Chapter 28

GAME THEORY AND EVOLUTIONARY BIOLOGY

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Contents

1. Introduction

The subject matter of evolutionary game theory is the analysis of conflict and cooperation in animals and plants. Originally game theory was developed as a theory of human strategic behavior based on an idealized picture of rational decision making. Evolutionary game theory does not rely on rationality assumptions but on the idea that the Darwinian process of natural selection drives organisms towards the optimization of reproductive success.

A seminal paper by Maynard Smith and Price (1973) is the starting point of evolutionary game theory but there are some forerunners. Fisher (1930, 1958) already used a game-theoretic argument in his sex ratio theory. Hamilton (1967) in a related special context conceived the notion of an unbeatable strategy. An unbeatable strategy can be described as a symmetric equilibrium strategy of a symmetric game. Trivers (1971) referred to supergame theory when he introduced the concept of reciprocal altruism. However, the efforts of the forerunners remained isolated whereas the conceptual innovation by Maynard Smith and Price immediately generated a flow of successful elaborations and applications. The book of Maynard Smith (1982a) summarizes the results of the initial development of the field. In the beginning there was little interaction between biologists and game theorists but nowadays the concept of an evolutionarily stable strategy and its mathematical exploration has been integrated into the broader field of non-cooperative game theory. An excellent overview concerning mathematical results is given by van Damme (1987) in Chapter 9 of his book on stability and perfection of Nash equilibria. Another overview paper with a similar orientation is due to Bomze (1986). However, it must be emphasized that the reader who is interested in substantial development, biological application, and conceptual discussion must turn to the biological literature which will be reviewed in Section 8.

The interpretation of game models in biology on the one hand and in economics and the social sciences on the other hand is fundamentally different. Therefore, it is necessary to clarify the conceptual background of evolutionary game theory. This will be done in the next section. We then proceed to introduce the mathematical definition of evolutionary stability for bimatrix games in Section 3; important properties of evolutionarily stable strategies will be discussed there. In Section 4 we shall consider situations in which the members of a population are not involved in pairwise conflicts but in a global competition among all members of the population. Such situations are often described by the words "playing the field". The mathematical definition o evolutionary stability for models of this kind will be introduced and its properties will be discussed. Section 5 deals with the dynamic foundations of evolutionary stability; most of the results covered concern a simple system of asexual reproduction called replicator dynamics; some remarks will be made about dynamic population genetics models of sexual reproduction. Section

6 presents two-sided asymmetric conflicts. It is first shown how asymmetric conflicts can be imbedded in symmetric games. A class of game models with incomplete information will be examined in which animals can find themselves in different roles such as owner and intruder in a territorial conflict. If the roles on both sides are always different, then an evolutionarily stable strategy must be pure. Section 7 is devoted to evolutionary stability in extensive games. problems arise with the usual normal form definition of an evolutionarily stable strategy. A concept which is better adapted to the extensive form will be defined and its properties will be discussed. In the last section some remarks will be made on applications and their impact on current biological throught.

2. Conceptual background

In biology strategies are considered to be inherited programs which control the individual's behavior. Typically one looks at a population of members of the same species who interact generation after generation in game situations of the same type. Again and again the joint action of mutation and selection replaces strategies by others with a higher reproductive success. This dynamic process may or may not reach a stable equilibrium. Most of evolutionary game theory focuses attention on those cases where stable equilibrium is reached. However, the dynamics of evolutionary processes in disequilibrium is also an active area of research (see Section 5).

2.1. Evolutionary stability

In their seminal paper John Maynard Smith and George R. Price (1973) introduced the notion of an evolutionarily stable strategy which has become the central equilibrium concept of evolutionary game theory. Consider a population in which all members play the same strategy. Assume that in this population a mutant arises who plays a different strategy. Suppose that initially only a very small fraction of the population plays the mutant strategy. The strategy played by the vast majority of the population is stable against the mutant strategy if in this situation the mutant strategy has the lower reproductive success. This has the consequence that the mutant strategy is selected against and eventually vanishes from the population. A strategy is called *evolutionarily stable* if it is stable, in the sense just explained, against any mutant which may arise.

A population state is *monomorphic* if every member uses the same strategy and *polymorphic* if more than one strategy is present. A mixed strategy has a monomorphic and a polymorphic interpretation. On the one hand we may think of a monomorphic population state in which every individual plays this mixed strategy.

On the other hand a mixed strategy can also be interpreted as a description of a polymorphic population state in which only pure strategies occur; in this picture the probabilities of the mixed strategy describe the relative frequencies of the pure strategies.

The explanation of evolutionary stability given above is monomorphic in the sense that it refers to the dynamic stability of a monomorphic population state against the invasion of mutants. A similar idea can be applied to a polymorphic population state described by a mixed strategy. In this polymorphic interpretation a potential mutant strategy is a pure strategy not represented in the population state. Stability of a polymorphic state requires not only stability against the invasion of mutants but also against small perturbations of the relative frequencies already present in the population.

Biologists are reluctant to relinquish the intuitive concept of evolutionary stability to a general mathematical definition since they feel that the great variety of naturally occurring selection regimes require an openness with respect to formalization. Therefore they do not always use the term evolutionarily stable strategy in the exact sense of the definition prevailing in the formal literature [Maynard Smith and Price (1973), Maynard Smith (1982)]. This definition and its connections to the intuitive notion of evolutionary stability will be introduced in Sections 3 and 4.

2.2. The Darwinian view of natural selection

Darwin's theory of natural selection is the basis of evolutionary game theory. A common misunderstanding of the Darwinian view is that natural selection optimizes the welfare of the species. In the past even eminent biologists explained phenomena of animal interaction by vaguely defined benefits to the species. It is not clear what the welfare of the species should be. Is it the number of individuals, the total biomass, or the expected survival of the species in the long run? Even if a reasonable measure of this type could be defined it is not clear how the interaction among species should result in its optimization.

The dynamics of selection among individuals within the same species is much quicker than the process which creates new species and eliminates others. This is due to the fact that the life span of an individual is negligibly short in comparison to that of the species. An adiabatic approximation seems to be justified. For the purpose of the investigation of species interaction equilibrium within the species can be assumed to prevail. This shows that the process of individual selection within the species is the more basic one which must be fully understood before the effects of species interaction can be explored. Today most biologists agree that explanations on the basis of individual selection among members of the same species are much more fruitful than arguments relying on species benefits [Maynard Smith (1976)].

In the 1960s a theory of group selection was proposed [(Wynne-Edwards (1962)] which maintains that evolution may favor the development of traits like restraint in reproduction which are favorable for a local group within a structured population even if they diminish the reproductive success of the individual. It must be emphasized that theoretical explanations of group selection can be constructed on the basis of individual selection. Inasfar as such explanations are offered the idea of group selection is not in contradiction to the usual Darwinian view. However, the debate on group selection has shown that extreme parameter constellations are needed in theoretical models in order to produce the phenomenon [Levins (1970), Boorman and Levitt (1972, 1973), Maynard Smith (1976), see also Grafen (1984) for recent discussions on the term group selection].

Only very few empirical cases of group selection are documented in the literature, e.g. the case of myxomatosis (a disease of rabbits in Australia). A quicker growth rate within the infected rabbit is advantageous for the individual parasite but bad for the group of parasites in the same animal since a shorter life span of the rabbit decreases the opportunities for infection of other rabbits [Maynard Smith (1989)].

The species and the group are too high levels of aggregation for the study of conflict in animals and plants. It is more fruitful to look at the individual as the unit of natural selection. Often an even more reductionist view is proposed in the literature; the gene rather than the individual is looked upon as the basic unit of natural selection [e.g. Williams (1966), Dawkins (1976, 1982)]. It must be admitted that some phenomena require an explanation in terms of genes which pursue their own interest to the disadvantage of the individual. For example, a gene may find a way to influence the process of meiosis in its favor; this process determines which of two genes of a pair of chromosomes in a parent is contributed to an egg or sperm. However, in the absence of strong hints in this direction one usually does not look for such effects in the explanation of morphological and behavioral traits in animals or plants. The research experience shows that the individual as the level of aggregation is a reasonable simplification. The significance of morphological and behavioral traits for the survival of the individual exerts strong pressure against disfunctional results of gene competition within the individual.

2.3. Payoffs

Payoffs in biological games are in terms of fitness, a measure of reproductive success. In many cases the fitness of an individual can be describd as the expected number of offspring. However, it is sometimes necessary to use a more refined definition of fitness. For example, in models for the determination of the sex ratio among offspring it is necessary to look more than one generation ahead and to count grandchildren instead of children [Fisher (1958), Maynard Smith (1982a)]. In models involving decisions on whether offspring should be born earlier or later

in the lifetime of the mother it may be necessary to weigh earlier offspring more heavily than later ones. Under conditions of exteme variations of the environment which affect all individuals with the same strategy in the same way the expected logarithm of the number of offspring may be a better definition of fitness than the usual one [Gillespie (1977)].

The significance of the fitness concept lies in its ability to connect short run reproductive success with long run equilibrium properties. Darwinian theory is not tautological. It does not say that those survive who survive. Instead of this it derives the structure of long-run equilibrium from the way in which short-term reproductive success measured by fitness depends on the environment and the population state. However, as it has been explained above, different types of processes of natural selection may require different ways of making the intuitive concept of reproductive success more precise.

2.4. Game theory and population genetics

Biologists speak of frequency-dependent selection if the fitness of a type depends on the frequency distribution over types in the population. This does not necessarily mean that several types must be present at equilibrium. Frequency-dependent selection has been discussed in the biological literature long before the rise of evolutionary game theory. Game-theoretic problems in biology can be looked upon as topics of frequency-dependent selection and therefore some biologists feel that game theory does not add anything new to population genetics. However, it must be emphasized that the typical population genetics treatment of frequency-dependent selection focuses on the genetic mechanism of inheritance and avoids the description of complex strategic interaction. Contrary to this the models of evolutionary game theory ignore the intricacies of genetic mechanisms and focus on the structure of strategic interaction.

The empirical investigator who wants to model strategic phenomena in nature usually has little information on the exact way in which the relevant traits are inherited. Therefore game models are better adapted to the needs of empirical research in sociobiology and behavioral ecology than dynamic models in population genetics theory. Of course the treatment of problems in the foundation of evolutionary game theory may require a basis in population genetics. However, in applications it is often preferable to ignore foundational problems even if they are not yet completely solved.

In biology the word genotype refers to a description of the exact genetic structure of an individual whereas the term phenotype is used for the system of morphological and behavioral traits of an individual. Many genotypes may result in the same phenotype. The models of evolutionary game theory are called phenotypical since they focus on phenotypes rather than genotypes.

2.5. Players

The biological interpretation of game situations emphasizes strategies rather than players. If one looks at strategic interactions within a population it is important to know the relative frequencies of actions, it is less interesting to know which member plays which strategy. Therefore, the question who are the players is rarely discussed in the biological literature.

It seems to be adequate to think of a "player" as a randomly selected animal. There are two ways of elaborating this idea. Suppose that there are N animals in the population. We imagine that the game is played by N players who are randomly assigned to the N animals. Each player has equal chances to become each one of the N animals. We call this the "many-player interpretation".

Another interpretation is based on the idea that there are only a small number of players, for example 2, which are assigned to the two roles (e.g. owner and intruder) in a conflict at random. Both have the same chance to be in each of both roles. Moreover, there may be a universe of possible conflicts from which one is chosen with the appropriate probability. There may be incomplete information in the sense that the players do not know exactly which conflict has been selected when they have to make their decision. We call this the "few-player interpretation".

The few-player interpretation can be extended to conflicts involving more than two animals. The number of animals in the conflict may even vary between certain limits. In such cases the number n of players is the maximal number of animals involved in a conflict and in any particular conflict involving m animals m players are chosen at random and randomly assigned to the animals.

2.6. Symmetry

In principle evolutionary game theory deals only with fully symmetric games. Asymmetric conflicts are imbedded in symmetric games where each player has the same chance to be on each side of the conflict. Strategies are programs for any conceivable situation. Therefore one does not have to distinguish between different types of players. One might think that it is necessary to distinguish, for example, between male and female strategies. But apart from the exceptional case of sex-linked inheritance, one can say that males carry the genetic information for female behavior and vice versa.

The mathematical definition of evolutionary stability refers to symmetric games only. Since asymmetric conflicts can be imbedded in symmetric games, this is no obstacle for the treatment of asymmetric conflicts. In the biological literature we often find a direct treatment of asymmetric conflicts without any reference to the symmetrization which is implicitly used in the application of the notion of evolutionary stability to such situations.

3.   Symmetric two-person games

3.1.   Definitions and notation

A symmetric two-person game $G = (S, E)$ consists of a finite nonempty *pure strategy set S* and a *payoff function E* which assigns a real number $E(s, t)$ to every pair (s, t) of pure strategies in *S*. The number $E(s, t)$ is interpreted as the payoff obtained by a player who plays *s* against an opponent who plays *t*.

A *mixed strategy q* is a probability distribution over *S*. The probability assigned to a pure strategy *s* is denoted by $q(s)$. The set of all mixed strategies is denoted by *Q*. The payoff function *E* is extended in the usual way to pairs of mixed strategies (p, q).

A *best reply* to *q* is a strategy *r* which maximizes $E(\cdot, q)$ over *Q*. An *equilibrium point* is a pair (p, q) with the property that *p* and *q* are best replies to each other. A symmetric equilibrium point is an equilibrium point of the form (p, p).

A strategy *r* is a *strict best reply* to a strategy *q* if it is the only best reply to *q*. A strict best reply must be a pure strategy. An equilibium point (p, q) is called strict if *p* and *q* are strict best replies to each other.

3.2.   The Hawk–Dove game

Figure 1 represents a version of the famous Hawk–Dove game [Maynard Smith and Price (1973)]. The words Hawk and Dove refer to the character of the two strategies *H* and *D* and have political rather than biological connotations. The game describes a conflict between two animals of the same species who are

Figure 1. The Hawk–Dove game

competing for a resource, for example a piece of food. Strategy H has the meaning of serious aggression, whereas D indicates peaceful behavior. If both choose H, the animals fight until one of them is seriously injured. Both contestants have the same probability to win the fight. The damage W caused by a serious wound is assumed to be higher than the value V of the resource. If only one of the animals plays the aggressive strategy H, this animal will win the resource and the other will flee. If both choose D, then some kind of unspecified random mechanism, for example a ritual fight, decides who gains the resource. Again, both players have the same chance to win. The numbers V and W are measured as changes in fitness. This is the usual interpretation of payoffs in biological games.

The game has two strict equilibrium points, namely (H, D) and (D, H), and one equilibrium point in mixed strategies, namely (r, r) with $r(H) = V/W$.

Only the symmetric equilibrium point is biologically meaningful, since the animals do not have labels 1 and 2. They cannot choose strategies dependent on the player number. Of course, one could think of correlated equilibria [Aumann (1974)], and something similar is actually done in the biological literature [Maynard Smith and Parker (1976), Hammerstein (1981)]. Random events like "being there first" which have no influence on payoffs may be used to coordinate the actions of two opponents. However, in a biological game the correlating random event should be modelled explicitly, since it is an important part of the description of the phenomenon.

3.3.   Evolutionary stability

Consider a large population in which a symmetric two-person game $G = (S, E)$ is played by randomly matched pairs of animals generation after generation. Let p be the strategy played by the vast majority of the population, and let r be the strategy of a mutant present in a small frequency. Both p and r can be pure or mixed. For the sake of simplicity we assume non-overlapping generations in the sense that animals live only for one reproductive season. This permits us to model the selection process as a difference equation.

Let x_t be the relative frequency of the mutant in season t. The *mean strategy* q_t of the population at time t is given by

$$q_t = (1 - x_t)p + x_t r.$$

Total fitness is determined as the sum of a basic fitness F and the payoff in the game. The mutant r has the total fitness $F + E(r, q_t)$ and the majority strategy p has the total fitness $F + E(p, q_t)$. The biological meaning of fitness is expressed by the mathematical assumption that the growth factors x_{t+1}/x_t and $(1 - x_{t+1})/(1 - x_t)$ of the mutant subpopulation and the majority are proportional with the same proportionality factor to total fitness of r and p, respectively. This yields the

following difference equation:

$$x_{t+1} = \frac{F + E(r, q_t)}{F + E(q_t, q_t)} x_t, \quad \text{for } t = 0, 1, 2, \ldots. \tag{1}$$

This process of inheritance describes an asexual population with randomly matched conflicts. We want to examine under what conditions x_t converges to 0 for $t \to \infty$. For this purpose, we look at the difference $x_t - x_{t+1}$:

$$x_t - x_{t+1} = \frac{E(q_t, q_t) - E(r, q_t)}{F + E(q_t, q_t)} x_t.$$

Obviously x_{t+1} is smaller than x_t if and only if the numerator of the fraction on the right-hand side is positive. We have

$$E(q_t, q_t) = (1 - x_t) E(p, q_t) + x_t E(r, q_t)$$

and therefore

$$E(q_t, q_t) - E(r, q_t) = (1 - x_t)[E(p, q_t) - E(r, q_t)].$$

This shows that $x_{t+1} < x_t$ holds if and only if the expression in square brackets on the right-hand side is positive, or equivalently if and only if the following inequality holds:

$$(1 - x_t)[E(p, p) - E(r, p)] + x_t[E(p, r) - E(r, r)] > 0. \tag{2}$$

It can also be seen that $x_{t+1} > x_t$ holds if and only if the opposite inequality is true.

Assume $E(p, p) < E(r, p)$. Then the process (1) does not converge to zero, since for sufficiently small x_t the expression on the left-hand side of inequality (2) is negative.

Now, assume $E(p, p) > E(r, p)$. Then for sufficiently small x_t the left-hand side of (2) is positive. This shows that an $\varepsilon > 0$ exists such that for $x_0 < \varepsilon$ the process (1) converges to zero.

Now, consider the case $E(p, p) = E(r, p)$. In this case the process (1) converges to zero if and only if $E(p, r) > E(r, r)$.

We say that p is *stable against* r if for all sufficiently small positive x_0 the process (1) converges to zero. What are the properties of a strategy p which is stable against every other strategy r? Our case distinction shows that p is stable against every other strategy r if and only if it is an evolutionarily stable strategy in the sense of the following definition:

Definition 1. An *evolutionarily stable strategy* p of a symmetric two-person game $G = (S, E)$ is a (pure or mixed) strategy for G which satisfies the following two conditions (a) and (b):

(a) *Equilibrium condition*: (p, p) is an equilibrium point.
(b) *Stability condition*: Every best reply r to p which is different from p satisfies

the following inequality:

$$E(p,r) > E(r,r) \tag{3}$$

The abbreviation ESS is commonly used for the term evolutionarily stable strategy.

A best reply to p which is different from p is called an alternative best reply to p. Since the stability condition only concerns alternative best replies, p is always evolutionarily stable if (p,p) is a strict equilibrium point.

Vickers and Cannings (1987) have shown that for every evolutionarily stable strategy p an ε exists such that inequality (2) holds for $0 < x_t < \varepsilon$ and every $r \neq p$. Such a bound ε is called a *uniform invasion barrier*.

Result 1. For all r different from p the process (1) converges to zero for all sufficiently small x_0 if and only if p is an evolutionarily stable strategy. Moreover, for every evolutionarily stable strategy a uniform invasion barrier ε can be found with the property that process (1) converges to zero fo all $0 < x_0 < \varepsilon$ for all r different from p.

The uniformity result of Vickers and Cannings (1987) holds for finite symmetric two-person games only. They present a counterexample with a countable infinity of strategies.

Comment. Result 1 shows that at least one plausible selection process justifies Definition 1 as an asymptotically stable dynamic equilibrium. However, it must be emphasized that this process is only one of many possible selection models, some of which will be discussed in Section 5.

Process (1) relates to the monomorphic interpretation of evolutionary stability which looks at an equilibrium state where all members of the population use the same strategy. This monomorphic picture seems to be adequate for a wide range of biological applications. In Section 5 we shall also discuss a polymorphic justification of Definition 1.

3.4. Properties of evolutionarily stable strategies

An evolutionarily stable strategy may not exist for symmetric two-person games with more than two pure strategies. The standard example is the Rock–Scissors–Paper game [Maynard Smith (1982a)]. This lack of universal existence is no weakness of the concept in view of its interpretation as a stable equilibrium of a dynamic pocess. Dynamic systems do not always have stable equilibria.

A symmetric two-person game may have more than one evolutionarily stable strategy. This potential multiplicity of equilibria is no drawback of the concept,

again in view of its dynamic interpretation. The history of the dynamic system decides which stable equilibrium is eached, if any equilibrium is reached at all.

The *carrier* of a mixed strategy p is the set of pure strategies s with $p(s) > 0$. The *extended carrier* of p contains in addition to this all pure best replies to p. The following two results are essentially due to Haigh (1975).

Result 2. Let p be an ESS of $G = (S, E)$. Then G has no ESS r whose carrier is contained in the extended carrier of p. [See Lemma 9.2.4. in van Damme (1987).]

Result 3. A symmetric two-person game $G = (S, E)$ has at most finitely many evolutionarily stable strategies.

It can be seen easily that Result 2 is due to the fact that r would violate the stability condition (3) for p. Result 3 is an immediate consequence of Result 2, since a finite game has only finitely many carriers.

An ESS p is called *regular* if $p(s) > 0$ holds for every pure best reply s to p. In other words, p is regular if its extended carrier coincides with its carrier. One meets irregular ESSs only exceptionally. Therefore, the special properties of regular ESSs are of considerable interest.

Regularity is connected to another property called essentiality. Roughly speaking, an ESS p of $G = (S, E)$ is *essential* if for every payoff function E_+ close to E the game $G_+ = (S, E_+)$ has an ESS p_+ near to p. In order to make this explanation more precise we define a distance of E and E_+ as the maximum of $|E(s, t) - E_+(s, t)|$ over all s and t in S. Similarly, we define a distance of p and p_+ as the maximum of $|p(s) - p_+(s)|$ over all s in S.

An ESS p of $G = (S, E)$ is *essential* if the following condition is satisfied. For every $\varepsilon > 0$ we can find a $\delta > 0$ such that every symmetric two-person game $G_+ = (S, E_+)$ with the property that the distance between E and E_+ is smaller than δ has an ESS p_+ whose distance from p is smaller than ε. The ESS p is strongly essential if not only an ESS but a regular ESS p_+ of this kind can be found for G_+.

The definition of essentiality is analogous to the definition of essentiality for equilibrium points introduced by Wu Wen-tsün and Jian Jia-he (1962).

Result 4. If p is a regular ESS of $G = (S, E)$ then p is a strongly essential ESS of G. [See Selten (1983), Lemma 9.]

An irregular ESS need not be essential. Examples can be found in the literature [Selten (1983), van Damme (1987)].

A *symmetric equilibrium strategy* is a strategy p with the property that (p, p) is an equilibrium point. Haigh (1975) has derived a useful criterion which permits to decide whether a symmetric equilibrium strategy is a regular ESS. In order to express this criterion we need some further notation. Consider a symmetric equilibrium strategy p and let $s_1, \ldots, s_n$ be the pure strategies in the carrier of p.

Define

$$a_{ij} = E(s_i, s_j) \tag{4}$$

for $i, j = 1, \ldots, n$. The payoffs a_{ij} form an $n \times n$ matrix:

$$A = (a_{ij}). \tag{5}$$

We call this matrix the carier matrix of p even if it does not only depend on p but also on the numbering of the pure strategies in the carrier. The definition must be understood relative to a fixed numbering.

Let $D = (d_{ij})$ be the following $n \times (n - 1)$ matrix with

$$d_{ij} = \begin{cases} 1, & \text{for } i = j < n, \\ -1, & \text{for } i = n, \\ 0, & \text{else.} \end{cases}$$

We say that Haigh's criterion is satisfied for p if the matrix $D^T A D$ is negative quasi-definite. The upper index T indicates transposition. Whether Haigh's criterion is satisfied or not does not depend on the numbering of the pure strategies in the carrier.

Result 5. Let p be a symmetric equilibrium strategy of $G = (S, E)$ whose carrier coincides with its extended carrier. Then p is a regular ESS if and only if it satisfies Haigh's criterion.

The notion of an ESS can be connected to various refinement properties for equilibrium points. Discussions of these connections can be found in Bomze (1986) and van Damme (1987). Here, we mention only the following result:

Result 6. Let p be a regular ESS p of $G = (S, E)$. Then (p, p) is a proper and strictly perfect equilibrium point of G. [Bomze (1986)].

4. Playing the field

In biological applications one often meets situations in which the members of a population are not involved in pairwise conflicts but in a global competition among all members of the population. Such situations are often described as "playing the field". Hamilton and May (1977) modelled a population of plants which had to decide on the fraction of seeds dropped nearby. The other seeds are equipped with an umbrella-like organ called pappus and are blown away by the wind. Fitness is the expected number of seeds which succeed to grow up to a plant. The mortality of seeds blown away with the wind is higher than that of seeds dropped nearby, but in view of the increased competition among the plant's own offspring, it is disadvantageous to drop too many seeds in the immediate neighborhood. In this

example every plant competes with all other plants in the population. It is not possible to isolate pairwise interactions.

In the following we shall explain the structure of playing-the-field models. Consider a population whose members have to select a strategy p out of a strategy set P. Typically P is a convex subset of an Euclidean space. In special cases P may be the set of mixed strategies in a finite symmetric game. In many applications, like the one mentioned above, P is a biological parameter to be chosen by the members of the population.

For the purpose of investigating monomorphic stability of a strategy p we have to look at bimorphic population states in which a mutant q is represented with a small relative frequency ε whereas strategy p is represented with the frequency $1 - \varepsilon$. Formally a bimorphic population state z can be described as a triple $z = (p, q, \varepsilon)$ with the interpretation that in the population p is used with probability $1 - \varepsilon$ and q is used with probability ε. In order to describe the structure of a playing-the-field model we introduce the notion of a population game.

Definition 2. A *population game* $G = (P, E)$ consists of a strategy set P and a payoff function E with the following properties:

(i) P is a nonempty compact convex subset of a Euclidean space.

(ii) The payoff function $E(r; p, q, \varepsilon)$ is defined for all $r \in P$ and all bimorphic population states (p, q, ε) with $p, q \in P$ and $0 \leqslant \varepsilon \leqslant 1$.

(iii) The payoff function E has the property that $E(r; p, q, 0)$ does not depend on q.

It is convenient to use the notation $E(r, p)$ for $E(r; p, q, 0)$. We call $E(\cdot, \cdot)$ the *short payoff function* of the population game $G = (P, E)$.

Regardless of q all triples $(p, q, 0)$ describe the same bimorphic population state where the whole population plays p. Therefore, condition (iii) must be imposed on E.

A strategy r is a *best reply* to p if it maximizes $E(\cdot, p)$ over P; if r is the only strategy in P with this property, r is called a *strict best reply* to p. A strategy p is a *(strict) symmetric equilibrium strategy* of $G = (P, E)$ if it is a (strict) best reply to itself.

The book by Maynard Smith (1982a) offers the following definition of evolutionary stability suggested by Hammerstein.

Definition 3. A strategy p for $G = (P, E)$ is *evolutionarily stable* if the following two conditions are satisfied:

(a) *Equilibrium condition*: p is a best reply to p.

(b) *Stability condition*: For every best reply q to p which is different from p an $\varepsilon_q > 0$ exists such that the inequality

$$E(p; p, q, \varepsilon) > E(q; p, q, \varepsilon) \tag{6}$$

holds for $0 < \varepsilon < \varepsilon_q$.

In this definition the invasion barrier ε_q depends on q. This permits the possibility that ε_q becomes arbitrarily small as q approaches the ESS p. One may argue that therefore the definition of evolutionary stability given above is too weak. The following definition requires a stronger stability property.

Definition 4. An ESS p of $G = (P, E)$ is called an *ESS with uniform invasion barrier* if an $\varepsilon_0 > 0$ exists such that (6) holds for all $q \in P$ with $q \neq p$ for $0 < \varepsilon < \varepsilon_0$.

It can be seen immediately that a strict symmetric equilibrium strategy is evolutionarily stable, if E is continuous in ε everywhere. Unfortunately, it is not necessarily true that a strict symmetric equilibrium strategy is an ESS with uniform invasion barrier even if E has strong differentiability properties [Crawford (1990a, b)].

Population games may have special properties present in some but not all applications. One such property which we call *state substitutability* can be expressed as follows:

$$E(r; p, q, \varepsilon) = E(r, (1 - \varepsilon)p + \varepsilon q), \tag{7}$$

for $r, p, q \in P$ and $0 \leqslant \varepsilon \leqslant 1$.

Under the condition of state substitutability the population game is adequately described by the strategy space P and the short payoff function $E(\cdot, \cdot)$. However, state substitutability cannot be expected if strategies are vectors of biological parameters like times spent in mate searching, foraging, or hiding. State substitutability may be present in examples where P is the set of all mixed strategies arising from a finite set of pure strategies. In such cases it is natural to assume that $E(r, q)$ is a linear function of the first component r, but even then it is not necessarily true that E is linear in the second component q. Animal conflicts involving many participants may easily lead to payoff functions which are high-order polynomials in the probabilities for pure strategies. Therefore, the following result obtained by Crawford (1990a, b) is of importance.

Result 7. Let $G = (P, E)$ be a population game with the following properties:

(i) P is the convex hull of finitely many points (the pure strategies).
(ii) State substitutability holds for E.
(iii) E is linear in the first component.

Then an ESS p is an ESS with uniform invasion barrier if a neighborhood U of p exists such that for every $r \in P$ the payoff function $E(r, q)$ is continuous in q within U. Moreover, under the same conditions a strict symmetric equilibrium strategy is an ESS of G.

A result similar to the first part of Result 7 is implied by Corollary 39 in Bomze and Pötscher (1989). Many other useful mathematical findings concerning playing-the-field models can be found in this book.

We now turn our attention to population games without state substitutability and without linearity assumptions on the payoff function. We are interested in the question under which condition a strict symmetric equilibrium strategy is an ESS with uniform invasion barrier. As far as we know, this important question has not been investigated in the literature. Unfortunately, our attempt to fill this gap will require some technical detail.

Let p be a strict symmetric equilibrium strategy of $G = (P, E)$. In order to facilitate the statement of continuity and differentiability conditions to be imposed on E, we define a deviation payoff function $F(t_1, t_2, r, \varepsilon)$:

$$F(t_1, t_2, r, \varepsilon) = E((1 - t_1)p + t_1 r; p, (1 - t_2)p + t_2 r, \varepsilon), \tag{8}$$

for $0 \leqslant t_i \leqslant 1$ $(i = 1, 2)$ and $0 \leqslant \varepsilon \leqslant 1$.

The deviation payoff function is a convenient tool for the examination of the question what happens if the mutant strategy r is shifted along the line $(1 - t)p + tr$ in the direction of p. Consider a mutant present in the relative frequency ε whose strategy is $(1 - t)p + tr$. Its payoff in this situation is $F(t, t, r, \varepsilon)$. The payoff for the strategy p is $F(0, t, r, \varepsilon)$. Define

$$D(t, r, \varepsilon) = F(0, t, r, \varepsilon) - F(t, t, r, \varepsilon). \tag{9}$$

The intuitive significance of (9) lies in the fact that the mutant is selected against if and only if the payoff difference $D(t, r, \varepsilon)$ is positive.

We shall use the symbols F_i and F_{ij} with $i, j = 1, 2$ in order to denote the first and second derivatives with respect to t_1 and t_2. The indices 1 and 2 indicate differentiation with respect to t_1 and t_2, respectively.

Result 8. Let $G = (P, E)$ be a population game and let p be a strict symmetric equilibrium strategy for G. Assume that the following conditions (i) and (ii) are satisfied for the deviation payoff function F defined by (8):

(i) The deviation payoff function F is twice differentiable with respect to t_1 and t_2. Moreover, F and its first and second derivatives with respect to t_1 and t_2 are jointly continuous in t_1, t_2, r, ε.

(ii) A closed subset R of the border of the strategy set P exists (possibly the whole border) with the following properties (a) and (b):

(a) Every $q \in P$ permits a representation of the form

$$q = (1 - t)p + tr, \quad \text{with } r \in R.$$

(b) The set R has two closed subsets R_0 and R_1 whose union is R, such that conditions (10) and (11) are satisfied:

$$\frac{d^2 E((1 - t)p + tr, p)}{dt^2}\bigg|_{t = 0} < 0 \qquad \text{for } r \in R_0, \tag{10}$$

$$\frac{\mathrm{d}E((1-t)p+tr,p)}{\mathrm{d}t}\bigg|_{t=0} < -\alpha \quad \text{for } r \in R_1, \tag{11}$$

where $\alpha >$ is a constant which does not depend on r.

Under these assumptions p is an ESS with uniform invasion barrier.

Proof. Consider the first and second derivatives $D'(t,r,\varepsilon)$ and $D''(t,r,\varepsilon)$ respectively of $D(t,r,\varepsilon)$ with respect to t:

$$D'(t,r,\varepsilon) = F_2(0,t,r,\varepsilon) - F_1(t,t,r,\varepsilon) - F_2(t,t,r,\varepsilon), \tag{12}$$

$$D''(t,r,\varepsilon) = F_{22}(0,t,r,\varepsilon) - F_{11}(t,t,r,\varepsilon) - F_{12}(t,t,r,\varepsilon) \tag{13}$$
$$- F_{21}(t,t,r,\varepsilon) - F_{22}(t,t,r,\varepsilon).$$

In view of (iii) in Definition 2 we have

$$F(t_1,0,r,\varepsilon) = E((1-t_1)p + t_1 r; p, p, \varepsilon) = E((1-t_1)p + t_1 r, p). \tag{14}$$

Since p is a strict symmetric equilibrium strategy, this shows that we must have $F_1(0,0,r,\varepsilon) \leqslant 0$. Consequently, in view of (12) we can conclude

$$D'(0,r,\varepsilon) \geqslant 0 \quad \text{for } 0 \leqslant \varepsilon \leqslant 1. \tag{15}$$

Equation (13) yields

$$D''(0,r,\varepsilon) = -F_{11}(0,0,r,\varepsilon) - 2F_{12}(0,0,r,\varepsilon).$$

In view of (8) we have $F_2(t_1,t_2,r,0) = 0$. This yields $F_{12}(0,0,r,0) = 0$. With the help of (iii) in the definition of a population game we can conclude

$$D''(0,r,0) = -\frac{\mathrm{d}^2 E((1-t)p+tr,p)}{\mathrm{d}t^2}\bigg|_{t=0} > 0, \quad \text{for } r \in R_0. \tag{16}$$

Similarly, (11) together with (12) yields

$$D'(0,r,0) = -\frac{\mathrm{d}E((1-t)p+tr,p)}{\mathrm{d}t}\bigg|_{t=0} > \alpha, \quad \text{for } r \in R_1. \tag{17}$$

Define

$$f(\mu) = \min_{\substack{0 \leqslant t \leqslant \mu \\ 0 \leqslant \varepsilon \leqslant \mu \\ r\varepsilon R_0}} D''(t,r,\varepsilon),$$

$$g(\mu) = \min_{\substack{0 \leqslant t \leqslant \mu \\ 0 \leqslant \varepsilon \leqslant \mu \\ r\varepsilon R_1}} D'(t,r,\varepsilon),$$

$$h(\mu) = \min_{\substack{\mu \leqslant t \leqslant 1 \\ 0 \leqslant \varepsilon \leqslant \mu \\ r\varepsilon R}} D(t,r,\varepsilon).$$

The functions $f(\mu), g(\mu)$, and $h(\mu)$ are continuous; this follows from the fact that the set of all triples (t, r, ε) over which the minimization is extended is compact, and that the function to be minimized is continuous by assumption in all three cases. We have $f(0) > 0$ in view of (16), and $g(0) > 0$ in view of (17). Moreover, we have

$$D(t, r, 0) = E(p, p) - E((1 - t)p + tr, p)$$

and therefore $h(\mu) > 0$ for sufficiently small $\mu > 0$, since p is a strict equilibrium point. Since f, g, and h are continuous, a number $\mu_0 > 0$ can be found such that for $0 \leqslant t \leqslant \mu_0$ and $0 \leqslant \varepsilon \leqslant \mu_0$ we have

$$D''(t, r, \varepsilon) > 0, \quad \text{for } r \in R_0,$$
$$D'(t, r, \varepsilon) > 0, \quad \text{for } r \in R_1,$$

and for $\mu_0 \leqslant t \leqslant 1$ and $0 \leqslant \varepsilon \leqslant \mu_0$ the following inequality holds:

$$D(t, r, \varepsilon) > 0$$

Together with (15) the last three inequalities show that μ_0 is a uniform invasion barrier. □

Remarks. Suppose that the strategy set P is one-dimensional. Then P has only two border points r_1 and r_2. Consider the case that $E(q, p)$ is differentiable with respect to q at (p, p). Then (10) is nothing else than the usual sufficient second-order condition for a maximum of $E(q, p)$ at $q = p$. It sometimes happens in applications [Selten and Shmida (1991)] that $E(q, p)$ has positive left derivative and negative right derivative with respect to q at $q = p$. In this case condition (11) is satisfied for r_1 and r_2. Result 8 is applicable here even if $E(q, p)$ is not differentiable with respect to q at $q = p$. It can be seen that (ii) in result 8 imposes only a mild restriction on the short payoff function E. The inequalities (10) and (11) with $<$ replaced by $\leqslant$ are necessarily satisfied if p is a symmetric equilibrium strategy.

Eshel (1983) has defined the concept of a continuously stable ESS for the case of a one-dimensional strategy set [see also Taylor (1989)]. Roughly speaking, continuous stability means the following. A population which plays a strategy r slightly different from the ESS p is unstable in the sense that every strategy q sufficiently close to r can successfully invade if and only if q is between r and p. One may say that continuous stability enables the ESS to track small exogenous changes of the payoff function E. As Eshel has shown, continuous stability requires

$$E_{11}(q, p) + E_{12}(q, p) \leqslant 0,$$

if E is twice continuously differentiable with respect to q and p. Here, the indices 1 and 2 indicate differentiation with respect to the first and second argument, respectively. Obviously, this condition need not be satisfied for an ESS p for which

the assumptions of Result 8 hold. Therefore, in the one-dimensional case an ESS with uniform invasion barrier need not be continuously stable.

Result 8 can be applied to models which specify only the short payoff function. It is reasonable to suppose that such models can be extended in a biologically meaningful way which satisfies condition (i) in Result 8. Condition (ii) concerns only the short payoff function.

Continuity and differentiability assumptions are natural for large populations. It is conceivable that the fitness function has a discontinuity at $\varepsilon = 0$; the situation of one mutant alone may be fundamentally different from that of a mutant in a small fraction of the population. However, in such cases the payoff for $\varepsilon = 0$ should be defined as the limit of the fitness for $\varepsilon \to 0$, since one is not really interested in the fitness of an isolated mutant.

It is doubtful whether the population game framework can be meaningfully applied to small finite populations. Mathematical definitions of evolutionary stability for such populations have been proposed in the literature [Schaffer (1988)]. However, these definitions do not adequately deal with the fact that in small finite populations [or, for that matter, in large populations – see Foster and Young (1990) and Young and Foster (1991)] the stochastic nature of the genetic mechanism cannot be neglected.

5. Dynamic foundations

Evolutionarily stable strategies are interpreted as stable results of processes of natural selection. Therefore, it is necessary to ask the question which dynamic models justify this interpretation. In Section 3.3 we have already discussed a very simple model of monomorphic stability. In the following we shall first discuss the replicator dynamics which is a model with continuous reproduction and exact asexual inheritance. Later we shall make some remarks on processes of natural selection in sexually reproducing populations without being exact in the description of all results.

We think that a distinction can be made between evolutionary game theory and its dynamic foundations. Therefore, our emphasis is not on the subject matter of this section. An important recent book by Hofbauer and Sigmund (1988) treats problems in evolutionary game theory and many other related subjects from the dynamic point of view. We recommend this book to the interested reader.

5.1. Replicator dynamics

The *replicator dynamics* has been introduced by Taylor and Jonker (1978). It describes the evolution of a polymorphic population state in a population whose members are involved in a conflict describd by a symmetric two-person game

$G = (S, E)$. Formally, the population state is represented by a mixed strategy q for G. The replicator dynamics is the following dynamic system:

$$\dot{q}(s) = q(s)[E(s, q) - E(q, q)], \quad \text{for all } s \in S. \tag{18}$$

As usually $\dot{q}(s)$ denotes the derivative of $q(s)$ with respect to time.

The replicator dynamics can be intuitively justified as follows. By a similar reasoning as in Section 3.3 concerning the process (1), in a discrete time model of non overlapping generations we obtain

$$q_{t+1}(s) = \frac{F + E(s, q_t)}{F + E(q_t, q_t)} q_t(s).$$

This yields

$$q_{t+1}(s) - q_t(s) = \frac{E(s, q_t) - E(q_t, q_t)}{F + E(q_t, q_t)} q_t(s).$$

If the changes from generation to generation are small, this difference equation can be approximated by the following differential equation:

$$\dot{q}(s) = \frac{E(s, q) - E(q, q)}{F + E(q, q)} q(s).$$

The denominator on the right-hand side is the same for all s and therefore does not influence the orbits. Therefore, this differential equation is equivalent to (18) as far as orbits are concerned.

A strategy q with $\dot{q}(s) = 0$ for all s in S is called a *dynamic equilibrium*. A dynamic equilibrium q is called *stable* if for any neighborhood U of q there exists a neighborhood V of q contained in U such that any trajectory which starts in V remains in U. A dynamic equilibrium q is called *asymptotically stable* if it is stable and if in addition to this there exists a neighborhood U of q such that any trajectory of (18) that starts in U converges to q.

It can be seen immediately that every pure strategy is a dynamic equilibrium of (18). Obviously, the property of being a dynamic equilibrium without any additional stability properties is of little significance.

A very important stability result has been obtained by Taylor and Jonker (1978) for the case of a regular ESS. Later the restriction of regularity has been removed by Hofbauer et al. (1979) and Zeeman (1981). This result is the following one:

Result 9. A strategy p for a symmetric two-person game $G = (S, E)$ is asymptotically stable with respect to the replicator dynamics if it is an ESS of G.

A strategy q can be asymptotically stable without being an ESS. Examples can be found in the literature [e.g. van Damme (1987), Weissing (1991)]. The question arises whether in view of such examples the ESS concept is a satisfactory static

substitute for an explicit dynamic analysis. In order to examine this problem it is necessary to broaden the framework. We have to look at the possibility that not only pure but also mixed strategies can be represented as types in the population.

A nonempty finite subset $R = \{r_1, \ldots, r_n\}$ of the set of all mixed strategies Q will be called a *repertoire*. The pure or mixed strategies r_i are interpreted as the types which are present in the population. For $i = 1, \ldots, n$ the relative frequency of r_i will be denoted by x_i. For a population with repertoire R a *population state* is a vector $x = (x_1, \ldots, x_n)$. The symbol q_x will be used for the mean strategy of the population at state x. The replicator dynamics for a population with repertoire R can now be described as follows:

$$\dot{x}_i = x_i[E(r_i, q_x) - E(q_x, q_x)] \quad \text{for } i = 1, \ldots, n, \tag{19}$$

with

$$q_x = \sum_{i=1}^{n} x_i r_i. \tag{20}$$

Two population states x and x' which agree with respect to their mean strategy are phenotypically indistinguishable in the sense that in both population states the pure strategies are used with the same probability by a randomly selected individual. Therefore we call the set of all states x connected to the same mean strategy q the *phenotypical equivalence class* for q.

Consider a repertoire $R = \{r_1, \ldots, r_n\}$ for a symmetric two-person game $G = (S, E)$. Let x^j be the population state whose jth component is 1; this is the population state corresponding to r_j. We say that r is *phenotypically attractive in R* if r belongs to the convex hull of R and a neighborhood U of r exists such that every trajectory of (19) starting in U converges to the phenotypical equivalence class of r. This definition is due to Franz Weissing in his unpublished diploma thesis.

Result 10.   A (pure or mixed) strategy p for a symmetric two-person game $G = (S, E)$ is stable and phenotypically attractive in every repertoire R whose convex hull contains p if and only if it is an ESS of G.

In a paper in preparation this result will be published by Weissing (1990). Cressman (1990) came independently to the same conclusion. He coined the notion of "strong stability" in order to give an elegant formulation of this result [see also Cressman and Dash (1991)].

Weissing proves in addition to Result 10 that a trajectory which starts near to the phenotypical equivalence class of the ESS ends in the phenotypical equivalence class at a point which, in a well defind sense, is nearer to the ESS than the starting point. This tendency towards monomorphism has already been observed in special examples in the literature [Hofbauer and Sigmund (1988)]. Weissing also shows that an asymptotically stable dynamic equilibrium p with respect to (18) is not

stable with respect to (19) in a repertoire which contains p and an appropriately chosen mixed strategy q. This shows that an asymptotically stable dynamic equilibrium with respect to (18) which fails to be an ESS can be destabilized by mutations, whereas the same is not true for an ESS. All these results together provide a strong justification for the view that at least as far as the replicator dynamics is concerned, the ESS concept is a satisfactory static substitute for an explicit dynamic analysis. However, it must be kept in mind that this view is based on the originally intended interpretation of an ESS as a strategy which is stable against the invasion of mutations and not as a polymorphic equilibrium in a temporarily existing repertoire.

5.2. Disequilibrium results

We now turn our attention to disequilibrium properties of the replicator dynamics. Schuster et al. (1981) have derived a very interesting result which shows that under certain conditions a completely mixed symmetric equilibium strategy can be interpreted as a time average. An equilibrium strategy is called *completely mixed* if it assigns positive probabilities to all pure strategies s. The *omega-limit* of an orbit q_t is the set of all its accumulation points. With the help of these definitions we are now able to state the result of Schuster et al. [see also Hofbauer and Sigmund (1988) p. 136].

Result 11. Let $G = (S, E)$ be a symmetric two-person game with one and only one completely mixed equilibrium strategy p, and let q_t be an orbit starting in $t = 0$ whose omega-limit is in the interior of the set of mixed strategies Q. Then the following is true:

$$\lim_{T \to \infty} \frac{1}{T} \int_0^T q_t(s)\, dt = p(s), \quad \text{for all } s \text{ in } S. \tag{21}$$

Schuster et al. (1979) have introduced a very important concept which permits statements for certain types of disequilibrium behavior of dynamical systems. For the special case of the replicator dynamics (18) this concept of permanence is defined as follows. The system (18) is *permanent* if there exists a compact set K in the interior of the set Q of mixed strategies such that all orbits starting in the interior of Q end up in K.

Permanence means that none of the pure strategies in S will vanish in the population if initially all of them are represented with positive probabilities. The following result [Theorem 1 in Chapter 19.5 in Hofbauer and Sigmund (1988)] connects permanence to the existence of a completely mixed symmetric equilibrium strategy.

Result 12.   If the system (18) is permanent then the game $G = (S, E)$ has one and only one completely mixed symmetric equilibrium strategy. Moreover, if (18) is permanent, equation (21) holds for every orbit q_t in the interior of Q.

In order to express the next result, we introduce some definitions. Consider a symmetric two-person game $G = (S, E)$. For every nonempty proper subset S' of S we define a restricted game $G' = (S', E')$. The payoff function E' as a function of pairs of pure strategies for G' is nothing else than the restriction of E to the set of these pairs. We call an equilibrium point of a restricted game $G' = (S', E')$ a *border pre-equilibrium* of G. The word border emphasizes the explicit exclusion of the case $S = S'$ in the definition of a restricted game. A border pre-equilibrium may or may ot be an equilibrium point of G. Note that the border pre-equilibria are the dynamic equilibria of (18) on the boundary of the mixed strategy set. The pure strategies are special border pre-equilibria. The following intriguing result is due to Jansen (1986) [see also Theorem 1 in Hofbauer and Sigmund (1988) p. 174].

Result 13.   The replicator system (18) is permanent for a game $G = (S, E)$ if there exists a completely mixed strategy p for G such that

$$E(p, q) > E(q, q) \tag{22}$$

holds for all border pre-equilibria q of G.

Superficially inequality (22) looks like the stability condition (3) in the definition of an ESS. However, in (22) p is not necessarily a symmetric equilibrium strategy, and q is not necessarily an alternative best reply to p. A better interpretation of (22) focuses on the fact that all border pre-equilibria q are destabilized by the same completely mixed strategy p. We may say that Result 13 requires the existence of a completely mixed universal destabilizer of all border pre-equilibria.

Suppose that p is a completely mixed ESS. Then (22) holds for all border pre-equilibria in view of (3), since they are alternative best replies. The proof of Result 9 shows that a completely mixed ESS is globally stable. This is a special case of permanence. The significance of (22) lies in the fact that it also covers cases where the replicator dynamics (18) does not converge to an equilibrium. In particular, Result 13 is applicable to symmetric two-person games for which no ESS exists.

5.3.   A look at population genetics

The replicator dynamics describes an asexual population, or more precisely a population in which, apart from mutations, genetically each individual is an exact copy of its parent. The question arises whether results about the replicator dynamics can be transferred to more complex patterns of inheritance. The investigation of

such processes is the subject matter of population genetics. An introduction to population genetic models is beyond our scope. We shall only explain some game-theoretically interesting results in this area.

Hines and Bishop (1983, 1984a, b) have investigated the case of strategies controlled by one gene locus in a sexually reproducing diploid population. A gene locus is a place on the chromosome at which one of several different alleles of a gene can be located. The word *diploid* indicates that an individual carries each chromosome twice but with possibly different alleles at the same locus.

It has been shown by Hines and Bishop that an ESS has strong stability properties in their one-locus continuous selection model. However, they also point out that the set of all population mean strategies possible in the model is not necessarily convex. Therefore, the population mean strategy can be "trapped" in a pocket even if an ESS is feasible as a population mean strategy. The introduction of new mutant alleles, however, can change the shape of the set of feasible mean strategies. Here we shall not describe the results for one-locus models in detail. Instead of this we shall look at a discrete time two-locus model which contains a one-locus model as a special case.

We shall now describe a standard two-locus model for viability selection in a sexually reproducing diploid population with random mating. We first look at the case without game interaction in which fitnesses of genotypes are exogenous and constant. Viability essentially is the probability of survival of the carrier of a genotype. Viability selection means that effects of selection on fertility or mating success are not considered.

Let $A_1, \ldots, A_n$ be the possible alleles for a locus A, and $B_1, \ldots, B_m$ be the alleles for a locus B. For the sake of conveying a clear image we shall assume that both loci are linked which means that both are on the same chromosome. The case without linkage is nevertheless covered by the model as a special case. An individual carries pairs of chromosomes, therefore, a genotype can be expressed as a string of symbols of the form A_iB_j/A_kB_l. Here, A_i and B_j are the alleles for loci A and B on one chromosome, and A_k and B_l are the alleles on both loci on the other chromosome. Since chromosomes in the same pair are distinguished only by the alleles carried at their loci, A_iB_j/A_kB_l and A_kB_l/A_iB_j are not really different genotypes, even if they are formally different. Moreover, it is assumed that the effects of genotypes are *position-independent* in the sense that A_iB_l/A_kB_j has the same fitness as A_iB_j/A_kB_l. The fitness of a genotype A_iB_j/A_kB_l is denoted by w_{ijkl}. For the reasons explained above we have

$$w_{ijkl} = w_{ilkj} = w_{kjil} = w_{klij}.$$

An offspring has one chromosome of each of its parents in a pair of chromosomes. A chromosome received from a parent can be a result of recombination which means that the chromosomes of the parent have broken apart and patched together such that the chromosome transmitted to the offspring is composed of parts of both chromosomes of the parent. In this way genotype A_iB_j/A_kB_l may transmit

a chromosome $A_i B_l$ to an offspring. This happens with probability $r \leqslant \frac{1}{2}$ called the *recombination* rate. The relative frequency of chromosomes with the same allele combination at time t is denoted by $x_{ij}(t)$. The model describes a population with nonoverlapping generations by a system of difference equations.

$$x_{ij}(t+1) = \frac{1}{W(t)} \left(r \sum_{kl} w_{ilkj} x_{il}(t) x_{kj}(t) + (1-r) \sum_{kl} w_{ijkl} x_{ij}(t) x_{kl}(t) \right],$$

for $i = 1, \ldots, n$ and $j = 1, \ldots, m$. \hfill (23)

Here, $W(t)$ is the mean fitness in the population:

$$W(t) = \sum_{ijkl} w_{ijkl} x_{ij}(t) x_{kl}(t).$$

The case that the two loci are on different chromosomes is covered by $r = \frac{1}{2}$. In model (23) the fitness w_{ijkl} of a genotype is constant. The selection described by the model is frequency-independent in the sense that fitnesses of genotypes do not depend on the frequencies $x_{ij}(t)$.

Moran (1964) has shown that in this model natural selection does not guarantee that the mean fitness of the population increases in time. It may even happen that the mean fitness of the population decreases until a minimum is reached. The same is true for the multilocus generalization of (23) and in many other population genetics models [Ewens (1968), Karlin (1975)]. Generally it cannot be expected even in a constant environment that the adaptation of genotype frequencies without any mutation converges to a population strategy which optimizes fitness.

The situation becomes even more difficult if game interaction is introduced into the picture. One cannot expect that the adaptation of genotype frequencies alone without any mutations moves results in convergence to an ESS unless strong assumptions are made. Suppose that the fitnesses w_{ijkl} depend on the strategic interaction in a symmetric two-person game $G = (S, E)$. Assume that a genotype $A_i B_j / A_k B_l$ plays a mixed strategy u_{ijkl} in Q. In accordance with the analogous condition for the fitnesses w_{ijkl} assume

$$u_{ijkl} = u_{ilkj} = u_{kjil} = u_{klij}.$$

Define

$$w_{ijkl}(t) = F + E(u_{ijkl}, q_t), \hfill (24)$$

with

$$q_t(s) = \sum_{ijkl} x_{ij}(t) x_{kl}(t) u_{ijkl}(s), \quad \text{for all } s \text{ in } S. \hfill (25)$$

Here, q_t is the mean strategy of the population. If in (23) and in the definition of $W(t)$ the w_{ijkl} are replaced by $w_{ijkl}(t)$ we obtain a new system to which we shall refer as the *system* (23) *with frequency-dependent selection*.

This system has been investigated by Ilan Eshel and Marcus Feldman (1984).

It is very difficult to obtain any detailed information about its dynamic equilibria. Eshel and Feldman avoid this problem. They assume that originally only the alleles $A_1, \ldots, A_{n-1}$ are present at locus A. They look at a situation where a genotype frequency equilibrium has been reached and examine the effects of the introduction of a new mutant allele A_n at the locus A. Initially A_n appears in a low frequency at a population state near the equilibrium.

The ingenious idea to look at the effects of a mutant at a genotype frequency equilibrium is an important conceptual innovation. Eshel (1991) emphasizes that it is important to distinguish between the dynamics of genotype frequencies without mutation and the much slower process of gene substitution by mutation. The dynamics of genotype frequencies without mutation cannot be expected to converge towards a game equilibrium unless special conditions are satisfied. Evolutionary game theory is more concerned about equilibria which are not only stable with respect to the dynamics of genotype frequencies without mutation, but also with respect to gene substitution by mutation. This stability against mutations is often referred to as external stability [Liberman (1983)]. Surprisingly, the conceptual innovation by Eshel and Feldman (1984) also helps to overcome the analytical intractability of multilocus models, since their questions permit answers without the calculation of genotype frequencies at equilibrium.

A *population state* of model (23) is a vector $x = (x_{11}, \ldots, x_{nm})$ whose components x_{ij} are the relative frequencies of the allele frequencies $A_i B_j$. The population mean strategy $q(x)$ is defined analogously to (25). For the purpose of examining qustions of external stability we shall consider the entrance of a mutant allele on locus A. We assume that originally only the alleles $A_1, \ldots, A_{n-1}$ are present. Later a mutant allele A_n enters the system. We assume that before the entrance of A_n the system has reached a dynamic equilibrium y with a population mean strategy p.

A particular specification of the frequency-dependent system (23) is described by a symmetric two-person game $G = (S, E)$ and a system of genotype strategies u_{ijkl}. It will be convenient to describe this system by two arrays, the *inside genotype strategy array*

$$U = (u_{ijkl}), \quad i, k = 1, \ldots, n-1, \quad j, l = 1, \ldots, m$$

and the *outside genotype strategy array*

$$U_n = (u_{njkl}), \quad k = 1, \ldots, n, \quad j, l = 1, \ldots, m.$$

The outside array contains all strategies of genotypes carrying the mutant allele (position independence requires $u_{njkl} = u_{kjnl}$). The inside array contains all strategies for genotypes without the mutant allele. A specific frequency-dependent system can now be described by a triple (G, U, U_n). We look at the numbers m, n and r as arbitrarily fixed with $n \geqslant 2$ and $m \geqslant 1$ and r in the closed interval between 0 and $\frac{1}{2}$.

We say that a sequence $q_0, q_1, \ldots$ of population mean strategies is *generated* by $x(0)$ in (G, U, U_n) if for $t = 0, 1, \ldots$ that strategy q_t is the population mean strategy of $x(t)$ in the sequence $x(0), x(1), \ldots$ satisfying (23) for this specification. For any

two strategies p and q for G the symbol $|p - q|$ denotes the maximum of all absolute differences $|p(s) - q(s)|$ over $s \in S$. Similarly, for any population states x and y the symbol $|x - y|$ denotes the maximum of all absolute differences $|x_{ij} - y_{ij}|$. An *inside population state* is a population state $x = (x_{11}, \ldots, x_{nm})$ with

$$x_{nj} = 0 \quad \text{for } j = 1, \ldots, m.$$

With these notations and ways of speaking we are now ready to introduce our definition of external stability. This definition is similar to that of Liberman (1988) but with an important difference. Liberman looks at the stability of population states and requires convergence to the original inside population state y after the entrance of A_n in a population state near y. We think that Libermans definition is too restrictive. Therefore we require phenotypic attractiveness in the sense of Weissing (see Section 5.1) instead of convergence. The stability of the distribution of genotypes is less important than the stability of the population mean strategy.

Definition 5. Let $y = (y_{11}, \ldots, y_{n-1,m}, 0, \ldots, 0)$ be an inside population state. We say that y is *phenotypically externally stable* with respect to the game $G = (S, E)$ and the inside genotype strategy array U if for every U_n the specification (G, U, U_n) of (23) has the following property: For every $\varepsilon > 0$ a $\delta > 0$ can be found such that for every population state $x(0)$ with $|x(0) - y| < \delta$ the sequence of population mean strategies $q_0, q_1, \ldots$ generated by $x(0)$ satisfies two conditions (i) and (ii) with respect to the population mean strategy p of y:

  (i) For $t = 0, 1, \ldots$ we have $|q_t - p| < \varepsilon$.
  (ii) $\lim_{t \to \infty} q_t = p$.

Eshel and Feldman (1984) have developed useful methods for the analysis of the linearized model (23). However, as far as we can see their results do not imply necessary or sufficient conditions for external stability. Here we shall state a necessary condition for arbitrary inside population states and a necessary and sufficient condition for the case of a monomorphic population. The word monomorphic means that all genotypes not carrying the mutant allele play the same strategy. We shall not make use of the linearization technique of Eshel and Feldman (1984) and Liberman (1988).

Result 14. If an inside population state y is externally stable with respect to a game $G = (S, E)$ and an inside genotype strategy array U, then the population mean strategy p of y is a symmetric equilibrium strategy of G.

Proof. Assume that p fails to be a symmetric equilibrium strategy of G. Let s be a pure best reply to p. Consider a specification (G, U, U_n) of (23) with

$$u_{njkl} = s, \quad \text{for } j, l = 1, \ldots, m, \quad k = 1, \ldots, n.$$

Equations (24) yields

$$w_{njkl}(t) = F + E(s, q_t), \quad \text{for } j, l = 1, \ldots, m, \quad k = 1, \ldots, n.$$

For $i = n$ Eq. (23) assumes the following form:

$$x_{nj}(t+1) = \frac{F + E(s, q_t)}{F + E(q_t, q_t)} \sum_{kl} [rx_{nl}(t)x_{kj}(t) + (1-r)x_{nj}(t)x_{kl}(t)], \quad \text{for } j = 1, \ldots, m.$$

$$(26)$$

Define

$$a(t) = \sum_{i=1}^{n-1} \sum_{j=1}^{m} x_{ij}(t), \tag{27}$$

$$b(t) = \sum_{j=1}^{m} x_{nj}(t). \tag{28}$$

We call $a(t)$ the *inside part* of $x(t)$ and $b(t)$ the *outside part* of $x(t)$. In view of

$$\sum_{k=1}^{n} \sum_{l=1}^{m} x_{nl}(t)x_{kj}(t) = b(t) \sum_{k=1}^{n} x_{kj}(t)$$

and

$$\sum_{k=1}^{n} \sum_{l=1}^{m} x_{nj}(t)x_{kl}(t) = x_{nj}(t)$$

the summation over the Eqs. (26) for $j = 1, \ldots, m$ yields

$$b(t+1) = \frac{F + E(s, q_t)}{F + E(q_t, q_t)} b(t). \tag{29}$$

Since s is a best reply to p and p is not a best reply to p, we have

$$E(s, p) > E(p, p).$$

Therefore, we can find an $\varepsilon > 0$ such that $E(s, q) > E(p, q)$ holds for all q with $|p - q| < \varepsilon$. Consider a population state $x(0)$ with $b(0) > 0$ in the ε − neighborhood of p. We examine the process (23) starting at $x(0)$. In view of the continuity of $E(\cdot, \cdot)$ we can find a constant $g > 0$ such that

$$\frac{F + E(s, q_t)}{F + E(q_t, q_t)} > 1 + g$$

holds for $|q_t - p| < \varepsilon$. Therefore eventually q_t must leave the ε − neighborhood of p. This shows that for the ε under consideration no δ can be found which satisfies the requirement of Definition 5. $\square$

The inside genotype strategy array $U = (u_{ijkl})$ with

$$u_{ijkl} = p, \quad \text{for } i, k = 1, \ldots, n-1, \quad j, l = 1, \ldots, m$$

is called the *strategic monomorphism* or shortly the *monomorphism* of p. A monomorphism U of a strategy p for $G = (S, E)$ is called *externally stable* if every inside population state y is externally stable with respect to G and U.

If only one allele is present on each locus one speaks of *fixation*. A monomorphism in our sense permits many alleles at each locus. The distinction is important since in the case of a monomorphism the entrance of a mutant may create a multitude of new genotypes with different strategies and not just two as in the case of fixation. Maynard Smith (1989) has pointed out that in the case of fixation the ESS-property is necessary and sufficient for external stability against mutants which are either recessive or dominant. The entrance of a mutant at fixation is in essence a one-locus problem. Contrary to this the entrance of a mutant at a monomorphism in a two-locus model cannot be reduced to a one-locus problem.

Result 15.   Let p be a pure or mixed strategy of $G = (S, E)$. The monomorphism of p is externally stable if and only if p is an ESS of G.

Proof.   Consider a specification (G, U, U_n) of (23), where U is the monomorphism of p. Let $x(0)$, $x(1), \ldots$ be a sequence satisfying (23) for this specification. Let the inside part $a(t)$ and the outside part $b(t)$ be defined as in (27) and (28). A genotype $A_i B_j / A_k B_l$ is called *monomorphic* if we have $i < n$ and $k < n$. The joint relative frequency of all monomorphic genotypes at time t is $a^2(t)$. A genotype $A_i B_j / A_k B_l$ is called a *mutant heterozygote* if we have $i = n$ and $k < n$ or $i < n$ and $k = n$. A genotype $A_i B_j / A_k B_l$ is called a *mutant homozygote* if $i = k = n$ holds.

At time t the three classes of monomorphic genotypes, mutant heterozygotes, and mutant homozygotes have the relative frequencies $a^2(t)$, $2a(t)b(t)$, and $b^2(t)$, respectively. It is useful to look at the average strategies of the three classes. The average strategy of the monomorphic genotype is p. The average strategies u_t of the mutant heterozygotes and v_t of the mutant homozygotes are as follows:

$$u_t = \frac{1}{a(t)b(t)} \sum_{j=1}^{m} \sum_{k=1}^{n-1} \sum_{l=1}^{m} x_{nj}(t) x_{kl}(t) u_{njkl}, \tag{30}$$

$$v_t = \frac{1}{b^2(t)} \sum_{j=1}^{m} \sum_{l=1}^{m} x_{nj}(t) x_{nl}(t) u_{njnl}. \tag{31}$$

The alleles $A_1, \ldots, A_{n-1}$ are called *monomorphic*. We now look at the average strategy α_t of all monomorphic alleles and the average strategy β_t of the mutant allele A_n at time t.

$$\alpha_t = a(t)p + b(t)u_t, \tag{32}$$

$$\beta_t = a(t)u_t + b(t)v_t. \tag{33}$$

A monomorphic allele has the relative frequency $a(t)$ of being in a monomorphic genotype and the relative frequency $b(t)$ of being in a mutant heterozygote. Similarly, the mutant is in a mutant heterozygote with relative frequency $a(t)$ and in a mutant homozygote with frequency $b(t)$. The mean strategy q_t of the population satisfies the following equations:

$$q_t = a(t)\alpha_t + b(t)\beta_t, \tag{34}$$

$$q_t = a^2(t)p + 2a(t)b(t)u_t + b^2(t)v_t. \tag{35}$$

We now look at the relationship between $a(t)$ and $a(t+1)$. Equation (23) yields:

$$a(t+1) = \frac{F + E(p, q_t)}{F + E(q_t, q_t)} \sum_{i=1}^{n-1} \sum_{j=1}^{m} \sum_{k=1}^{n-1} \sum_{l=1}^{m} [r x_{il}(t) x_{kj}(t) + (1-r) x_{ij}(t) x_{kl}(t)]$$

$$+ \frac{1}{F + E(q_t, q_t)} \sum_{i=1}^{n-1} \sum_{j=1}^{m} \sum_{l=1}^{m} r[F + E(u_{ilnj}, q_t)] x_{il}(t) x_{nj}(t)$$

$$+ \frac{1}{F + E(q_t, q_t)} \sum_{i=1}^{n-1} \sum_{j=1}^{m} \sum_{l=1}^{m} (1-r)[F + E(u_{ijnl}, q_t)] x_{ij}(t) x_{nl}(t).$$

It can be seen without difficulty that this is equivalent to the following equation:

$$a(t+1) = \frac{1}{F + E(q_t, q_t)} \{a^2(t)[F + E(p, q_t)] + a(t)b(t)[F + E(u_t, q_t)]\}.$$

In view of the definition of α_t this yields

$$a(t+1) = \frac{F + E(\alpha_t, q_t)}{F + E(q_t, q_t)} a(t).$$

It follows by (34) that we have

$$\frac{F + E(\alpha_t, q_t)}{F + E(q_t, q_t)} = 1 + \frac{E(\alpha_t, q_t) - E(q_t, q_t)}{F + E(q_t, q_t)}$$

$$= 1 + \frac{b(t)E(\alpha_t, q_t) - b(t)E(\beta_t, q_t)}{F + E(q_t, q_t)}.$$

This yields (36). With the help of $a(t) + b(t) = 1$ we obtain a similar equation for $b(t)$.

$$a(t+1) = \left(1 + b(t)\frac{E(\alpha_t, q_t) - E(\beta_t, q_t)}{F + E(q_t, q_t)}\right) a(t), \tag{36}$$

$$b(t+1) = \left(1 + a(t)\frac{E(\beta_t, q_t) - E(\alpha_t, q_t)}{F + E(q_t, q_t)}\right) b(t). \tag{37}$$

Obviously, the difference $E(\alpha_t, q_t) - E(\beta_t, q_t)$ is decisive for the movement of $a(t)$ and $b(t)$. We now shall investigate this difference. For the sake of simplicity we

drop t in $u_t, v_t, \alpha_t, \beta_t, q_t, a(t)$ and $b(t)$. It can be easily verified that the following is true:

$$\begin{aligned}
E(\alpha, q) - E(\beta, q) = {} & a^3[E(p, p) - E(u, p)] \\
& + a^2 b\{2[E(p, u) - E(u, u)] + E(u, p) - E(v, p)\} \\
& + ab^2\{2[E(u, u) - E(v, u)] + E(p, v) - E(u, v)\} \\
& + b^3[E(u, v) - E(v, v)].
\end{aligned} \tag{38}$$

We now prove the following *assertion*: If p is an ESS of G and $u \neq p$ or $v \neq p$ holds, then $E(\alpha, q) - E(\beta, q)$ is positive for all sufficiently small $b > 0$. – It is convenient to distinguish four cases:

(i) u is not a best reply to p. Then the first term in (38) is positive.

(ii) u is a best reply to p with $u \neq p$. Then the first term in (38) is zero and the second one is positive.

(iii) $u = p$ and v is not a best reply to p. Here, too the first term in (38) is zero and the second one is positive.

(iv) $u = p$ and v is a best reply to p. We must have $v \neq p$. The first three terms vanish and the fourth one is positive.

The discussion has shown that in all four cases $E(\alpha, q) - E(\beta, q)$ is positive for sufficiently small $b > 0$.

In the case $u = v = p$ we have $\alpha = \beta$. In this case the difference $E(\alpha, q) - E(\beta, q)$ vanishes. Consider a sequence $x(0), x(1), \ldots$ generated by the dynamic system. Assume that p is an ESS. If $b(0)$ is sufficiently small, then $b(t)$ is nonincreasing. The sequence of population mean strategies $q_0, q_1, \ldots$ generated by $x(0)$ remains in an ε-neighborhood of p with $\varepsilon > b(0)$. The sequence $q_0, q_1, \ldots$ must have an accumulation point q. Assume that q is different from p. In view of the continuity of (23) this is impossible, since for q_t sufficiently near to q the inside part $b(t)$ would have to decrease beyond the inside part b of q. Therefore, the sequence $q_0, q_1, \ldots$ converges to p. We have shown that every inside population state is externally stable if p is an ESS.

It remains to show that p is not externally stable if it is not an ESS. In view of Result 14 we can assume that p is a symmetric equilibrium strategy, but not an ESS. Let v be a best reply to p with

$$E(p, v) \leqslant E(v, v).$$

Since p is a symmetric equilibrium strategy, but not an ESS, such a strategy can be found. We look at the specification (G, U, U_n) with the following outside array:

$$u_{njkl} = p, \quad \text{for } j, l = 1, \ldots, m \text{ and } k = 1, \ldots, n - 1,$$
$$u_{njnl} = v, \quad \text{for } j, l = 1, \ldots, m.$$

Consider a sequence $x(0), x(1), \ldots$ generated by the dynamic system. The mean strategies u_t and v_t do not depend on t. We always have $u_t = p$ and $v_t = v$. Assume $E(p, v) < E(v, v)$. In this case (38) shows that $E(\alpha_t, q_t) - E(\beta_t, q_t)$ is always negative.

In view of the continuity of (23) the sequence of the $b(t)$ always converges to 1 for $b(0) > 0$. In the case $E(p, v) = E(v, v)$ the difference $E(\alpha_t, q_t) - E(\beta_t, q_t)$ always vanishes and we have

$$q_t = [1 - b^2(0)]p + b^2(0)v, \quad \text{for } t = 0, 1, \dots.$$

In both cases the sequence $q_0, q_1, \dots$ of the population mean strategies does not converge to p, whenever $b(0) > 0$ holds. Therefore, p is not externally stable. □ □

The proof of 14 reveals additional stability properties of a monomorphism whose phenotype is an ESS p. Consider a specification (G, U, U_n) of (23) and let U be the monomorphism of genotype p. We say that a population state c is *nearer* to the monomorphism U than a population state x' or that x' is *farther* from U than x if the outside part b of x is smaller than the outside part b' of x'. We say that a population state x is *shifted* towards the monomorphism if for every sequence $x(0), x(1), \dots$ generated by (23) starting with $x(0) = x$ every $x(t)$ with $t = 1, 2, \dots$ is nearer to the monomorphism than x; if for $x(0) = x$ every $x(t)$ with $t = 1, 2, \dots$ is not farther away from the monomorphism than x we say that x is not *shifted away* from the monomorphism. An ε-neighborhood N_ε of an inside state y is called *drift resistant* if all population states $x \in N_\varepsilon$ with a population mean strategy different from p are shifted towards the monomorphism and no population state $x \in N_\varepsilon$ is shifted away from the monomorphism. An inside state y is called *drift resistant* if for some $\varepsilon > 0$ the ε-neighborhood N_ε of y is drift resistant. The monomorphism U is *drift resistant* if for every U_n every inside state y is drift resistant in (G, U, U_n).

Result 16. Let p be an ESS of G. Then the monomorphism U of phenotype p is drift resistant.

Proof. As we have seen in the proof of Result 15 the dynamics of (23) leads to Eq. (37) which together with (38) has the consequence that a population state x with a sufficiently small outside part b is not shifted farther away from the monomorphism and is shifted towards the monomorphism if its population mean strategy is different from p. □

Water resistant watches are not water proof. Similarly drift resistance does not offer an absolute protection against drift. A sequence of perturbances away from the monomorphism may lead to a population state outside the drift resistant ε-neighborhood. However, if perturbances are small relative to ε, this is improbable and it is highly probable that repeated perturbances will drive the mutant allele towards extinction. Of course, this is not true for the special case in which all genotypes carrying the mutant allele play the monomorphic ESS p. In this case the entrance of the mutant creates a new monomorphism, with one additional allele, which again will be drift resistant.

6. Asymmetric conflicts

Many conflicts modelled by biologists are asymmetric. For example, one may think of territorial conflicts where one of two animals is identified as the territory owner and the other one as the intruder (see Section 8.2). Other examples arise if the opponents differ in strength, sex, or age. Since a strategy is thought of as a program for all situations which may arise in the life of a random animal, it determines behavior for both sides of an asymmetric conflict. Therefore, in evolutionary game theory asymmetric conflicts are imbedded in symmetric games.

In the following we shall describe a class of models for asymmetric conflicts. Essentially the same class has first been examined by Selten (1980). In the models of this class the animals may have incomplete information about the conflict situation. We assume that an animal can find itself in a finite number of *states of information*. The set of all states of information is denoted by U. We also refer to the elements of U as *roles*. This use of the word role is based on applications in the biological literature on animal contests. As an example we may think of a strong intruder who faces a territory owner who may be strong or weak. On the one hand, the situation of the animal may be described as the role of a strong intruder and, on the other hand, it may be looked upon as the state of information in this role.

In each role u an animal has a nonempty, finite set C_u of choices. A *conflict situation* is a pair (u, v) of roles with the interpretation that one animal is in the role u, and the other in the role v. The game starts with a random move which selects a conflict situation (u, v) with probability w_{uv}. Then the players make their choices from the choice sets C_u and C_v respectively. Finally they receive a payoff which depends on the choices and the conflict situation. Consider a conflict situation (u, v) and let c_u and c_v be the choices of two opponents in the roles u and v respectively; under these conditions $h_{uv}(c_u, c_v)$ denotes the payoffs obtained by the player in the role u; for reasons of symmetry, the payoff of the player in the role of v is $h_{vu}(c_v, c_u)$.

We define an asymmetric conflict as a quadruple

$$M = (U, C, w, h). \tag{39}$$

Here, U, the *set of information states or roles*, is a nonempty finite set; C, the *choice set function*, assigns a nonempty finite choice set C_u to every information state u in U; the *basic distribution*, w, assigns a probability w_{uv} to every conflict situation (u, v); finally, h, the *payoff function*, assigns a payoff $h_{uv}(c_u, c_v)$ to every conflict situation (u, v) with $w_{uv} > 0$ together with two choices c_u in C_u and c_v in C_v. The probabilities w_{uv} sum up to 1 and have the symmetry property

$$w_{uv} = w_{vu}.$$

Formally the description of a model of type (39) is now complete. However, we would like to add that one may think of the payoffs of both opponents in a conflict

situation (u, v) as a bimatrix game. Formally, it is not necessary to make this picture explicit, since the payoff for the role v in the conflict situation (u, v) is determined by h_{vu}.

A *pure strategy* s for a model of the type (39) is a function which assigns a choice c_u in C_u to every u in U. Let S be the set of all pure strategies.

From here we could directly proceed to the definition of a symmetric two-person game (S, E) based on the model. However, this approach meets serious difficulties. In order to explain these difficulties we look at an example.

Example. We consider a model with only two roles u and v, and $w_{uu} = w_{vv} = \frac{1}{2}$ and $C_u = C_v = \{H, D\}$. The payoff functions h_{uu} and h_{vv} are payoffs for Hawk–Dove games (see Figure 1) with different parameters W. We may think of (u, u) and (v, v) as different environmental conditions like rain and sunshine which influence the parameter W. The pure strategies for the game $G = (S, E)$ are HH, HD, DH, and DD, where the first symbol stands for the choice in u and the second symbol for the choice in v. Let p_1 be the ESS for the Hawk–Dove game played at (u, u) and p_2 be the ESS of the Hawk–Dove game played at (v, v). We assume that p_1 and p_2 are genuinely mixed. The obvious candidate for an ESS in this model is to play p_1 at u and p_2 at v. This behavior is realized by all mixed strategies q for G which satisfy the following equations:

$$q(HH) + q(HD) = p_1(H),$$

$$q(HH) + q(DH) = p_2(H).$$

It can be seen immediately that infinitely many mixed strategies q satisfy these equations. Therefore, no q of this kind can be an ESS of G, since all other strategies satisfying the two equations are alternative best replies which violate the stability condition (b) in the Definition 1 of evolutionary stability. Contrary to common sense the game G has no ESS.

The example shows that the description of behavior by mixed strategies introduces a spurious multiplicity of strategies. It is necessary to avoid this multiplicity. The concept of a behavior strategy achieves this purpose.

A *behavior strategy* b for a model of the type (39) assigns a probability distribution over the choice set C_u of u to every role u in U. A probability distribution over C_u is called a *local strategy* at u. The probability assigned b to a choice c in C_u is denoted by $b(c)$. The symbol B is used for the set of all behavior strategies b.

We now define an expected payoff $E(b, b')$ for every pair (b, b') of behavior strategies:

$$E(b, b') = \sum_{(u,v)} w_{uv} \sum_{c \in C_u} \sum_{c' \in C_v} b(c) b'(c') h_{uv}(c, c'). \tag{40}$$

The first summation is extended over all pairs (u, v) with $w_{uv} > 0$. The payoff $E(b, b')$ has the interpretation of the expected payoff of an individual who plays b in a

population playing b'. We call

$$G_M = (B, E)$$

the *population game associated with* $M = (U, C, w, h)$.

$E(b, b')$ is a bilinear function of the probabilities $b(c)$ and $b'(c')$ assigned by the behavior strategies b and b' to choices. Therefore, the definition of evolutionary stability by two conditions analogous to those of Definition 1 is adequate. In the case of a bilinear payoff function E Definitions 1 and 3 are equivalent. A behavior strategy b is a best reply to a behavior strategy b' if it maximizes $E(\cdot, b')$ over B. A behavior strategy b^* for G_M is *evolutionarily stable* if the following conditions (a) and (b) are satisfied:

(a) *Equilibrium condition*: b^* is a best reply to b^*.

(b) *Stability condition*: Every best reply b to b^* which is different from b^* satisfies the following inequality:

$$E(b^*, b) > E(b, b) \tag{41}$$

An evolutionarily stable strategy b^* is called *strict* if b^* is the only best reply to b^*. It is clear that in this case b^* must be a pure strategy.

In many applications it never happens that two animals in the same role meet in a conflict situation. For example, in a territorial conflict between an intruder and a territory owner the roles of both opponents are always different, regardless of what other characteristics may enter the definition of a role. We say that $M(U, C, w, h)$ satisfies the condition of *role asymmetry* [information asymmetry in Selten (1980)] if the following is true:

$$w_{uu} = 0, \quad \text{for all } u \text{ in } U. \tag{42}$$

The following consequence of role asymmetry has been shown by Selten (1980).

Result 17. Let M be a model of the type (39) with role asymmetry and let $G_M = (B, E)$ be the associated population game. If b^* is an evolutionarily stable strategy for G_M, then b^* is a pure strategy and a strict ESS.

Sketch of the proof. If an alternative best reply is available, then one can find an alternative best reply b which deviates from b^* only in one role u_1. For this best reply b we have $E(b, b^*) = E(b^*, b^*)$. This is due to the fact that in a conflict situation (u_1, v) we have $u_1 \neq v$ in view of the role asymmetry assumption. Therefore, it never matters for a player of b whether an opponent plays b or b^*. The equality of $E(b, b^*)$ and $E(b^*, b^*)$ violates the stability condition (41). Therefore, the existence of an alternative best reply to b^* is excluded.

If the role asymmetry condition is not satisfied, an ESS can be genuinely mixed. This happens in the example given above. There the obvious candidate for an ESS corresponds to an ESS in G_M. This ESS is the behavior strategy which assigns the local strategies p_1 and p_2 to u and v, respectively.

A special case of the class of models of the type (39) has been examined by Hammerstein (1981). He considered a set U of the form

$$U = (u_1, \ldots, u_n, v_1, \ldots, v_n)$$

and a basic distribution w with $w(u, v) > 0$ for $u = u_i$ and $v = v_i$ $(i = 1, \ldots, n)$ and $w(u, v) = 0$ for $u = u_i$ and $v = v_j$ with $i \neq j$. In this case an evolutionarily stable strategy induces strict pure equilibrium points on the n bimatrix games played in the conflict situations (u_i, v_i). In view of this fact it is justified to speak of a strict pure equilibrium point of an asymmetric bimatrix game as an evolutionarily stable strategy. One often finds this language used in the biological literature. The simplest example is the Hawk–Dove game of Figure 1 with the two roles "owner" and "intruder".

7. Extensive two-person games

Many animal conflicts have a sequential structure. For example, a contest may be structured as a sequence of a number of bouts. In order to describe complex sequential interactions one needs extensive games. It is not possible to replace the extensive game by its normal form in the search for evolutionarily stable strategies. As in the asymmetric animal conflicts in Section 6, the normal form usually has no genuinely mixed ESS, since infinitely many strategies correspond to the same behavior strategy. It may be possible to work with something akin to the agent normal form, but the extensive form has the advantage of easily identifiable substructures, such as subgames and truncations, which permit decompositions in the analysis of the game.

7.1. Extensive games

In this section we shall assume that the reader is familiar with basic definitions concerning games in extensive form. The results presented here have been derived by Selten (1983, 1988). Unfortunately, the first paper by Selten (1983) contains a serious mistake which invalidates several results concerning sufficient conditions for evolutionary stability in extensive two-person games. New sufficient conditions have been derived in Selten (1968).

Notation. The word *extensive game* will always refer to a finite two-person game with perfect recall. Moreover, it will be assumed that there are at least two choices at every information set. A game of this kind is described by a septuple

$$\Gamma = (K, P, U, C, p, h, h').$$

K is the *game tree*. The set of all endpoints of K is denoted by Z.

$P = (P_0, P_1, P_2)$ is the *player partition* which partitions the set of all decision points into a random decision set P_0 and decision sets P_1 and P_2 for players 1 and 2.

U is the *information partition*, a refinement of the player partition.

C is the *choice partition*, a partition of the set of alternatives (edges of the tree) into choices at information sets u in U. The set of all random choices is denoted by C_0. For $i = 1, 2$ the set of all choices for player i is denoted by C_i. The choice set at an information set u is denoted by C_u. The set of all choices on a play to an endpoint set is denoted by $C(z)$.

p is the *probability assignment* which assigns probabilities to random choices.

h and h' are the *payoff functions* of players 1 and 2, respectively which assign payoffs $h(z)$ and $h'(z)$ to endpoints z.

For every pair of behavior strategies (b, b') the associated payoffs for players 1 and 2 are denoted by $E(b, b')$ and $E'(b, b')$, respectively.

No other strategies than behavior strategies are admissible. Terms such as *best reply*, *equilibrium point*, etc. must be understood in this way. The probability assigned to a choice c by a behavior strategy b is denoted by $b(c)$.

We say that an information set u of player 1 is *blocked* by a behavior strategy b' of player 2 if u cannot be reached if b' is played. In games with perfect recall the probability distribution over vertices in an information set u of player 1 if u is reached depends only on the strategy b' of player 2. On this basis a *local payoff* $E_u(r_u, b, b')$ for a local strategy r_u at u if b and b' are played can be defined for every information set u of player 1 which is not blocked by b'. The local payoff is computed starting with the probability distribution over the vertices of u determined by b' under the assumption that at u the local strategy r_u is used and later b and b' are played.

A local *best reply* b_u at an information set u of player 1 to a pair of behavior strategies (b, b') such that u is not blocked by b' is a local strategy at u which maximizes player 1's local payoff $E_u(r_u, b, b')$. We say that b_u is a *strict local best reply* if b_u is the only best reply to (b, b') at u. In this case b_u must be a pure local strategy, or in other words a choice c at u.

7.2. Symmetric extensive games

Due to structural properties of game trees, extensive games with an inherent symmetry cannot be represented symmetrically by an extensive form. Thus two simultaneous choices have to be represented sequentially. One has to define what is meant by a symmetric two-person game.

Definition 6. A *symmetry* f of an extensive game $\Gamma = (K, P, U, C, p, h, h')$ is a mapping from the choice set C onto itself with the following properties (a)–(f):

(a) If $c \in C_0$, then $f(c) \in C_0$ and $p(f(c)) = p(c)$.

(b) If $c \in C_1$ then $f(c) \in C_2$.

(c) $f(f(c)) = c$ for every $c \in C$.

(d) For every $u \in U$ there is a $u' \in U$ such that for every choice c at u, the image $f(c)$ is a choice at u'. The notation $f(u)$ is used for this information set u'.

(e) For every endpoint $z \in Z$ there is a $z' \in Z$ with $f(C(z)) = C(z')$, where $f(C(z))$ is the set of all images of choices in $C(z)$. The notation $f(z)$ is used for this endpoint z'.

(f) $h(f(z)) = h'(z)$ and $h'(f(z)) = h(z)$.

A symmetry f induces a one-to-one mapping from the behavior strategies of player 1 onto the behavior strategies of player 2 and vice versa:

$$b' = f(b), \quad \text{if } b'(f(c)) = b(c), \quad \text{for every } c \in C_1,$$
$$b = f(b'), \quad \text{if } b' = f(b).$$

An extensive game may have more than one symmetry. In order to see this, consider a game Γ with a symmetry f. Let Γ_1 and Γ_2 be two copies of Γ, and let f_1 and f_2 be the symmetries corresponding to f in Γ_1 and Γ_2, respectively. Let Γ_3 be the game which begins with a random move which chooses one of both games Γ_1 and Γ_2 both with probability $\frac{1}{2}$. One symmetry of Γ_3 is composed of f_1 and f_2, and a second one maps a choice c_1 in Γ_1 on a choice c_2 in Γ_2 which corresponds to the same choice c in Γ as c_1 does.

In biological aplications there is always a natural symmetry inherent in the description of the situation. "Attack" corresponds to "attack", and "flee" corresponds
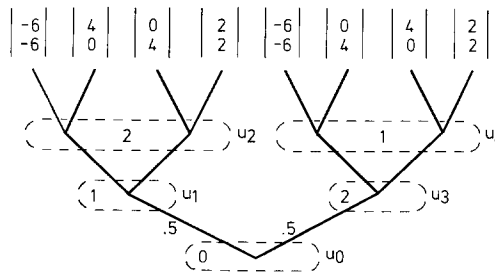
Figure 2. Example of a game with two symmetries. This game starts with a random move after which players 1 and 2 find themselves in a Hawk–Dove contest. Their left choices mean to play Hawk, right choices mean to play Dove. The initial random move can be *distinguishing* or *neutral* in the following sense. Suppose that the left random choice determines player 1 as the original owner of a disputed territory and the right random choice determines player 2 as the original owner. In this case the random move distinguishes the players so that they can make their behavior dependent on the roles "owner" and "intruder". On the other hand, suppose that the random move determines whether there is sunshine (left) or an overcast sky (right). This is the neutral case where nothing distinguishes player 1 and player 2. The two possible symmetries of this game specify whether the random move is distinguishing or neutral. If the symmetry maps the information set u_1 to u_3, it is distinguishing. If it maps u_1 to u_2, it is neutral [Selten (1983)].

to "flee" even if a formal symmetry may be possible which maps "attack" to "flee". Therefore, the description of the natural symmetry must be added to the extensive form in the evolutionary context (see Figure 2).

Definition 7. A *symmetric extensive game* is a pair (Γ, f), where Γ is an extensive game and f is a symmetry of Γ.

7.3. Evolutionary stability

A definition of evolutionary stability suggests itself which is the analogue of Definition 1. As we shall see later, this definition is much too restrictive and will have to be refined. Since it is the direct analogue of the usual ESS definition we call it a direct ESS.

Definition 8. Let (Γ, f) be a symmetric extensive game. A *direct ESS* for (Γ, f) is a behavior strategy b^* for player 1 in Γ with the following two properties (a) and (b):

(a) *Equilibrium condition*: $(b^*, f(b^*))$ is an equilibrium point of Γ.

(b) *Stability condition*: If b is a best reply to $f(b^*)$ which is different from b^*, then we have

$$E(b^*, f(b)) > E(b, f(b)).$$

A behavior strategy b^* which satisfies (a) but not necessarily (b) is called a *symmetric equilibrium strategy*. An equilibrium point of the form $(b^*, f(b^*))$ is called a *symmetric equilibrium point*.

The definition of a direct ESS b^* is very restrictive, since it implies that every information set u of Γ must be reached with positive probability by the equilibrium path generated by $(b^*, f(b^*))$ [Selten (1983) Lemma 2 and Theorem 2, p. 309]. This means that most biological extensive form models can be expected to have no direct ESS. Nevertheless, the concept of evolutionary stability can be defined in a reasonable way for extensive two-person games.

Since every information set is reached with positive probability by $(b^*, f(b^*))$, no information set u of player 1 is blocked by $f(b^*)$. Therefore, a local payoff $E_u(r_u, b^*, f(b^*))$ is defined at all information sets u of player 1 if b^* is a direct ESS of (Γ, f). We say that a direct ESS b^* is *regular* if at every information set u of player 1 the local strategy b_u^* assigned by b^* to u chooses every pure local best reply at u with positive probability.

The definition of perfectness [Selten (1975)] was based on the idea of mistakes which occur with small probabilities in the execution of a strategy. In the biological context it is very natural to expect such mistakes; rationality is not assumed and genetic programs are bound to fail occasionally for physiological reasons if no

others. Therefore, it is justified to transfer the trembling hand approach to the definition of evolutionary stability in extensive games. However, in contrast to the definition of perfectness, it is here not required that every choice must be taken with a small positive probability in a perturbed game. The definition of a perturbed game used here permits zero probabilities for some or all choices. Therefore, the game itself is one of its perturbed games.

A *perturbance* α for (Γ, f) is a function which assigns a minimum probability $\alpha_c \geqslant 0$ to every choice c of player 1 and 2 in Γ such that (a) the choices at an information set u sum to less than 1 and (b) the equation $\alpha_c = \alpha_d$ always holds for $d = f(c)$. A *perturbed game* of (Γ, f) is a triple $\Gamma' = (\Gamma, f, \alpha)$ in which α is a perturbance for (Γ, f). In the perturbed game Γ' only those behavior strategies are admissible which respect the minimum probabilities of α in the sense $b(c) \geqslant \alpha_c$. Best replies in Γ' are maximizers of $E(\cdot, b')$ or $E(b, \cdot)$ within these constraints. The definition of a *direct ESS* for Γ' is analogous to Definition 6. A *regular direct ESS* of a perturbed game is also defined analogously to a regular direct ESS of the unperturbed game.

The maximum of all minimum probabilities assigned to choices by a perturbance α is denoted by $|\alpha|$. If b and b^* are two behavior strategies, then $|b - b^*|$ denotes the maximum of the absolute difference between the probabilities assigned by b and b^* to the same choice. With the help of these auxiliary definitions we can now give the definition of a (regular) limit ESS.

Definition 9. A behavior strategy b^* of player 1 for a symmetric extensive two-person game (Γ, f) is a (*regular*) *limit ESS* of (Γ, f) if for every $\varepsilon > 0$ at least one perturbed game $\Gamma' = (\Gamma, f, \alpha)$ with $|\alpha| < \varepsilon$ has a (regular) direct ESS b with $|b - b^*| < \varepsilon$.

Loosely speaking, a limit ESS b^* is a strategy which can be arbitrarily closely approximated by a direct ESS of a perturbed game. For a biological game model this means that in a slightly changed game model with small mistake probabilities for some choices a direct ESS close to b^* can be found.

Since the special case of a perturbance $\alpha_c = 0$ for all choices c of players 1 and 2 is not excluded by the definition of a perturbed game, a direct ESS is always a limit ESS.

7.4. Image confrontation and detachment

In the following we shall state a result which can be looked upon as the analogue of Result 17 for symmetric extensive games. Let (Γ, f) be a symmetric extensive game. We say that an information set u in Γ is *image confronted* if at least one play in Γ intersects both u and $f(u)$; otherwise u is called *image detached*. The following result can be found in Selten (1983):

Result 18.   Let b^* be a limit ESS for a symmetric extensive game (Γ, f). Then the following is true:

(a) The pair $(b^*, f(b^*))$ is an equilibrium point of (Γ, f).
(b) If u is an image detached information set in (Γ, f), then the local strategy b_u^* is pure, or in other words $b(c) = 1$ holds for one choice c at u.

Result 18 narrows down the search for ESS candidates. In many models most information sets are image detached, since the opponents in a sequential conflict who are initially indistinguishable may quickly become distinguishable by the history of the game. Thus one of both animals may be identifiable as that one which attacked first; thereby all later information sets become image detached.

7.5.   Decomposition

In the determination of subgame perfect equilibrium points one can replace a subgame by the payoff vector for one of its equilibrium points and then determine an equilibrium point of the truncation formed in this way. The equilibrium points of the subgame and the truncation together form an equilibrium point of the whole game. Unfortunately, a direct ESS or a limit ESS does not have the same decomposition properties as a subgame perfect equilibrium point. A direct ESS or a limit ESS cannot be characterized by purely local conditions. Counterexamples can be found in the literature (van Damme 1987, Selten 1988). Nevertheless, a limit ESS does have some decomposition properties which are useful in the analysis of extensive game models. In order to describe these decomposition properties we now introduce the definitions of an "upper layer" and an "abridgement".

We say that an information set v *preceeds* an information set u if at least one play intersects both information sets and if on every play which intersects both information sets the vertex in v comes before the vertex in u. An *upper layer* of a symmetric extensive two-person game (Γ, f) is a nonempty subset V of the set of all information sets U in Γ which satisfies the following conditions (i) and (ii):

(i) If $v \in V$ then $f(v) \in V$
(ii) If $v \in V$ preceeds $u \in U$ then $u \in V$.

An information set v in an upper layer V is called a starting set in V if no other information sets $u \in V$ preceed v. The vertices of starting sets in V are called starting points in V.

Let V be an upper layer of (Γ, f). For every strategy b of player 1 for Γ we construct a new symmetric two-person game called the *b-abridgement* of (Γ, f) with respect to V. The b-abridgement is a game (Γ_*, f_*) constructed as follows. All vertices and edges after the starting point of V are removed from the game tree. The starting points of V become end points. The payoffs at a starting point

x are the conditional payoff expectations in the original game if x is reached and b and $f(b)$ are played later on. The other specifications of (Γ_*, f_*) are obtained as restrictions of the corresponding specifications of (Γ, f) to the new game tree.

A strategy b of player 1 for (Γ, f) is called *quasi-strict* at an information set u if a number $\varepsilon > 0$ exists for which the following is true: If r is a strategy in the ε-neighborhood of b and if $f(r)$ does not block u, then the local strategy b_u which b assigns to u is a strong local best reply to r and $f(r)$ in Γ.

Obviously, b is quasi-strict at u if b_u is a strict best reply. Moreover, if b is quasi-strict at u, then b_u is a pure local strategy, or in other words a choice at u.

The following result is the Theorem 4 in Selten (1988).

Result 19. Let (Γ, f) be a symmetric extensive two-person game, let b be a strategy of player 1 for Γ and let V be an upper layer of (Γ, f). Moreover, let (Γ_*, f_*) be the b-abridgement of (Γ, f) with respect to V. Then b is a regular limit ESS of (Γ, f) if the following two conditions (i) and (ii) are satisfied:

(i) For every information set v of player 1 which belongs to V the following is true: b is quasi-strict at v in (Γ, f).

(ii) The strategy b_* induced on (Γ_*, f_*) by b is a regular limit ESS of (Γ_*, f_*).

Results 18 and 19 are useful tools for the analysis of evolutionary extensive game models. In many cases most of the information sets are image detached and the image detached information sets form an upper layer. In the beginning two animals involved in a conflict may be indistinguishable, but as soon as something happens which makes them distinguishable by the history of the conflict all later information sets become image detached. A many-period model with ritual fights and escalated conflicts [Selten (1983, 1988)] provides an example. Result 18 helps to find candidates for a regular limit ESS and Result 19 can be used in order to reach the conclusion that a particular candidate is in fact a regular limit ESS. Further necessary conditions concerning decompositions into subgames and truncations can be found in Selten (1983). However, the sufficient conditions stated there in connection to subgame–truncation decompositions are wrong.

8. Biological applications

Evolutionary game theory can be applied to an astonishingly wide range of problems in zoology and botany. Zoological applications deal, for example, with animal fighting, cooperation, communication, coexistence of alternative traits, mating systems, conflict between the sexes, offspring sex ratio, and the distribution of individuals in their habitats. botanical applications deal, for example, with seed dispersal, seed germination, root competition, nectar production, flower size, and sex allocation. In the following we shall briefly review the major applications of evolutionary game theory. It is not our intent to present the formal mathematical

structure of any of the specific models but rather to emphasize the multitude of
new insights biologists have gained from strategic analysis. The biological literature
on evolutionary games is also reviewed in Maynard Smith (1982a), Riechert &
Hammerstein (1983), Parker (1984), Hines (1987), and Vincent & Brown (1988).

8.1. Basic questions about animal contest behavior

Imagine the following general scenario. Two members of the same animal species
are contesting a *resource*, such as food, a territory, or a mating partner. Each
animal would increase its Darwinian fitness by obtaining this resource (the *value
of winning*). The opponents could make use of dangerous weapons, such as horns,
antlers, teeth, or claws. This would have negative effects on fitness (the *cost of
escalation*). In this context behavioral biologists were puzzled by the following
functional questions which have led to the emergence of evolutionary game theory:

Question 1.   Why are animal contests often settled *conventionally*, without resort
to injurious physical escalation; under what conditions can such conventional
behavior evolve?

Question 2.   How are conflicts resolved; what can decide a non-escalated contest?

Classical ethologists attempted to answer Question 1 by pointing out that it
would act against the good of the species if conspecifics injured or killed each
other in a contest. Based on this argument, Lorenz (1966) even talked of "behavioral
analogies to morality" in animals. He postulated the fairly widespread existence
of an innate inhibition which prevents animals from killing or injuring members
of the same species.

However, these classical ideas are neither consistent with the methodological
individualism of modern evolutionary theory, nor are they supported by the facts.
Field studies have revealed the occurrence of fierce fighting and killing in many
animal species when there are high rewards for winning. For example, Wilkinson
and Shank (1977) report that in a Canadian musk ox population 5–10 percent of
the adult bulls may incur lethal injuries from fighting during a single mating season.
Hamilton (1979) describes battlefields of a similar kind for fig wasps, where in
some figs more than half the males died from the consequences of inter-male
combat. Furthermore, physical escalation is not restricted to male behavior. In
the desert spider *Agelenopsis aperta* females often inflict lethal injury on female
opponents when they fight over a territory of very high value [Hammerstein and
Riechert (1988)].

Killing may also occur in situations with moderate or low rewards when it is
cheap for one animal to deal another member of the same species the fatal blow.
For example, in lions and in several primate species males commit infanticide by

killing a nursing-female's offspring from previous mating with another male. This infanticide seems to be in the male's "selfish interest" because it shortens the period of time until the female becomes sexually receptive again (Hausfater and Hrdy 1984).

Another striking phenomenon is that males who compete for access to a mate may literally fight it out on the female's back. This can sometimes lead to the death of the female. In such a case the contesting males destroy the very mating partner they are competing for. This happens, for example, in the common toad [Davies and Halliday (1979)]. During the mating season the males locate themselves near those ponds where females will appear in order to spawn. The sex ratio at a given pond is highly male-biased. When a single male meets a single female he clings to her back as she continues her travel to the spawning site. Often additional males pounce at the pair and a struggle between the males starts on the female's back. Davies & Halliday describe a pond where more than 20 percent of the females carry the heavy load of three to six wrestling males. They also report that this can lead to the death of the female who incurs a risk of being drowned in the pond.

It is possible to unravel this peculiar behavior by looking at it strictly from the individual male's point of view. His individual benefit from interacting with a female would be to fertilize her eggs and thus to father her offspring. If the female gets drowned, there will be no such benefit. However, the same zero benefit from this female will occur if the male completely avoids wrestling in the presence of a competitor. Thus it can pay a male toad to expose the female to a small risk of death.

The overwhelming evidence for intra-specific violence has urged behavioral biologists to relinquish the Lorenzian idea of a widespread "inhibition against killing members of the same species" and of "behavioral analogies to morality". Furthermore, this evidence has largely contributed to the abolishment of the "species welfare paradigm". Modern explanations of contest behavior hinge on the question of how the behavior contributes to the individual's success rather than on how it affects the welfare of the species. These explanations relate the absence or occurrence of fierce fighting to costs and benefits in terms of fitness, and to biological constraints on the animals' strategic possibilities.

We emphasize that the change of paradigm from "species welfare" to "individual success" has paved the way for non-cooperative game theory in biology (Parker and Hammerstein 1985). The *Hawk–Dove* game in Figure 1 (Maynard Smith and Price 1973) should be regarded as the simplest model from which one can deduce that natural selection operating at the individual level may forcefully restrict the amount of aggression among members of the same species, and that this restriction of aggression should break down for a sufficiently high value of winning. In this sense the Hawk–Dove game provides a modern answer to Question 1, but obviously it does not give a realistic picture of true animal fighting.

The evolutionary analysis of the Hawk–Dove game was outlined in Section 3. Note, however, that we confined ourselves to the case where the game is played

between genetically unrelated opponents. Grafen (1979) has analyzed the *Hawk–
Dove game between relatives* (e.g. brothers or sisters). He showed that there are
serious problems with adopting the well known biological concept of "inclusive
fitness" in the context of evolutionary game theory [see also Hines & Maynard
Smith (1979)]. The inclusive fitness concept was introduced by Hamilton (1964)
in order to explain "altruistic behavior" in animals. It has had a major impact on
the early development of sociobiology. Roughly speaking, *inclusive fitness* is a
measure of reproductive success which includes in the calculation of reproductive
output the effects an individual has on the number of offspring of its genetic
relatives. These effects are weighted with a coefficient of relatedness. The inclusive
fitness approach has been applied very successfully to a variety of biological
problems in which no strategic interaction occus.

8.2.   Asymmetric animal contests

We now turn to Question 2 about how conflict is resolved. It is typical for many
animal contests that the opponents will differ in one or more aspect, e.g. size, age,
sex, ownership status, etc. If such an asymmetry is discernible it may be taken as
a cue whereby the contest is conventionally settled. This way of settling a dispute
is analyzed in the theory of asymmetric contests (see Section 6 for the mathematical
background).

It came as a surprise to biologists when Maynard Smith and Parker (1976)
stated the following result about simple contest models with a single asymmetric
aspect. A contest between an "owner" and an "intruder" can be settled by an
evolutionarily stable "owner wins" convention even if ownership does not positively
affect fighting ability or reward for winning (e.g. if ownership simply means prior
presence at the territory). Selten (1980) and Hammerstein (1981) clarified the
game-theoretic nature of this result. Hammerstein extended the idea by Maynard
Smith and Parker to contests with several asymmetric aspects where, for example,
the contest is one between an owner and an intruder who differ in size (strength).
He showed that a *payoff irrelevant* asymmetric aspect may decide a contest even
if from the beginning of the contest another asymmetric aspect is known to both
opponents which is *payoff relevant* and which puts the conventional winner in an
inferior strategic position. For example, if escalation is sufficiently costly, a weaker
owner of a territory may conventionally win against a stronger intruder without
having more to gain from winning.

This contrasts sharply with the views traditionally held in biology. Classical
ethologists either thought they had to invoke a "home bias" in order to explain
successful territorial defense, or they resorted to the well known logical fallacy
that it would be more important to avoid losses (by defending the territory) than
to make returns (by gaining access to the territory). A third classical attempt to
explain the fighting success of territory holders against intruders had been based

on the idea that the owner's previous effort already put into establishing and maintaining the territory would bias the value of winning in the owner's favor and thus create for him a higher incentive to fight. However, in view of evolutionary game theory modern biologists call this use of a "backward logic" the Concorde fallacy and use a "forward logic" instead. The value of winning is now defined as the individual's future benefits from winning.

The theory of asymmetric contests has an astonishingly wide range of applications in different parts of the animal kingdom, ranging from spiders and insects to birds and mammals [Hammerstein (1985)]. Many empirical studies demonstrate that asymmetries are decisive for conventional conflict resolution [e.g. Wilson (1961), Kummer et al. (1974), Davies (1978), Riechert (1978), Yasukawa and Bick (1983), Crespi (1986)]. These studies show that differences in ownership status, size, weight, age, and sex are used as the cues whereby contests are settled without major escalation. Some of the studies also provide evidence that the conventional settlement is based on the logic of deterrence and thus looks more peaceful than it really is (the animal in the winning role is ready to fight). This corresponds nicely to qualitative theoretical results about the structure of evolutionarily stable strategies for the asymmetric contest models mentioned above. More quantitative comparisons between theory and data are desirable, but they involve the intriguing technical problem of measuring game-theoretic payoffs in the field. Biological critics of evolutionary game theory have argued that it seems almost impossible to get empirical access to game-theoretic payoffs [see the open peer commentaries of a survey paper by Maynard Smith (1984)].

Question 3. Is it possible to determine game-theoretic payoffs in the field and to estimate the costs and benefits of fighting?

Despite the pessimistic views of some biologists, there is a positive answer to this question. Hammerstein and Riechert (1988) analyze contests between female territory owners and intruders of the funnel web spider *Agelenopsis aperta*. They use data [e.g. Riechert (1978, 1979, 1984)] from a long-term field study about demography, ecology, and behavior of these desert animals in order to estimate all *game payoffs* as *changes in the expected lifetime number of eggs laid*. Here the matter is complicated by the fact that the games over web sites take place long before eggs will be laid. Subsequent interactions occur, so that a spider who wins today may lose tomorrow against another intruder, and today's loser may win tomorrow against another owner.

In the major study area (a New mexico population), web site tenancy crucially affects survival probability, fighting ability, and the rate at which eggs are produced. The spiders are facing a harsh environment in which web sites are in short supply. Competition for sites causes a great number of territorial interactions. At an average web site which ensures a moderate food supply, a contest usually ends without leading into an injurious fight. For small differences in weight, the
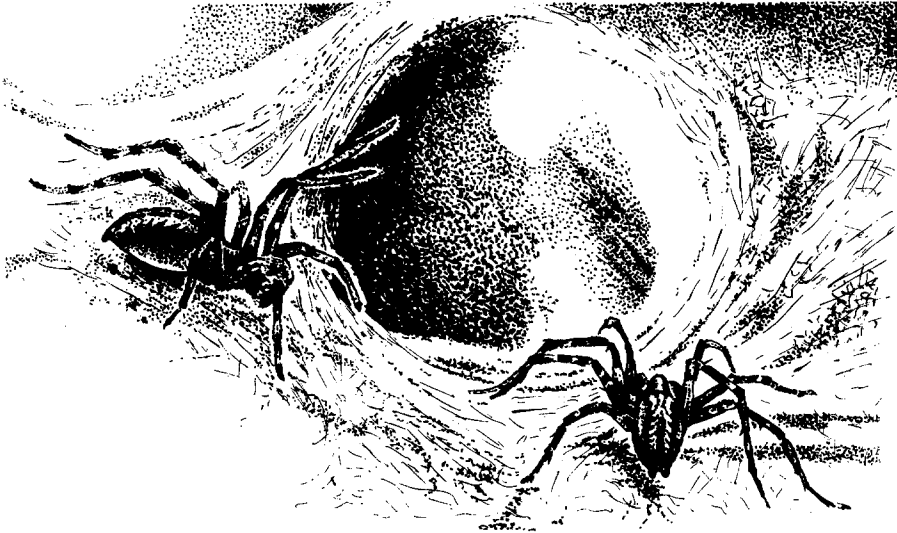
Figure 3. Fighting in the desert spider *Agelenopsis aperta*. The left animal is an intruder who challenges the owner of a territory. The contest takes place on the owner's funnel web. Typically the opponents do not touch each other and keep a minimum distance of approximately one inch. The web is used as a "scale" in order to determine relative body weight. The heavier spider wins conventionally if there is an important weight difference. Otherwise ownership is respected in most cases. (Drawing by D. Schmidl after a photograph by S.E. Riechert.)

owner–intruder asymmetry typically settles the dispute in favor of the owner. For great differences in weight, the weight asymmetry settles it in favor of the heavier spider. Apparently the information about relative weight is revealed when the spiders are shaking the web. This follows from the observation that in most contests the spiders do not even touch each others' bodies, and from the fact that vision is relatively poor in these creatures whose sensory systems are more specialized on dealing with vibratory and chemical information. Experiments with artificial weights glued on the spider's abdomen also support this view.

In order to examine carefully whether we understand the evolutionary logic of fighting in these desert animals it is clearly impotant to deal with Question 3 about measuring payoffs in the field. However, only the immediate consequences of a contest and not the game payoffs can be measured directly. For example, the outcome of a territorial fight between two spiders may be that one of the contestants has lost *two legs* during a vicious biting match, and that the opponent has gained the territory which yields a daily energy intake of *72 joule* per day. Here, we are dealing with very different currencies: how do joules compare to leg amputations?

The currency problem can be solved by converting legs and joules into the leading currency of evolutionary biology, i.e. fitness. This requires numerical simulations of future life histories for healthy and injured spiders with different

starting conditions. In the study by Hammerstein and Riechert these simulations are based on data from 15 years of desert field work. The results are used to calculate, for example, the value of winning as the difference in expected future egg mass between a healthy owner and a healthy wanderer. The wanderer's expected egg mass can be interpreted as a biological *opportunity cost*.

A glance at the outcome of these calculation reveals an interesting aspect of this spider society. The estimated benefit of winning is 20 mg for an average site and 72 mg for an excellent site. These values differ by a factor of more than 3. In contrast, the immediate benefits in terms of daily weight gain are not even twice as good for excellent sites (5.1 versus 7.9 mg). This "multiplier effect" can be explained as follows. An individual who occupies an excellent site gains weight at a rate which is near the maximum for this population. As a result, an individual's weight relative to the population mean will increase as long as it inhabits the excellent site. This is important for remaining in possession of the site because weight counts in territorial defense. Therefore, an originally "richer" spider will have better future chances of maintaining its wealth than an otherwise equal "poorer" individual. This anthropomorphic feature of the spider society explains the multiplier effect.

The negative consequences of fighting can be calculated on the same scale as the value of winning (egg mass). Leg loss costs 13 mg and death costs 102 mg in the New Mexico population. Furthermore, the risk of injury is known for escalated fights. Using these data it can be shown that intruders would pay a high price for "breaking the rules" of this society by disregarding the status of an owner of similar weight. This cost is high enough to ensure the evolutionary stability of the "owner wins" convention.

In order to give a consistent picture of the spider territorial system the assumption had to be made that an individual spider has little information about how its weight compares to the rest of the population, and good informtion about its relative size in a given contest situation. Otherwise small spiders would have to engage in more fierce fights with small opponents because they would then be in a "now or never" situation. Grafen (1987) calls asymmetries *devisive* when they put animals in such now or never situations. This feature does not seem to prevail in the spider population because of the apparent lack of an individual's information about its "position" in the population weight distribution. At this point it should be emphasized that game-theoretic studies of field data often reveal details about information that is not available to an animal although it would be advantageous for the individual to have this information. Such constraints, for example, were also discovered in a famous field study about digger wasps [Brockmann et al. (1979)]. These wasps face a strategic decision to either work hard and digg a burrow or to save this effort and enter an existing burrow which may or may not be in use by a conspecific animal. Surprisingly, the wasps seem to be unable to distinguish between empty and occupied burrows although in view of the fighting risk it would be important to have this capability.

The analysis of spider behavior by Hammerstein and Riechert (1988) is based on a way of modelling called the *fixed background approach*. This means that payoffs for a given contest are calculated from field data about habitat structure, demography, and observed behavior of the population under investigation. The "fixed background" is a mathematical representation of biological facts about the existing population. In other theoretical studies that are more detached from empirical information one can also adopt the *variable background approach*. Here, the entire sequence of an individual's contests with varying opponents is modelled within a single large population game. Houston and McNamara (1988a, 1991) study the Hawk–Dove game from this point of view.

8.3. War of attrition, assessment, and signalling

The Hawk–Dove game and related models emphasize the problem of when an individual should initiate injurious biting or other forms of esclated fighting behavior. It is assumed that the onset of true aggression is a discrete step rather than a gradual transition (such a discrete step occurs, for example, in the spider example presented above). Maynard Smith (1974) introduced the "war of attrition" as a different model that captures ways of fighting in which costs arise in a smoother, gradual way. This modelling approach emphasizes the following problem:

Question 4. When should an animal stop a costly fighting activity?

Bishop and Cannings (1978a, b) analyzed the symmetric war of attrition and another variant of this game with random rewards about which the contestants have private information. Hammerstein and Parker (1981) analyzed the asymmetric war of attrition, i.e. a conflict where a role difference between two opponents is known to both of them with some small error. They showed that typically the benefit–cost ratio V/C should be decisive: the individual with the higher benefit–cost ratio should win (here, V is the value of winning, C is the constant time rate of cost, and both parameters may differ for different roles). This result has an important implication, namely that common-sense rules for conflict resolution are the only evolutionarily stable solutions in the asymmetric war of attrition model! Needless to say that this is in sharp contrast with the results obtained for models of the Hawk–Dove type (see previous section).

The original war of attrition model is lacking an important feature. Behavioral biologists find it hard to imagine a real animal contest in which no assessment of the opponent takes place during an ongoing aggressive interaction. This has led to an interesting refinement of the war of attrition model by Enquist and Leimar. They developed the "sequential assessment game" in which the opponents acquire information about their true fighting abilities throughout an agonistic interaction [Enquist and Leimar (1983, 1987, 1988), Leimar (1988)]. The beauty of the sequen-

tial assessment game is its potential for creating quantitative predictions that can be tested by empirical biologists. Enquist et al. (1990) demonstrate this for fighting in the cichlid fish *Nannacara anomala*, Leimar et al. (1991) for fighting in the bowl and doily spider *Frontinella pyramitela* [see also Austad (1983)].

The problem of assessment is closely related to the problem of signalling and communication in animal contests. When animals assess each other, it may pay an individual to convey information about strength by use of signals rather than by actual fighting [e.g. Clutton-Brock and Albon (1979)]. Evolutionary game theory has strongly influenced the biological study of signalling. It caused behavioral biologists to address the strategic aspects of animal communication.

Question 5. What is communicated by animal display behavior?

It seems obvious that animals should demonstrate strength or resource holding potential during an agonistic display. However, it is much less clear as to whether or not animals should communicate behavioral intentions, such as the intention to escalate. Maynard Smith (1982b) expressed the extreme view that the intention to escalate could not be communicated by a cheap signal, such as barking. He argued that if such a signal did indeed deter opponents it would be profitable to use this signal even in situations where no escalation is intended. As a result of this cheating the signal would then lose its meaning.

It was Maynard Smith's merit to bring this problem of cheating to the attention of behavioral biologists. However, he clearly pushed the cheating argument a little too far. Enquist (1985) provided the first biological model in which cheap signals do relate to intended fighting behavior at evolutionary equilibrium. As far as the empirical side of this problem is concerned, Caryl (1979) has reanalyzed a number of bird studies on aggresion in the light of Maynard Smith's idea. He concluded that the displays are far from being good predictors of physical attack. In contrast, Enquist et al. (1985) povide an example of aggressive behavior in fulmars, where the behavior shown by an individual at an early stage during a contest is related to this individual's persistence at a later stage. Andersson (1984) discusses the astonishingly high degree of interspecific variation found in threat displays.

So far we addressed the use of cheap signals in animal communication. More recent developments in biological signalling theory deal with the evolution of costly signals. Zahavi (1975, 1977, 1987) made the first major attempt to consider horns, antlers, and other structures as costly signals used in animal communication. He formulated the so-called handicap principle which roughly states that animals should demonstrate their quality to a rival or a potential mate by building costly morphological structures that in some sense handicap the signaller. The handicap principle was formulated in a verbal way by a field biologist. It attracted major criticism by Maynard Smith (1976, 1985) and other theoreticians who rejected Zahavi's idea on the ground of simple model considerations. However, recently

Pomiankowski (1987) and Grafen (1990a, b) used more intricate models from population genetics and game theory to re-establish Zahavi's principle. This shows nicely how biologists may sometimes learn more quickly about game rationality from studying real animals than by dealing with mathematical models.

8.4. The evolution of cooperation

There are a number of different ways (see Questions 6–9) in which cooperation between animals can be explained from an evolutionary point of view. Hamilton (1964) argued convincingly that altruistic behavior towards genetic relatives becomes understandable if one includes into the evolutionary measure of success (fitness) not only the altruist's own offspring but also the effect of the altruistic act on the receiver's reproductive output. The so-called *kin selection theory* weighs this effect on the receiver's offspring with the coefficient of genetical relatedness between donor and receiver. Hamilton's theory therefore takes indirect gene transmission via relatives into account.

Question 6. Is genetic relatedness an important key to the understanding of animal cooperation?

Because of its emphasis on genetic relatedness, kin selection theory does not attempt to explain cooperation between non-relatives. Except for this limitation in scope it has become the most successful theory about cooperation in animals. It is crucial, for example, for the understanding of castes and reproductive division of labor in highly social species of ants, bees, wasps, and termites. The remarkable complexity of social organization in ant colonies was recently surveyed by Hölldobler and Wilson (1990). Interestingly, many of the features of a typical ant colony are also found in a highly social mammal called the naked mole-rat [Sherman et al. (1991)]. Again, elementary kin selection theory rather than evolutionary game theory seems to provide the essential ideas for the understanding of sociality in this mammal. Kin selection also plays an important role in the explanation of helping and cooperative breeding in various bird species [Stacey and Koening (1990)].

Question 7. Does the (non-genetic) inheritance of resources or mating partners lead to animal cooperation?

Reyer (1990) described a cooperatively breeding bird population in which two kinds of cooperation occur that call for very different explanations. In the Pied Kingfisher, young male birds stay with their parents and help them to raise brothers and sisters instead of using the reproductive season for their own breeding attempts. This is explicable by straight forward kin selection arguments. In contrast, other

young birds of the same species are also helpers but are not genetically related to the receivers of their help.

Reyer was able to show that the latter helpers through their help increased their future chances of becoming the breeding female's mating partner in the subsequent season. Note here that the mating market in Reyer's population is fairly asymmetrical. Female partners are scarce "resources". There is a game involved in the sense that it would be in the breeding pair's interest to impose a high work load on the helper whereas the helper would be better off by inheriting the female without incurring the cost of help. There seem to be a number of other biological examples where games of a similar kind are being played.

Question 8. Do animals cooperate because of partially overlapping interests?

Houston and Davies (1985) give an example of cooperation in birds where it may happen that two unrelated males care cooperatively for the same female's offspring. Here the point is that both have copulated with this female and both have a positive probability of being the father of the offspring they are raising. There is nevertheless a game-like conflict between the males as to how much each contributes to the joint care. Houston and Davies used ESS models to analyze the consequences of unequal mating success for the amount of male parental care. They also included the female as a third player in this game.

Question 9. Has evolution taught its organisms the logic of repeated games?

Trivers (1971) introduced the idea into evolutionary theory that a long-term benefit of an altruistic act may result from the fact that it will be reciprocated later by the receiver. He caused biologists to search for the phenomenon of reciprocal altruism. In his seminal paper, Trivers already referred to the game-theoretic literature on cooperation in a repeated game, such as the supergame of the prisoner's dilemma. After more than a decade of search for reciprocal altruism, however, it became clear that this search has not been very successful [Packer (1986)] except for the discovery of elaborate alliances in primates [e.g. Seyfart and Cheney (1984)].

In non-primates, only a few cases are known that have at least some flavor of reciprocity. Perhaps the most interesting example was provided by Wilkinson (1984) who studied vampire bats in Costa Rica. In the population under investigation, female vampire bats roost in groups of several individuals. They fly out every night searching for a blood meal. If they fail to obtain such a meal for two consecutive nights, death from starvation is very likely to occur. Females who return to the roost without a blood meal solicit help from other females by licking under their wings. If their begging is successful, blood will be donated by regurgitation. Wilkinson demonstrated that bats who had previously received help from a begging individual had a stronger tendency to provide help than others.

Although Trivers (1971) had already introduced the idea of cooperation in repeated games, this idea entered the biological literature for a second time when Axelrod and Hamilton (1981) analyzed the repeated Prisoner's dilemma game in the context of evolutionary game theory. They emphasize that cooperation could not very easily start to evolve in a population of non-cooperating animals because a threshold value for the proportion of cooperators in the population would have to be exceeded in order to make cooperation a successful evolutionary strategy. Here, kin selection may once again play an important role if one attempts to understand the initial spread of cooperation.

Axelrod and Hamilton also stated that "tit for tat" would be an evolutionarily stable strategy. This, however, is not quite correct because "tit for tat" fails to satisfy the second condition for evolutionary stability [Hammerstein (1984), Selten and Hammerstein (1984)]. Boyd and Richerson (1988) discussed further problems with the logic of biological cooperation in groups of more than two individuals. Nowak and Sigmund (1992) studied repeated conflict in heterogeneous populations.

Brown and Brown (1980) and Caraco and Brown (1986) interpreted the phenomenon of food sharing in communally breeding birds as cooperation based on the repeated structure of an evolutionary game. Their key argument is the following. When neighboring parents share the task of delivering food to their offspring, this may result in a fairly steady supply of nutrition even when an individual's daily foraging success varies a lot. This benefit from food sharing may be achievable in a game equilibrium, since foraging takes place repeatedly.

The idea that "tit for tat"-like cooperation might evolve caused Milinski (1987) to run a series of experiments in which he manipulated cooperation in sticklebacks. These fish swim towards a predator in order to inspect the enemy. Milinski studied pairwise predator inspection trips. Using a mirror, he replaced the partner of a stickleback by the animal's own mirror image. Depending on the mirror's angle, the artificial companion behaved in a more or less cooperative way by either following or swimming away. With a cooperative mirror image, the sticklebacks approached the predator more closely than with a non-cooperative mirror image.

At first glance this seems to be explicable in a fairly simple way through the effect of risk dilution, and there seems to be no need to invoke the far-sighted logic of repeated game interaction. However, Milinski offers a number of reasons that indicate the importance of the repeated structure [see also Milinski et al. (1990a, b)]. He created a lively discussion of the predator inspection phenomenon [e.g. Lazarus and Metcalfe (1990), Milinski (1990)] and caused other fish biologists to search for similar phenomena in their species [Dugatkin (1988, 1991), Dugatkin and Alfieri (1991)].

Fischer (1980, 1981, 1988) suggested another example of animal behavior that seemed to have some similarity with the "tit for tat" strategy. His study object is a fish called the black hamlet. This is a simultaneous hermaphrodite who produces sperm and eggs at the same time. When mating takes place between a pair of fish, each fish alternates several times between male and female role. Fischer argues

that eggs are relatively few and expensive compared with sperm, and that, therefore, it is easy for a hamlet to get its own eggs fertilized by another fish. Thus a fish can use the eggs in its possession to trade them in for the opportunity to fertilize the eggs of another fish. The egg exchange takes place in a sequence containing several distinct spawning bouts.

To trade, or not to trade; that is the question Friedman and Hammerstein (1991) asked about the Hamlet's peculiar mating behavior. They modelled the conflict as a population game in which the search for other partners after desertion of a given partner is explicitly taken into account. It follows from their analysis that there is less similarity with a repeated prisoner's dilemma game and with "tit for tat" than Fischer (1988) had originally suggested. Friedman and Hammerstein show in particular that cheating does not pay in the Hamlet's egg trading, and that there is no scope for specialization on male function. Enquist and Leimar (1993) analyzed more generally the evolution of cooperation in mobile organisms.

8.5. The great variety of biological games

A final "tour d'horizon" will take us through a number of different biological applications. Evolutionary conflict seems to exist in almost any area of animal and plant behavior where individuals interact directly or indirectly. Consider, for example, the problem of parental care. Both father and mother of a young animal would benefit from offering parental care if this increased their offspring's chances of survival. However, when there is a cost involved in parental care, both father and mother would often be better off if they could transfer some or all of the work load to the other sex.

A similar point can be made about the problem of mate searching. Although both sexes have an interest in finding each other for the purpose of mating, an individual of either sex would benefit from saving the cost of mate searching. Once the sexes have found each other, there may be a conflict as to whether or not mating should take place. It may pay off for one sex to mate but not for the other.

The problem of conflict over parental investment was first described by Trivers (1972). However, through his way of looking at this problem he came close to committing the so-called Concorde fallacy [Dawkins and Carlisle (1976)]. Maynard Smith (1977) analyzed conflict over parental investment in the context of evolutionary game theory. Hammerstein (1981) provided a formal justification for his modelling approach. Grafen and Sibly (1978) further discussed the evolution of mate desertion. Mate searching games and conflict over mating were studied by Bengtsson (1978), Packer (1979), Parker (1979), and Hammerstein and Parker (1987).

Finding a mate can be facilitated if one sex calls in order to attract a mate. This is what some males – the callers – do, for example, in the natterjack toad. Other males in this species – the satellites – remain silent and try to intercept females as they approach the caller. If everybody is silent, there is a high incentive to behave

as a caller. If everybody calls, some males have a high incentive to remain silent. Arak (1988) used game theory in order to model the evolution of this system.

Alternative male mating tactics are also found in various other parts of the animal kingdom. For example, in a population of the white-faced dragonfly males either defend territories on the pond or they act as transients in the vegetation surrounding the pond. Waltz and Wolf (1988) used ESS theory in order to understand the dragonfly mating strategies. Another dragonfly mating system was investigated in a similar spirit by Poethke and Kaiser (1987).

Before mating takes place a male may have to defend the female against other males who show an interest in the same partner (pre-copulatory mate guarding). Even after mating a male may have to defend the female against other males if a new mate would still be able to fertilize a considerable fraction of the eggs (post-copulatory mate guarding). These conflicts were analyzed by Grafen and Ridley (1983), Ridley (1983), and Yamamura (1986, 1987).

Related to the problem of mate guarding and access to a mate is the evolution of male armament. In many species males have a greater body size than females, and they are equipped with morphological structures that may serve as weapons in a fight. The evolution of such features resembles an arms race that can be treated as an evolutionary game [Parker (1983)]. However, the equilibrium approach of ESS theory may not always be appropriate [Maynard Smith and Brown (1986)] for this kind of problem.

Males use their weapons not only against their rivals. In several species of primates and in lions, males have a tendency to kill the offspring of a nursing female after they chased away the father of this offspring. This infant killing seems to considerably shorten the time span that elapses until the female becomes sexually receptive again. Hausfater et al. (1982), and Glass et al. (1985) argued that infant killing is an equilibrium strategy of an evolutionary game. One can look in a similar way at the phenomenon of siblicide and at other forms of sib competition [Dickins and Clark (1987), Parker et al. (1989)].

Fortunately, there are many cases in nature where less violent means than infant killing serve the purpose of gaining access to a mate. For example, the female may have to be "conquered" by donation of a nuptial gift that would resemble a box of chocolates in the human world. Parker and Simmons (1989) studied game-theoretic models of nuptial feeding in insects.

Yet another problem concerning the sexes is that of sex ratio among a female's offspring. Throughout the animal kingdom there is a strong tendency to produce both sexes in roughly equal numbers. This fact was already known to Darwin (1871) who reviewed sex ratio data for various groups of animals with little success in explaining the 1:1 property. It was indeed left to Fisher (1930, 1958) and to Shaw and Mohler (1953) to give a convincing explanation of this phenomenon. There is an implicit game-theoretic structure in Fisher's way of reasoning. This structure was revealed by Maynard Smith (1982a) who reformulated Fisher's thoughts in the formal framework of evolutionary game theory. Maynard Smith

(1980) also introduced a new theory of sexual investment in which the evolution of the sex ratio is subject to severe constraints. Reviews of sex ratio theory can be found in Charnov (1982), Karlin and Lessard (1986), and Bull and Charnov (1988).

When animals live in groups, such as a flock of birds, game-like situations arise from the problem of how individuals should avoid dangers caused by predators. There is an obvious conflict concerning the safest locations within the group. However, there is also an evolutionary conflict with regard to the individual rate of scanning for predators. Properties of this vigilance game were investigated by Pulliam et al. (1982), Parker and Hammerstein (1985), Motro (1989), Motro and Cohen (1989), Lima (1990), and McNamara and Houston (1992).

The distribution of foraging animals over a patchy habitat can be studied theoretically under the extreme assumption that each individual is *free* to choose its foraging patch and can change between patches at no cost. Fretwell and Lucas (1970) and Fretwell (1972) pointed out that *ideally* each animal should move to the patch were its success will be highest. When competitive ability is equal this should result in a distribution over patches with the property that (a) individuals in different patches have equal gains, and that (b) average success is the same for all patches. This pattern of habitat utilization is called the *ideal free distribution*.

A number of experiments [e.g. Milinski (1979), Harper (1982)] have shown that prediction (b) is supported by facts even when there are differences in competitive ability so that (a) does not hold. This has led to interesting theoretical work by Houston and McNamara (1988b) who enrich the game-theoretic analysis with additional methods from statistical mechanics [see also Parker and Sutherland (1986)]. A review of models in relation to the ideal free distribution is given by Milinski and Parker (1991). Yamamura and Tsuji (1987) examine the use of patchily distributed resources as a game that is closely related to standard models in optimal foraging theory.

Organisms are not always free to choose their location. An interesting example of unfree choice of location is that of seed dispersal. Here the parental plant can impose its "will" on the offspring by attaching morphological structures to it that will enforce migration. Hamilton and May (1977) used evolutionary game theory in order to discuss the question of how (enforced) seed dispersal is affected by intraspecific competition. They found that substantial dispersal should occur even when the habitat is homogeneous, constant, and saturated, and when there are high levels of seed mortality during dispersal. This is in sharp contrast with the view previously held in ecology that seed dispersal serves the main purpose of colonizing new empty patches. The seminal paper by Hamilton and May stimulated various authors to analyze dispersal as an evolutionary game [Comins et al. (1980), Comins (1982), Hastings (1983), Stenseth (1983), Levin et al. (1984), Holt (1985), Frank (1986), Lomnicki (1988), Taylor (1988), Cohen and Motro (1989)].

A somewhat related matter is the game between individuals of a parasitoid who have to decide where to lay their eggs. This game can lead to the phenomenon of

superparasitism where the number of eggs laid in a host is far greater than the number of offspring that can emerge from this host. Oviposition in a previously parasitized host can be observed even when only one offspring will emerge from this host. Originally, biologists tended to interpret this phenomenon as a mistake made by the egg-laying parasitoid. However, with the help of evolutionary game theory superparasitism can be understood much more convincingly as an adaptive phenomenon [van Alphen and Visser (1990)].

Parental plants can impose their "will" not only on the spatial distribution of their offspring, but also on the temporal distribution of when the seeds should germinate; different degrees of encapsulation lead to different germination patterns. These patterns have to be adapted to the environment in competition with other members of the same species. Germination games and the problem of dormancy were investigated by Ellner (1985a, b; 1986, 1987).

There are more games played by plants. Desert shrubs use their root systems in order to extract water and nutrients from the soil. Near the surface, water is in short supply and there are many indications that neighboring plants compete for access to this scarce resource. Riechert and hammerstein (1983) modelled root competition as a population game and showed that the evolutionarily stable root strategy would not result in optimal resource exploitation at the species level. This result casts some doubt on classical ideas in ecology that are based on species welfare considerations.

The root game can be extended to a co-evolutionary case where plants of different species interact. Co-evolutionary games were first studied by Lawlor and Maynard Smith (1976). Riechert and Hammerstein (1983) introduced a modelling approach to co-evolution in which the game-theoretic nature of interspecific conflict is made more explicit. They analyzed the problem of root evolution under the simultaneous occurrence of intra- and interspecific competition for water. Their model shows that co-evolution should lead to the use of different soil strata by different species, and that similar species should show the phenomenon of character displacement in areas were they overlap. As a matter of fact, most communities of desert plants are stratified in this sense. A number of other papers relate co-evolution to the framework of evolutionary game theory [e.g. Eshel and Akin (1983), Brown and Vincent (1987), Eshel (1978), Leimar et al. (1986)].

So far we have discussed applications of evolutionary game theory to either zoology or botany. However, some ESS models relate to both disciplines. This is most obvious in the field of pollination biology. There is a game-like conflict between plants and insects where the plant uses its flower to advertise nectar. Once a pollinator visits the flower, the insect's pollination service is rendered regardless of whether or not nectar is found. Given that this is the case, why should a plant offer nectar at all and how much nectar should it provide? Cochran (1986) explained the existence of non-rewarding orchids using her own empirical work. In contrast, Selten and Shmida (1991) answered the question of why a population of rewarding plants can be in stable equilibrium.

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