } h^{\overline{a}} > 1$$

where the difference in the probabilities should increase when $h^{\overline{a}}$ becomes larger. Since $w\left(\cdot\right)$ refers to an individual animal, one will typically assume that $w\left(N^{a}\right)$ decreases when N^{a} increases, both for $a = \underline{a}$ and for $a = \overline{a}$.

On the other hand the probability that an individual animal can escape after being spotted by a predator can be much lower for solitary grazers than for social ones. Here it is assumed that a solitary grazer can allocate the time $s_{i}^{\underline{a}}$ to grazing and the remaining time span $t^{\underline{a}} - s_{i}^{\underline{a}}$ of his total time $t^{\underline{a}}$ to being on the alert. Different strategies $s_{i}^{\underline{a}} \in S^{\underline{a}}$ thus reflect different allocations of time to grazing and being on the alert.

Social grazers, who exist in herds of average size $h^{\overline{a}}$, rely on labor distribution: Whereas the number $s_{i}^{\overline{a}} \in S^{\overline{a}}$ of animals in the herd are on the alert, all the

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$h^{\overline{a}} - s^{\overline{a}}_i$ remaining animals can graze. Although the strategies $s^a_{\underline{i}}$ and $s^{\overline{a}}_j$ of solitary, respectively social grazers have quite a different interpretation, they nevertheless may imply the time sharing between grazing and being on the alert. If $t^{\overline{a}}$ denotes the available time of social grazers, then

$$s^a_{\underline{i}} = \frac{h^{\overline{a}} - s^{\overline{a}}_j}{h^{\overline{a}}} t^{\overline{a}}$$

would imply the same grazing time for solitary and social grazers. In social grazers $\overline{a} \in A$, of course, also the herd size $h^{\overline{a}}$ might be subjected to evolutionary adaptation.

One might wonder how mutation in the sense that herds of social grazers $\overline{a} \in A$ change from $s^{\overline{a}}_i$ to $s^{\overline{a}}_j$ can take place in social grazers $\overline{a} \in A$. If a mutant $s^a_{\underline{j}} \in S^{\overline{a}}$ invades an $s^{\overline{a}}_i$-monomorphic population of social grazers, one might assume that herds invidually switch to s^a_j with positive, but small probability ε whereas they continue to rely on $s^{\overline{a}}_i$ with probability $1 - \varepsilon$.

Let $q(\cdot)$ denote the (conditional) probability of escape after being spotted by a predator. In view of the interpretation of the strategies we assume

$$q\left(s^a_{\underline{i}}\right) < q\left(s^a_{\underline{j}}\right) \ \text{ for } s^a_{\underline{i}} > s^a_{\underline{j}}$$

and

$$q\left(s^{\overline{a}}_i\right) > q\left(s^{\overline{a}}_j\right) \ \text{ for } s^{\overline{a}}_i > s^{\overline{a}}_j.$$

Thus the overall survival probability $S(a)$ of a grazer $a \in \{\underline{a}, \overline{a}\}$ is

$$S\left(s^a_i\right) = 1 - w(\cdot)\left[1 - q(\cdot)\right] \ \text{ for all } s^a_i \in S^a.$$

To keep our example as simple as possible we assume that the fitness $\widehat{n}^a\left(s^a_i; H\right)$ of species $a \in \{\underline{a}, \overline{a}\}$ using strategy $s^a_i \in S^a$ is the product of grazing time and survival probability $S\left(s^i_a\right)$, i.e.

$$\widehat{n}^{\underline{a}}\left(s^a_{\underline{i}}; H\right) = s^a_{\underline{i}}\left(1 - w\left(N^{\underline{a}}\right)\left[1 - q\left(s^a_{\underline{i}}\right)\right]\right)$$

and

$$\widehat{n}^{\overline{a}}\left(s^{\overline{a}}_i; H\right) = \frac{h^{\overline{a}} - s^{\overline{a}}_i}{h^{\overline{a}}} t^{\overline{a}}\left(1 - w\left(N^{\overline{a}}, h^{\overline{a}}\right)\left[1 - q\left(s^{\overline{a}}_i\right)\right]\right).$$

Let H be a habitat which is evolutionarily stable and sustainable ($H \in \mathcal{H}$). If

(C) $\hat{n}^{\overline{a}}\left(s_i^{\overline{a}}; H\right) > \hat{n}^{\underline{a}}\left(s_j^{\underline{a}}; H\right)$ for $n_i^{\overline{a}}, n_j^{\underline{a}} > 0$

then this means that the number $N^{\overline{a}}$ of social grazers will increase more than the number $N^{\underline{a}}$ of solitary grazers. Soon or later thus social grazers will outnumber solitary grazers. If, for instance,

$$\underline{N}^{\underline{a}} + \underline{N}^{\overline{a}} > \overline{N}^{\underline{a}+\overline{a}}(\varphi) > max\left\{\underline{N}^{\underline{a}}, \underline{N}^{\overline{a}}\right\}$$

this surely implies the elimination of solitary grazers $\underline{a} \in A$ when the initial population size $N^{\overline{a}}$ of social grazers satisfies $N^{\overline{a}} \geq \underline{N}^{\overline{a}}$.

Let us discuss inequality (C), whose explicit formulation is

(C') $\frac{h^{\overline{a}}-s_i^{\overline{a}}}{h^{\overline{a}}}t^{\overline{a}}\left(1 - w\left(N^{\overline{a}}, h^{\overline{a}}\right)\left[1 - q\left(s_i^{\overline{a}}\right)\right]\right) > s_j^{\underline{a}}\left(1 - w\left(N^{\underline{a}}\right)\left[1 - q\left(s_j^{\underline{a}}\right)\right]\right)$

for strategies $s_i^{\overline{a}}$ with $n_i^{\overline{a}} > 0$ and $s_j^{\overline{a}}$ with $n_j^{\overline{a}} > 0$, in more detail in order to see whether it is likely to be fulfilled or not. Since herd size will usually be much larger than 1, especially for grazers who inhabitate large plains, the grazing time $t^{\overline{a}}\left(h^{\overline{a}} - s_i^{\overline{a}}\right)/h^{\overline{a}}$ of social grazers will be far longer than $s_j^{\underline{a}}$, the grazing time of solitary grazers. This renders the condition $S\left(s_i^{\overline{a}}\right) > S\left(s_j^{\underline{a}}\right)$ or

(C'') $\frac{1-q\left(s_j^{\underline{a}}\right)}{1-q\left(s_i^{\overline{a}}\right)} > \frac{w\left(N^{\overline{a}}, h^{\overline{a}}\right)}{w\left(N^{\underline{a}}\right)}$

as far too restrictive. Nevertheless we want to argue that even condition (C'') is likely to hold. Of course, the right hand side of (C'') can be much larger than 1. On the other hand $q\left(s_i^{\overline{a}}\right)$ should be considerably larger than $q\left(s_j^{\underline{a}}\right)$ where also this difference will typically increase with the herd size $h^{\overline{a}}$.

Thus especially in habitats with large herd size $h^{\overline{a}}$ of social grazers, e.g. in habitats with wide and open grazing grounds where differences in the probabilities of being spotted by predators are less important, even the far too restrictive condition (C'') for (C) or (C') will hold true. Solitary grazers will then hardly be able to survive

so that ecological stability of H will usually imply $N^{\underline{a}} = 0$, i.e. the extinction of solitary grazers. Habitats favoring solitary grazers should thus be those where differences in the probabilities of being spotted by predators are essential. This typically will require a rich vegetation (a jungle world) and/or uneven ground (hilly habitats) which provide ample hiding places. Here one typically will expect also small herd sizes $h^{\overline{a}}$ of social grazers what seriously restricts the advantages of cooperative behavior.

4. Conclusions

Our main motivation is to account for the high degree of cooperative behavior in many species of the animal kingdom. Often this can and is explained by **kin selection** (Trivers, 1985). At least in mammals this is, however, a rather questionable assumption although it, of course, explains a great deal of cooperation is smaller units (families, e.g. of mother and their offspring in chimpanzees, see Goodall, 1971, de Waal, 1982, or of a male with his harem and the offspring of his wives, Kummer, 1995). There seems to be a need to justify cooperative behavior in larger groups (communities) which cannot be explained by kin selection.

Of course, in rare circumstances cooperative behavior may be also individually optimal, i.e. it can be justified by strategy selection, e.g. in the sense of evolutionarily stable strategies. An insuppressible food call (see Goodall, 1971, for a vivid example) may, for instance, be individually optimal if the food, provided by the habitat, comes in large quantities and is perishable. Like in human societies it seems, however, that shirking, i.e. refraining from the usual degree of cooperativeness, often appears to be individually better.

What we stress here is another aspect of competition, namely that between species. Of the many species, which could exist, only those which make efficient use of whatever is available will survive interspecies competition. Cooperativeness can then be derived from the condition of species survival. Only a species whose strategy selection does not allow to question its relative cooperativeness

can prevent its distinction as illustrated by our example of solitary and social grazers.

There are various ways in which a species can guarantee that strategy selection does not question the degree of cooperation in larger groups. In social grazers the animals, who are supposed to watch out for predators, may be the ones who are most exposed, i.e. they would be the most likely prey of predators. It is then clearly optimal to watch out for predators as hard as possible (what is hardly true for human police (wo)men who are known to shirk a lot).

Another possibility is to link access to females to the investments in watching out for predators. So often the α-male is the one who invests most of his time in being on the alert. Also here the evolutionarily stable strategy will not question the cooperativeness of behavior, here in the sense that few animals are on the alert allowing all others to graze peacefully.

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