

# Species survival and evolutionary stability in sustainable habitats\*

## The concept of ecological stability

Robert Aumann<sup>1</sup>, Werner Güth<sup>2</sup>

<sup>1</sup> Mathematics Institute, The Hebrew University of Jerusalem, Givat Ram, Jerusalem 91904, Israel

<sup>2</sup> Humboldt-University of Berlin, Department of Economics, Institute for Economic Theory III, Spandauer Straße 1, 10178 Berlin, Germany (e-mail: gueth@wiwi.hu-berlin.de)

**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. We do not only analyze interspecies competition and the conditions for species survival, but also 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.

**JEL-classification:** C70, C72

**Key words:** Ecological stability – Species survival – Inter- and intraspecies competition

## 1 Introduction

Having survived means

- (i) belonging 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.

---

\* The helpful comments of an anonymous editor as well as the support from the Deutsche Forschungsgemeinschaft (SFB 373, Quantifikation und Simulation ökonomischer Prozesse) is gratefully acknowledged.

Correspondence to: W. Güth

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; 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, and 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 such as chimpanzees or bonobos which are closely related to mankind, but also less developed species such as birds [e.g. the great tit, see Aumann (1987), as well as Regelmann and Curio (1986)] – display cooperative behavior, e.g. by collectively watching out for predators, by collectively fighting against predators, etc. A further impressive example is (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 as though 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 being less involved in cooperative behavior. 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 becoming 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. refraining from any kind of cooperation, seems for most socially living species no alternative since the end will most surely be starvation. A solitary lion will, for instance, hardly be successful in hunting. Such changes in behavior will thus have to be explained by substituting species, i.e. by interspecies competition to which we refer as species survival.

This does not exclude the possibility that a similar species exists which only differs in the social structuring of the species population. 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 the possibility 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, we first define the concept of ecological stability, which then is illustrated by our example of solitary and social grazers. As in evolutionary biology and game theory, stability conditions can be either static or dynamic. In our Conclusions we 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, existing and 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 herbivorous and which were carnivorous.

We do not necessarily want to defend our definition of a habitat  $H$  by its components  $D^a$ , i.e. the population distributions over strategies in  $S^a$  for all  $a \in A$ , as well as by its other characteristics  $\varphi$ , 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  $\varphi$ .

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 inbreeding and/or to guarantee sufficient chances for mating. Also catastrophic, e.g. climatic events, species specific epidemics, 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  $\overline{N}^a$ .

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

**Table 1.** Notation of Section 2

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

stochastic events, the new habitat  $H$  will have  $\hat{n}_i^a$  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  $D^a$  is *evolutionarily stable* if

$$(ES.1) \quad (i) \quad \hat{n}^a(s_i^a; H) = \max_{s_j^a \in S^a} \hat{n}^a(s_j^a; H) \text{ or} \\ (ii) \quad n_i^a = 0$$

and if for all  $s_i^a$  and  $s_j^a$  satisfying part (i) of (ES.1)

$$(ES.2) \quad \hat{n}^a(s_i^a; \tilde{H}) > \hat{n}^a(s_j^a; \tilde{H}) \text{ if } \tilde{n}_i^a < n_i^a \text{ and } \tilde{n}_j^a > n_j^a,$$

where  $\tilde{H}$  differs from  $H$  at most in the components  $n_i^a$  and  $n_j^a$ , respectively  $\tilde{n}_i^a$  and  $\tilde{n}_j^a$ . According to condition (ES.1), any existing ( $n_i^a > 0$ ) mutant  $s_i^a$  must be optimally adjusted (maximize  $\hat{n}_a(\cdot; H)$ ) to the environment, as described by  $H$ . If two such mutants coexist, because of (ES.2) their frequencies are in equilibrium in the sense that, for any other frequency constellations, there is a tendency towards this equilibrium.

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

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

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 dynamics can, of course, be stochastic, e.g. in the form of probabilities

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

for observing  $n_{t+1}^a (s_i^a; H_t)$  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  $D^a$  be a stationary solution of the dynamic process and an at least local attractor, i.e. when starting in some open neighborhood of  $D^a$  the process will converge to  $D^a$  over time.

In the following, it will be assumed that, for all existing species  $a \in A$ , the distribution  $D^a$  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  $a \in A$ ,

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

Similar to evolutionary stability, 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  $\varphi$  of the habitat  $H = (D; \varphi)$  with  $D = (D^a)_{a \in A}$  determining  $N$  does not change over time. A habitat  $H = (D; \varphi)$  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

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

that the habitat  $H$  is *sustainable* holds. The explicit meaning of (SH) will often be in restrictions of the number 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.

Species survival limits the number of animals of a certain species  $a \in A$  since this must be in proportion to 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  $\varphi$  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.

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

and  $\widehat{n}^{\underline{a}}(s_i^{\underline{a}}; H) = \widehat{n}^{\overline{a}}(s_j^{\overline{a}}; H)$  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.

Two other species  $\widetilde{a}$  and  $\widehat{a}$  in  $A$  may, however, rely on a different food supply in the habitat  $H$ . Let  $\widetilde{a}$  be, for instance, the prey species which is the 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  $D^{\widetilde{a}}$  of  $H$  in the sense that  $\overline{N}^{\widehat{a}}$  will increase when  $N^{\widetilde{a}}$  becomes larger. Thus, when trying to model interspecies competition, i.e. when asking which species  $a \in A$  finally satisfies 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 becomes 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 to now our discussion of interspecies competition has focused on the way in which species may become extinct. It may, however, be necessary to outline also the way in which 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 1). To keep things as simple as possible let

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

with the following interpretation:

- $\underline{a}$  the solitary grazers
- $\bar{a}$  the social grazers
- $\tilde{a}$  the only predator species

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

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

whereas

$$\bar{N}^{\tilde{a}}(H) = N^{\underline{a}} + N^{\bar{a}}.$$

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

Imagine a hunting process during which the predator first has to spot a prey and then try to catch it. For the prey animals this offers two ways of increasing survival probability, namely by avoiding being spotted (usually related to camouflage and herd size) and by trying to escape after being spotted (usually related to relative speed and – for the individual animal – to herd size). Let  $w(N^{\underline{a}})$  denote the probability by which an individual animal of species  $\underline{a} \in A$ , whose total number is  $N^{\underline{a}}$ , is spotted by a predator. For social grazers  $\bar{a} \in A$

this probability will also depend on the herd size  $h^{\bar{a}}$ , so that  $w(N^{\bar{a}}, h^{\bar{a}})$  is the corresponding probability for social grazers. Clearly, one should have

$$w(N^a) < w(N^{\bar{a}}, h^{\bar{a}}) \text{ for } N^a = N^{\bar{a}} \text{ and } h^{\bar{a}} > 1$$

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

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  $s_i^a$  to grazing and the remaining time span  $t^a - s_i^a$  of his total time  $t^a$  to being on the alert. Different strategies  $s_i^a \in S^a$  thus reflect different allocations of time to grazing and being on the alert.

Social grazers, who exist in herds of average size  $h^{\bar{a}}$ , rely on labor distribution: while the number  $s_j^{\bar{a}} \in S^{\bar{a}}$  of animals in the herd are on the alert, all the  $h^{\bar{a}} - s_j^{\bar{a}}$  remaining animals can graze. Although the strategies  $s_i^a$  and  $s_j^{\bar{a}}$  of solitary, respectively social, grazers have quite a different interpretation, they nevertheless both imply time sharing between grazing and being on the alert. If  $t^{\bar{a}}$  denotes the available time of social grazers, then

$$s_i^a = \frac{h^{\bar{a}} - s_j^{\bar{a}}}{h^{\bar{a}}} t^{\bar{a}}$$

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

One might wonder how mutation, in the sense that herds of social grazers  $\bar{a} \in A$  change from  $s_k^{\bar{a}}$  to  $s_j^{\bar{a}}$ , can take place in social grazers  $\bar{a} \in A$ . If a mutant  $s_j^{\bar{a}} \in S^{\bar{a}}$  invades an  $s_k^{\bar{a}}$ -monomorphic population of social grazers, one might assume that herds individually switch to  $s_j^{\bar{a}}$  with positive, but small probability  $\varepsilon$ , whereas they continue to rely on  $s_k^{\bar{a}}$  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

$$q(s_i^a) < q(s_h^a) \text{ for } s_i^a > s_h^a$$

and

$$q(s_k^{\bar{a}}) > q(s_j^{\bar{a}}) \text{ for } s_k^{\bar{a}} > s_j^{\bar{a}}.$$

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

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

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

$$\widehat{n}^a(s_i^a; H) = s_i^a (1 - w(N^a) [1 - q(s_i^a)])$$

and

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

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

$$(C) \quad \widehat{n}^{\bar{a}}(s_j^{\bar{a}}; H) > \widehat{n}^a(s_i^a; H) \text{ for } n_j^{\bar{a}}, n_i^a > 0$$

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

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

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

Let us discuss inequality (C), the explicit formulation of which is

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

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

$$(C'') \quad \frac{1 - q(s_i^a)}{1 - q(s_j^{\bar{a}})} > \frac{w(N^{\bar{a}}, h^{\bar{a}})}{w(N^a)}$$

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 one. On the other hand,  $q(s_j^{\bar{a}})$  should be considerably larger than  $q(s_i^a)$ , where this difference will typically increase with herd size  $h^{\bar{a}}$ .

Thus especially in habitats with large herd size  $h^{\bar{a}}$  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 the ecological stability of  $H$  will usually imply  $N^a = 0$ , i.e. the extinction of solitary grazers. Habitats favoring solitary grazers should thus be those in which 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 small herd sizes  $h^{\bar{a}}$  of social grazers, which seriously restrict 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 a rather questionable assumption, although it, of course, explains a great deal of cooperation in smaller units [families, e.g. of mother and her 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.

When explaining cooperation, the narrow concept of intraspecies competition, as formalized by the concepts of evolutionary stability such as evolutionarily stable strategies or stable constellations for certain evolutionary dynamics, often fails since free-riding mutants fare better in intraspecies competition. Our basic intuition has been, however, that species in which such an advantage prevails, will often have been the ones which became extinct, respectively which overexploited their habitat. As a consequence, we have attempted to formulate the broader concept of ecological stability, which supplements evolutionary stability by the requirements of species survival and sustainability of the habitat. Naturally such a more comprehensive idea can be used to account for other behavioral aspects, e.g. the various forms of symbiosis which appear, such as interspecies cooperation. Here we have concentrated on intraspecies cooperation since we were inspired by such aspects in animal behavior.

Of course, in rare circumstances cooperative behavior may be also individually optimal, meaning 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. As in human societies it seems, however, that shirking (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 questioning its relative cooperativeness can prevent its extinction as illustrated by our example of solitary and social grazers.

This is not to deny that intraspecies competition may sometimes imply cooperation, too. 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 that are supposed to watch out for predators may be the ones most exposed, i.e. they would be the most likely prey. It is then clearly optimal to watch out for predators as much as possible (what is hardly true for human police men who are known to shirk a lot).

Another possibility is to link access to females to investments in watching out for predators. So often the  $\alpha$ -male (the leading male animal with a more or less exclusive right to fertilize female animals) is the one who invests most of his time on alert. Here the evolutionarily stable strategy will not question the cooperativeness of behavior, in the sense that few animals are on the alert allowing all others to graze peacefully.

## References

1. Aumann RJ (1987) Game theory. In: Eatwell J, Milgate M, Newman P (eds) *The new palgrave, a dictionary of economics*, Vol 2, E to J, pp 460–482. The MacMillan Press Limited, London (reprinted 1994)
2. Maynard Smith J (1982) *Evolution and the theory of games*. Cambridge University Press, Cambridge
3. Maynard Smith J, Price G (1973) The logic of animal conflict. *Nature* 264: 15–18
4. de Waal F (1982) *Chimpanzee politics*. Jonathan Cape, London
5. Goodall J (1971) *In the shadow of man*. Houghton Mifflin Company, London (revised 1983)
6. Hammerstein P, Selten R (1994) Game theory and evolutionary biology. In: Aumann J, Hart S (eds) *Handbook of game theory*, Vol 2, pp 929–993. Elsevier, Amsterdam
7. Kummer H (1995) *In quest of the sacred baboon: a scientist's journey*. Princeton University Press, Princeton
8. Ostrom E, Shivakoti G, Shukla A, Thapa G, Varughese G (1997) People, participation and sustainable development: The dynamics of natural resource systems. *Indiana University Workshop in Political Theory and Policy Analysis*
9. Regelman K, Curio E (1986) How do grackles (Parus Major) pair mates cooperate in broad defense? *Behavior* 97: 10–36
10. Trivers R (1985) *Social evolution*. Benjamin-Cummings, Menlo Park, CA
11. Weibull JW (1995) *Evolutionary game theory*. The MIT Press, Cambridge, MA