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GAME THEORY IN THE ECOLOGICAL CONTEXT

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INTRODUCTION

Ecology is that branch of science that aims at explaining the relationships between organisms and their physical and biotic environments. Model building is generally used in ecology as the first step towards meeting this goal. The model should be a simplified representation of reality that provides insight into the structure and function of often complex systems (49). Of the many models applied to ecological problems, those based on the principle of optimization, borrowed from economics, have frequently been used (88). In economic optimization models, a dependent variable (money) is maximized, using some cost-benefit function. Ecologists' reliance on the optimality construct is related to the fact that its structure is similar to the evolutionary biologist's view of the mechanics of evolutionary processes—that natural selection, operating on phenotypic variance, drives populations towards optimal, fine-tuned responses to environmental variables. Instead of money, the dependent variable that will be maximized here is Darwinian fitness. The methodology and problems associated with the application of optimality theory to ecological problems have received extensive treatment in several reviews (16, 52, 62, 77, 76). Despite some criticisms (see 88), many ecologists think that "optimization models have been, and are likely to remain, the principal conceptual framework for thinking about evolutionary trends at the phenotypic level" (78).

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[1] Order of authorship determined by one round of Game of Chicken

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The species optimization criteria most often used in ecology are best applied to those cases in which the performance of an individual is independent of (i.e. it is neither affected by nor has an effect on) the performance of other members of the population to which it belongs. If this condition does not hold, then one must apply the evolutionary game theory approach in order to model the process. This review is intended to provide ecologists with both the necessary background and the incentives to use the evolutionary game theory construct in place of species optimization, where it is appropriate.

The biological variant of game theory originated with Maynard Smith & Price (68); the reader should consult Maynard Smith's recent book (66) for a full treatment of the subject. It is not our intent to critique Maynard Smith's book in this review but rather to emphasize those areas that are not detailed in his treatment, namely: (*a*) the links between classical and evolutionary game theory; (*b*) the application of evolutionary game theory to ecological problems; and (*c*) the degree to which the predictions of optimization deviate from those of game theoretic models when selection is frequency dependent. The links between classical game theory and its evolutionary biological interpretation are usually underestimated and sometimes misunderstood. We attempt to clarify this relationship. We then introduce a simple botanical paradigm to demonstrate the ideas and methodology associated with evolutionary games. This model is extended from the simplest case involving pairwise interactions between neighboring plants to one involving local population competition. Both intra- and interspecific competition are considered. As we develop this paradigm, we compare the predictions produced by considering the problem as one simply of species' optimal resource allocation, as opposed to one involving frequency-dependent selection—the differences in the outcomes of these two methods of analysis are far from trivial. Finally, we consider other situations where evolutionary game theory has been or should be applied.

CLASSICAL AND EVOLUTIONARY GAME THEORY: A GENERAL DISCUSSION

Game theory is the study of conflicts of interest in which the value of a particular set of actions undertaken by a "decision-maker" depends not only on his own choices but also on those of others. The term game theory is used because the mathematical representation of this type of conflict is similar to that of many parlor games—e.g. chess, bridge, poker, and tic-tac-toe. The implications of game theory, however, are much more profound, having considerable importance in economics and business (e.g. 30, 58, 70, 99, 101), the social sciences and politics (e.g. 9, 20, 97), the military (e.g. 1), social psychology (e.g. 6, 32, 87), and, most recently, evolutionary biology (e.g. 37, 66, 68, 108). Nevertheless, the terminology used in parlor games and in the theory of games is similar. The decision makers are termed players and the objective function of optimization theory is called the payoff function. This function assigns a value or measure of success to the benefits received from playing a particular strategy, which specifies how a player will act in all potential situations. The game, then, is a collection of rules known to all players that determines what each player can possibly do and the outcome of using particular choices or strategies.

Von Neumann and Morgenstern (110) originally developed game theory as a mathematical tool for the social sciences. Its aim was to illuminate the problem of rational (i.e. conscious) decision making in interpersonal conflicts (see 55 for a discussion). This process involved the mathematically intricate task of dealing simultaneously with the strategical planning of at least two players, each of whom was trying to obtain the best possible payoff in his own personal interest. In classical game theory, a player's payoff is measured subjectively and is defined by personal value judgements of what constitutes success. In contrast, a neo-Darwinian analysis of this type of contest replaces the subjective notion of success with an objective criterion. The player's payoff is measured as the change in expected Darwinian fitness resulting from playing a particular strategy. There is one other major conceptual difference between classical game theory and evolutionary game theory. In most classical applications, game theory focuses on decisions made by humans using cognitive choice. The evolutionary application of this construct focuses on decisions "made by" the process of natural selection—individual plants and animals are merely the performers of an inherited program. In this context, the term decision refers to the long-term outcome of selection under a given set of environmental conditions. Interactions may be direct or indirect and between two, a few, or many individuals.

The essential similarity between the ways in which neo-Darwinists and classical game theorists analyze contests is in the emphasis both place on individual success rather than on the success of groups or aggregates of individuals. This criterion is especially important, of course, to biological applications of the theory, since the theory of natural selection emphasizes contributions to the reproductive success of individuals rather than of populations or other higher categories. In both neo-Darwinian and classical game theory, one cannot use simple optimization criteria in identifying a successful strategy: the payoff maximum changes with the relative frequency that different strategies are used in the population or group of players. How is a solution to a contest reached then? In the classical noncooperative game, upon which evolutionary game theory is based, the Nash equilibrium point (74) provides the basic solution. Cooperative game theory does not emphasize strategic solutions and often considers payoffs to groups of individuals. Noncooperative game theory, on the other hand, includes both cooperative and noncooperative contexts in which the solution is based on benefits to individual players; this latter type is more appropriate for evolutionary theory (e.g. see 45). The Nash equilibrium point is defined as that combination of strategies among players for which it would not pay for any one of them to deviate from his strategy, given that nobody else deviated from theirs; there is often more than one equilibrium point. Within the context of Bayesian decision theory, then, the quantity a player tries to optimize is his expected or average payoff.

In the early history of game theory, other quantities were also examined, especially the concept of the worst possible outcome. The so-called maximin philosophy (sometimes referred to as minimax) was based on the idea that a player should choose that strategy which maximizes the payoff from the worst possible outcomes. Though some researchers still apply it in limited contexts (e.g. 86), the maximin principle has not been central to classical game theory since the publication of Nash's work (74). This fact has not been recognized in some of the comparisons that biologists make between classical game theory and evolutionary game theory. Maynard Smith (60), for example, placed too much emphasis on the differences between minimax and the concept of the Evolutionarily Stable Strategy (ESS), instead of emphasizing the close similarity between the Nash equilibrium concept and the evolutionary game solution. The solution used in the evolutionary game (ESS), in fact, represents a subset of the Nash equilibrium points (40, 103). As Maynard Smith & Price (68) defined it for pairwise animal conflicts, the ESS has the property that a population of individuals adopting the strategy I is stable against invasion by initially rare mutants adopting any other strategy J. For I to be an ESS, the expected payoff in fitness E of I played against itself must either (*i*) be greater than that of any other strategy J played against I: $E(I,I) > E(J,I)$, or (*ii*) if $E(I,I) = E(J,I)$, then the payoff received from playing I against J must be greater than the payoff J receives when played against itself, i.e. $E(I,J) > E(J,J)$. This ESS condition is based on the assumption of random pairing of conflict partners.

From the standpoint of Darwinian fitness, therefore, a successful strategy (or trait) must not only be well adapted to its environment but also adaptive with respect to potential competition with conspecifics and perhaps even with heterospecifics. The success of this trait critically depends on which traits or phenotypes are present in the population and in what proportions. A given phenotype's fitness is thus frequency dependent and would classically be considered within the theory of frequency-dependent selection, as it has been developed by Lewontin (51), Lloyd (54), and Slatkin (104). Within this theoretical framework, one can look for character states that are in a dynamically stable equilibrium under selection. The ESS solution approximates such states.

It is unreasonable to expect that ESS theory should ultimately be converted into a branch of population genetics. It has been developed to provide insight into the evolution of phenotypes in the more complex ecological situations, without having any detailed knowledge of the genetic system underlying the traits. One only assumes that enough genetic variability exists on which natural selection can work. For computational simplicity, in fact, ESS analyses are usually based on assumptions of asexual inheritance. As such, the ESS is defined as the phenotype toward which members of a species population would evolve given parthenogenetic (i.e. haploid) inheritance. Where sexual (i.e. diploid) inheritance has been incorporated into the ESS model, results have been obtained similar to those achieved with the haploid model for the two-strategy game involving unselected players (31, 46, 65, 107). There is a problem, however, with polymorphic populations exhibiting more than two strategies. Gadgil et al (31) indicate that in these circumstances more genotypes meet stability criteria than indicated by ESS analysis. Nevertheless, it appears as if the more complex the genetic system, the greater is the probability that an ESS will be reached (B. Charlesworth, cited in 54, 104). The ESS solution, then, can be applied reliably to most ecological contexts involving frequency-dependent selection.

THE NATURE OF A GAME: CLASSICAL GAME THEORY

The Prisoner's Dilemma Game

There has been considerable confusion in the recent biological literature about what the central concepts of classical game theory are and how they relate to evolutionary theory. While introducing the basic elements of strategic analysis, we will sketch the major goals and methodology of classical (i.e. noncooperative) game theory.

Consider the famous classical paradigm that has been the subject of more than 2000 papers within the social sciences—"The Prisoner's Dilemma" (55). We shall introduce this game by first giving its most popular interpretation and then defining its formal structure. The interpretation reads as follows: Two persons are arrested for committing a minor crime that is generally punished with a one-year prison sentence. However, they are also suspected of being guilty of a major crime for which they would be imprisoned for an additional 9 years. While there is firm evidence for the first charge, the evidence for the second is insubstantial and a confession is essential to the prosecution's case. The district attorney offers the following deal in order to obtain the needed confession. If one of the prisoners confesses that both have committed the major crime, he will be freed immediately (i.e. he will serve no time in prison), whereas his partner in the crimes will have to serve a ten-year prison term. If both confess, however, they will be forgiven the minor crime but not the major one, so each will serve a nine-year term. Clearly, if neither individual confesses, both will only have to pay the penalty for having committed the minor crime (i.e. a one-year prison term). Both suspects are interrogated simultaneously and in separate rooms.

Obviously, the attorney has created a situation in which both prisoners, although former partners, find themselves in a conflict of interest: each would be best off if he confessed and the other did not. It must be emphasized at this point that noncooperative game theory does not attempt to describe or predict actual human behavior in the game situation, since it assumes that the decisions are made by perfectly rational players (something humans are not known to be). Game theory thus has a "normative" aim—its solutions are based on how a fictitious individual, provided with unlimited powers of calculation and consistent preferences, should best pursue his interests.

To model the outlined dilemma, or any such conflict, as a game, one must carefully specify the following:

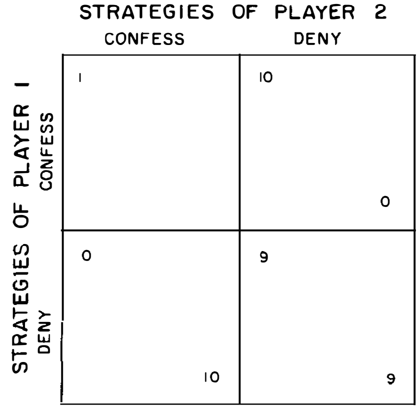
1. Who are the players and what are each player's interests? (How strongly would each prefer one outcome over another in the comparison between any two outcomes of the total conflict?)
2. What are the actions each player can choose from?
3. How do the actions of the players affect the outcome of the conflict?

The specifications used in the classical Prisoner's Dilemma Game are as follows:

1. There are two players—the prisoners, not the attorney—whose interests are measured in terms of years saved from the maximum penalty.
2. Each prisoner has only two choices: to "confess" or to "deny."
3. The outcome in this case—the degree of penalty—corresponds to the rules set by the attorney.

The standard way of describing these features mathematically is to write down a payoff matrix as shown in Figure 1. Each cell of this matrix corresponds to one of the four ways in which the conflict can be resolved. The payoffs indicated in the respective cells refer to the years *saved* from completion of the maximum penalty. (By convention, the payoff to player 1 is represented in the upper left corner of a given cell and to player 2 in the lower right corner).

In order to analyze a game like Prisoner's Dilemma, it is useful to think in terms of so-called best reply strategies. Suppose, for example, that it were assumed that player 2 chooses to deny. How should player 1 act in order to maximize his payoff? According to the payoff matrix (Figure 1), he would clearly have to confess (since 10 years saved is more than 9) which is therefore called player 1's best reply strategy against deny. Furthermore, if it were



		STRATEGIES OF PLAYER 2	
		CONFESS	DENY
STRATEGIES OF PLAYER 1	CONFESS	1	10 0
	DENY	0 10	9 9

Figure 1 The Prisoner's Dilemma Game: In each cell, the upper left entry denotes the payoff to player 1, the lower right entry denotes the payoff to player 2. Payoffs here represent the years *saved* from the maximum penalty of 10 years in prison for the individual playing the strategy indicated in the cell against the strategy exhibited by the other player.

assumed that the opponent chooses to confess, player 1's best reply strategy would also be to confess. Since the game is symmetrical (i.e. players are merely distinguished as 1 or 2 for our convenience), the same argument holds for player 2. From this example, one can draw the following seemingly trivial but important conclusion about Prisoner's Dilemma: Whatever choice of strategy the opponent makes, it is always better for a player to confess than to deny. Obviously, the only rational solution to this game, then, would be for both opponents to confess, since otherwise they would receive lower payoffs, i.e. they would not have chosen the strategic means that best served their respective interests.

Generally, games have much less obvious solutions and it is often difficult to define what constitutes rational behavior in the context of strategic interaction. It is basically a conceptual question of: How can one optimize against an opponent's behavior, if one does not know what the opponent will do? Harsanyi & Selten (45) have recently provided a comprehensive approach to this problem. We will not deal here with all of the intricacies they discuss in defining a rational solution for strategic interaction. There is one fundamental property, however, that any game theory concept of rationality must have, since it is based on the maximization of utility or payoffs. If each player expects his opponent to behave according to the rational solution, neither should have any incentive to deviate from the rational solution himself. In mathematical terms, for the two person game the pair of strategies for the two players must satisfy the following necessary condition: each of these two strategies must be a best reply to the other. Such a pair of strategies is called an equilibrium pair or equilibrium point (74). The Prisoner's Dilemma Game shown in Figure 1 is a symmetric game and, as such, only symmetric equilibrium points in which both players play the same strategy are rational solutions. In actuality, the Prisoner's Dilemma Game has only one equilibrium pair, so the point is academic in this case. Its significance will become apparent in our discussion of the Game of Chicken with mixed strategies, which has three equilibrium pairs.

The Game of Chicken

The "Game of Chicken" (e.g. 9) is a very simple model of a sport that was especially fashionable among American teenagers in the 1950s. In this game (frequently played by Riechert), two persons steer their bicycles or cars towards one another at top speed. If we ignore the more complex strategic features of timing that might be incorporated into a proper model of this situation, each player's decision is simply between "swerving" and "not swerving" at the last possible instant. The loser is defined as that individual who swerves first in order to avoid a head-on collision. Suppose that the loser has to pay the winner $10 and that the average cost of repairing a bike following a collision is $100. The payoffs are as follows: If both players choose not to swerve, they each suffer a $100 penalty (a negative payoff of -100); if both swerve, the payoff to each is 0, since no money is either lost or gained; if only one player swerves, he will pay $10 (a negative payoff of -10) and the other will receive $10 (a positive payoff of $+10$).

The Game of Chicken is presented in matrix form in Figure 2. Player 1's best reply strategies are indicated by arrows 1 and 3 and player 2's by 2 and 4. The arrows are a pictorial representation of what is called the game's best reply structure. Each arrow points in the direction of the decision that yields the highest payoff against a given opposing strategy. The points where two arrows meet are necessarily equilibrium points. In the Game of Chicken, they are: A—player 1 swerves and player 2 does not swerve, and B—player 2 swerves and player 1 does not swerve. Since the Game of Chicken is symmetric (i.e. the players do not differ from one another, but are merely designated as 1 or 2 for our convenience), only a symmetric equilibrium point can be a rational solution. This condition holds because the individuals would not know who should act as player 1 and who as player 2. The two equilibrium points identified by the arrow technique are not symmetric and hence cannot be rational solutions. Does the Game of Chicken really have no symmetric equilibrium point and thus no rational solution? Classical game theorists believe that there should be a rational solution to most conflicts. Thus they have developed the following construct to overcome the kind of problem encountered in this game. Instead of dealing only with the pure strategies—swerve and not swerve—an enlarged set of mixed strategies is taken into consideration. A mixed strategy is a specifica-

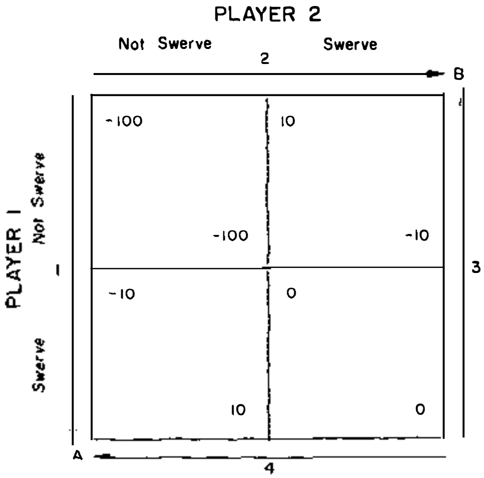


Figure 2 Game of Chicken: The arrows indicate the best reply strategies. Arrow 1, for example, indicates that player 1's best reply to "not swerve" is "swerve." Arrow 4 indicates that player 2's best reply to "swerve" is "not swerve." Equilibrium pairs of pure strategies correspond to points at which arrows meet. There are two such points in this game: A) player 1 will "swerve"–player 2 will "not swerve"; B) player 2 will "swerve"–player 1 will "not swerve".

tion of the probabilities with which each pure strategy will be exhibited by a player in a particular game—e.g. swerve with probability 0.2 and do not swerve with probability 0.8. The original pure strategies then are just special cases of mixed strategies.

What then is the solution to the Game of Chicken? If an individual plays a mixed strategy I against another mixed strategy J, his expected payoff is $E(I,J)$, which he wishes to optimize. $E(I,J)$ is defined as a probability-weighted sum of the payoffs a player would receive in each cell of the matrix shown in Figure 2:

$$E(I,J) = \sum_{i,j=1}^{n} I_i J_j a_{ij}, \qquad 1.$$

where I_i is the probability that an I player exhibits the ith pure strategy, J_j is the probability that a J player exhibits the jth pure strategy, n is the number of pure strategies, and a_{ij} is the payoff of playing i against j (according to the payoff matrix). Figure 3 gives an example of how $E(I,J)$ is calculated.

In the strategic context that is extended to include mixed strategies, a strategy I is called a best reply to another strategy J if it satisfies the inequality

$$E(I,J) \geqslant E(K,J) \qquad 2.$$

		PROBABILITIES, STRATEGY J	
		3/4 Not Swerve	1/4 Swerve
PROBABILITIES, STRATEGY I	2/5 Not Swerve	$-100 \cdot \frac{2}{5} \cdot \frac{3}{4}$	$10 \cdot \frac{2}{5} \cdot \frac{1}{4}$
	3/5 Swerve	$-10 \cdot \frac{3}{5} \cdot \frac{3}{4}$	$0 \cdot \frac{3}{5} \cdot \frac{1}{4}$

Figure 3 Demonstration of the calculation of the expected (i.e. average) payoff associated with playing a mixed strategy *I* against a mixed strategy *J* in the Game of Chicken. Here, *I* is to play "not swerve" and "swerve" with probabilities of 2/5 and 3/5, respectively; *J* is to play "not swerve" and "swerve" with probabilities of 3/4 and 1/4, respectively. The expected payoff to the player who adopts *I*, if it is played against *J*, is defined as the sum of all four entries. Therefore, $E(I,J) = -33.5$

for all strategies *K*. Furthermore, *I* is called an equilibrium strategy if *I* is a best reply to *I*. The fundamental property characterizing such an equilibrium strategy *I* is that all those pure strategies to which *I* assigns a positive probability are also best replies to *I*. In the Game of Chicken, this condition means that if *I* is an equilibrium strategy (i.e. a rational solution), then the following two statements can be made: (*a*) Not swerve is also a best reply to *I*; (*b*) Swerve is also a best reply to *I*. Therefore, $E(\text{not swerve}, I) = E(\text{swerve}, I)$. Let p equal the probability that an *I* player does not swerve. From Figure 2, then $E(\text{not swerve}, I) = -100p + 10(1-p)$ and $E(\text{swerve}, I) = -10p + 0(1-p)$, which implies that $p = 0.1$ and $1-p = 0.9$. The equilibrium strategy for the Game of Chicken is thus to swerve, with a probability of 0.9 and not swerve, with a probability of 0.1. The equilibrium payoff, $E(I, I)$, of this equilibrium strategy is -1. (Note that truly rational beings would not play this Game of Chicken at all, since the equilibrium payoff is negative.)

EVOLUTIONARY GAME THEORY: THE ROOT GAME PARADIGM

Since its conception, evolutionary game theory has largely developed around a simple model of animal conflict—Maynard Smith & Price's (68) Hawk-Dove Game. The structure of this game is well known and a good review of the general game and its modifications is available in Maynard Smith (66). Our interest is in a simple ecological example which, though analyzable as a two individual or pairwise contest, might be extended to the *n*-person context characteristic of most ecological applications. We have chosen competition for water in desert plants as our didactic example. Arguments similar to the ones developed here are particularly relevant to such real world problems as the analysis of fragmented phenotypes in clonal plants (75).

Let us assume that desert plants compete for water [however, see (34)]. Three sources of water are available to these plants which vary in depth: 0–0.2 m, 0.21–1.0 m, and greater than 1 m (106). Plants' lateral root systems utilize water at or near the surface (for our purposes, that available within 1 m of the surface), while underground sources of water are exploited by the elongated taproots. In the desert ecosystem, the efficient utilization of one water source (surface or underground) precludes the use of the other (106). Hence desert plants tend to specialize in one or the other type of root system. Succulents, for instance, primarily develop their lateral root systems and utilize surface water for the most part, while many other species are true phreatophytes and only tap underground water (98). Ludwig [in Solbrig et al (106)] states that most perennial shrub species have the potential for either extensive lateral or taproot development. It is this group of plants that we will consider in our example.

Pairwise Interactions

In our basic "Root Game," we are analyzing the individual shrub's "decision" to emphasize the development of either the lateral or taproot component of its water (and nutrient) procurement system. Although an individual plant usually competes with more than one neighboring individual, we will only model the interaction between nearest neighbors in this simple case, making the game a pairwise intraspecific contest. The two strategies available to our perennial shrub species are "lateral" and "tap." Our payoffs are proximal ones—the quantities of water obtained per unit time. We assume, however, that these payoffs have the following relationship with changes in Darwinian fitness: The quantities of water and dissolved nutrients taken up are proportional to reproductive output. The average amount of water uptake by a lateral root system per unit time, in the absence of a competing nearest neighbor, is defined as S for surface water (0–1 m in depth). Likewise, U denotes the expected quantity of water obtained by the taproot system from such underground water sources as depressions and washes. For the two individual game, we assume that the competitive effect of nearest-neighbor lateral root systems is $S/2$—i.e. that two neighboring plants using lateral root systems each receive one half of the available surface water. No such competitive effect is included in the basic model for the taproot system, since it is assumed that, once located, this source of water can adequately support the needs of two shrubs. Each root type thus has a constraint. In the case of the lateral system, a little water is usually available but in low enough quantities that the presence of neighbors exhibiting the same lateral system limits the quantity each shrub can obtain. For the taproot, there is no competition for water since there is an adequate supply once some is found. We assume, however, that the distribution of underground water is patchy and hence not as spatially reliable as surface water. In this initial analysis, we must also assume that both players in the game decide which root system to emphasize at the same time—perhaps they are colonizers following a frost or fire kill in a local area.

Figure 4 shows the Root Game and indicates the best reply strategies under the assumption that $U < S/2$ (i.e. underground water is very difficult to locate). With this assumption, the best reply structure of the Root Game (the arrow configuration) is the same as the Prisoner's Dilemma Game already discussed. If shrubs behaved as if they were rational thinking beings, they would thus develop only lateral roots in this context. If, however, $U > S/2$, the best reply strategies would be different. The reader may easily change the arrows in Figure 4: Arrow 1 no longer points upwards but downward and arrow 2 now points to the right. The best reply structure is now identical to that in the Game of Chicken (Figure 2). Games with this latter structure have two asymmetric equilibrium points consisting of pure strategies. But, as has already been discussed, the rational solution of such a game is a mixed equilibrium strategy. Both shrubs would play the same mixed equilibrium strategy I if they were rational, since I is by definition a best reply to itself.

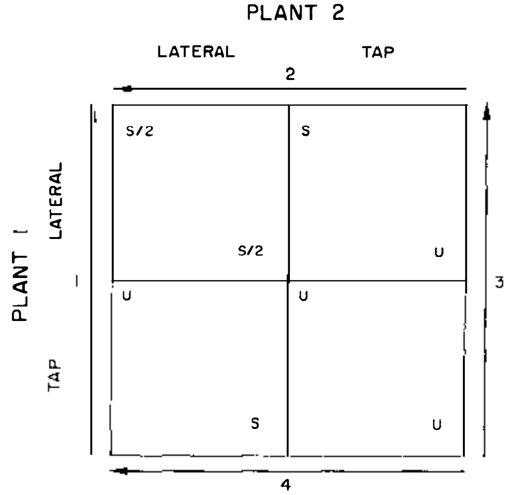


Figure 4 Root Game: The arrows indicate the best reply strategies when $U < S/2$, where U = supply of underground water and S = quantity of surface water available to a lateral root. Note the similarity in the reply structure with the Prisoner's Dilemma Game (Figure 1).

EVOLUTIONARILY STABLE STRATEGIES Biologists gain little from discussing which root systems shrubs should develop if they were rational beings. In fact, however, the outcome of frequency-dependent selection operating on phenotypic traits corresponds reasonably well to what rationality would suggest. Let us consider why this is the case, since the heuristic value of evolutionary game theory is based on this fact. Biological game theory asks the following question: Which strategies (i.e. phenotypes) should one expect to find in a population as the long-term outcomes of natural selection, given that game-like conflict occurs among members of the population generation after generation. In asking this question, the pure and mixed strategies of the Root Game are considered as inheritable traits—i.e. they are subject to choice by selection and not to choice by the individual plant. Now if a single strategy, I, is a long-term outcome of selection and thus is permanently maintained under given environmental conditions, it must have the following property: No mutant strategy, J, should have a higher expected fitness than I in this population of I-playing shrubs. If all of the strategies of the Root Game are considered as potential mutant strategies, this means that I must necessarily be a best reply to I. As in game theory the term best reply means that: $E(I,I) \geqslant E(J,I)$ for all strategies J. Strategy I must satisfy this criterion in order to be a rational solution of the symmetric Root Game, since it means that the pair of strategies (I,I) is a symmetric or Nash equilibrium point.

In many cases, then, the solution to the evolutionary game is identical to that of the classical game. The evolutionary game deviates from the classical game if another strategy J is as successful as I in the population of I players. Then a second condition must be met: For I to be an evolutionarily stable strategy, J must be at a selective disadvantage as it increases in frequency. Such an alternative best reply to I can only have this selective disadvantage if $E(I,J) > E(J,J)$, since $E(I,I) = E(J,I)$.

An Evolutionarily Stable Strategy (ESS) is therefore defined as a strategy, I, that satisfies the following two conditions:

(*i*) Equilibrium Property
I is a best reply to I (i.e. $E(I,I) \geqslant E(J,I)$ for all strategies J).

(*ii*) Stability Property
If J is an alternative best reply to I, then it is better to play I against J than J against J. Formally this second condition is stated as: If $E(J,I) = E(I,I)$, then $E(I,J) > E(J,J)$.

The definition of an ESS given here is equivalent to Maynard Smith's and Price's (59, 68) original formulations. Selten (103) and Hammerstein (41, 42) are responsible for identifying the two conditions as a game theoretic equilibrium and an additional stability property, respectively. This identification, which was first used by Hammerstein and Parker (40, 43), is important since it reveals that the main property (*i*) of an ESS is equivalent to that of a symmetrical Nash equilibrium point in classical game theory.

The calculations of an ESS for the Root Game with the parameter values of $U < S/2$ are easy. We do not need any further algebra, since the arrows in Figure 4 tell us that the lateral strategy is the only best reply to itself—$E(\text{lateral},\text{lateral}) > E(J,\text{lateral})$ for all other strategies J. In this case, we do not have to check condition (*ii*), since there is no alternative best reply strategy. If $U > S/2$, no pure strategy exists that is a best reply to itself, since the arrows are arranged as in the Game of Chicken (Figure 2). However, as pointed out earlier, a 2 × 2 matrix game with this best reply structure has a mixed equilibrium strategy. We calculate this strategy by using the same method as we used in the Game of Chicken. Suppose that I is an equilibrium strategy of building a lateral root system with positive probability p and a taproot system with positive probability $1 - p$. The characteristic property of I, then, is that both lateral and tap are best replies to I, i.e. $E(\text{lateral}, I) = E(\text{tap}, I) = E(I,I)$. From $E(\text{lateral}, I) = pS/2 + (1-p)S$ and $E(\text{tap}, I) = U$, it follows that $p\,S/2 + (1-p)S = U$. Solving this equation for p yields the equilibrium probability:

$$p = 2(1 - U/S). \qquad 3.$$

This mixed strategy I defined by p is only an ESS if it can be demonstrated that I satisfies the second ESS condition (*ii*), because we know that lateral and tap, for example, are also best replies to I.

In analyzing the second ESS condition, let us suppose that J is an alternative best reply to I and that J develops a lateral root system with probability q. From Figure 4, then, the expected payoff to I when played against J is:

$$E(I,J) = pq\,S/2 + p(1-q)S + (1-p)U, \qquad 4.$$

and the expected payoff to J of playing against itself is:

$$E(J,J) = q^2\,S/2 + q(1-q)S + (1-q)U. \qquad 5.$$

After some calculations, one gets:

$$E(I,J) - E(J,J) = (S - qS/2 - U)(p-q). \qquad 6.$$

This expression is always positive if $p = 2(1-U/S)$, and $q \neq p$, since the bracketed items on the right of the equality sign in Equation 6 are simultaneously either negative or positive. We have thus demonstrated for the case of $U < S/2$ that it is an evolutionarily stable strategy to build a lateral root system with a probability of $p = 2(1 - U/S)$.

The Root Game thus has one ESS for each choice of model parameters: If $U < S/2$, it is an ESS to expand the lateral system; and if $U > S/2$, the ESS is a mixed one of expanding the lateral system with a probability of $p = 2(1 - U/S)$ and emphasizing the tap system with probability of $1-p$. These results need not hold for other evolutionary games. In some cases, there may be no ESS at all and in others there may be several, any one of which may be the outcome of selection realized in a particular historical context. Multiple ESS's are more likely to be encountered in the larger strategy sets consisting of three or more phenotypes. The mathematics used in identifying ESS's for larger games are beyond the scope of this general review, so we refer the reader to Bishop & Cannings (8) and Haigh (35) for examples of treatments of the subject.

EVOLUTIONARY STABILITY VS OPTIMAL RESOURCE EXPLOITATION A common way of analyzing ecological problems is to assume that selection has driven a population to a state in which resources are optimally exploited. However, this approach may lead to inaccurate conclusions if selection is frequency dependent. Let us examine our root problem in terms of simple optimal resource exploitation and compare the estimates derived from the two methods of analysis.

The goal of a shrub population—in the sense of the species optimum—is to adopt the strategy J that permits the maximum uptake of water per individual. The following function F should be maximized:

$$f(J) = E(J,J) = U - qU + qS - q^2 S/2, \qquad 7.$$

We calculate the maximum taking the derivative of $E(J,J)$ with respect to q. This operation yields the expression:

$$dE(J,J)/dq = S - qS - U, \qquad 8.$$

which is 0 for $q = 1 - U/S$. The maximum water uptake per individual would thus be achieved if the probability that the modeled shrub population would develop a lateral root is $1 - U/S$. On the other hand, the ESS probability of emphasizing a lateral root system would be 1 if $U < S/2$ and $2(1 - U/S)$ if $U > S/2$. Thus, for a wide range of parameter values, ESS analysis of the problem predicts that twice as many plants in a local population would emphasize taproots than predicted by optimization criteria (Figure 5A).

The two methods of analysis also produce divergent predictions with respect to the water uptake achieved by the two strategies. Let us compare the expected payoff $E(I,I)$ for the ESS strategy I with the payoff $E(J,J)$ predicted for the species optimal strategy J. If $U < S/2$, then $E(I,I) = S/2$. Otherwise $E(I,I) = U$, since we know that $E(I,I) = E(\text{tap},I)$. After some calculation, one also gets

$$E(J,J) = q^2 S/2 + q(1-q)S + (1-q)U = (S^2 + U^2)/2S. \qquad 9.$$

The water uptake predicted by the optimal solution is consistently higher than the ESS solution to the problem (Figure 5B). Depending on the values of the parameters used, the differences may be as great as 25%.

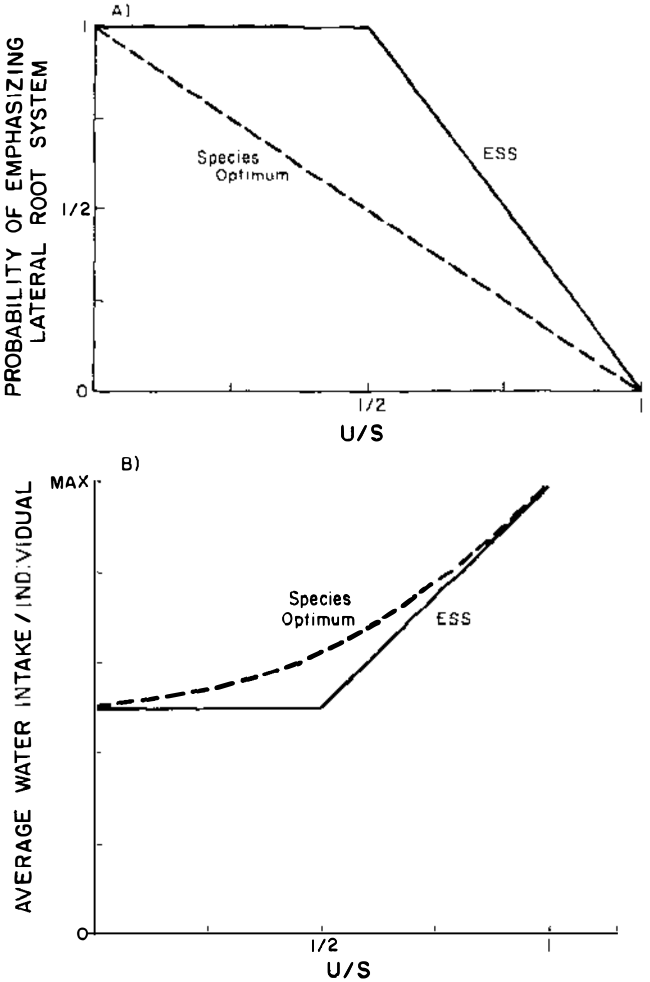


Figure 5 A comparison of the predictions of ESS vs species-optimum analyses of a hypothetical root-competitive system over a range of environmental contexts: A) the proportion of phenotypes emphasizing lateral roots in a population as a function of the ratio of underground water to surface water; B) a comparison of predicted water uptake per individual as a function of the same ratio as in A, but with a fixed value of S. In both A and B, dashed lines equal species-optimum predictions for given parameters; solid lines equal ESS predictions.

ADDITIONAL EXAMPLES In the context of animal conflict, Maynard Smith & Price (68) proposed the Hawk-Dove Game as a standard paradigm for evolutionary game theory. In the simplest version of this game, corresponding to our root game, contestants may play either an aggressive strategy called escalate or a nonaggressive strategy called display. The ESS of the Hawk-Dove game is a mixed strategy, namely to escalate with a low probability and display with a high probability if fighting is costly and vice versa if it is not. In extreme cases, the ESS may even be the pure strategy of escalating.

The game becomes more complicated when the two players are assigned distinct roles, A and B, such as owner and intruder in territorial conflicts (59, 67). The ESS is then to escalate in one role and to display in the other. Selten (103) has demonstrated mathematically that if there is a role difference that can be perceived by the players, then the ESS must always be a pure strategy in these asymmetric contests. Role asymmetries, then, are typically used in the conventional (i.e. nonfighting) determination of contest winners and losers. There can be more than one asymmetry in a contest and, as the complexity increases, so does the task of locating the ESS's for the game. This increasing difficulty occurs because, in order to identify an ESS, all of the roles that an individual potentially will fill during its life must be included in the analysis. The evolutionary game describing asymmetric contests is, in principle, a symmetric game. However, Hammerstein (40, 42) has developed a method in which models of asymmetric contests can be decomposed into subgames where asymmetric Nash equilibrium points become relevant to evolutionary game theory. This modification has greatly simplified the analysis of this type of game.

Role differences are generally associated either with differences in fighting ability or in rewards associated with winning (the so-called correlated asymmetries). It is possible, however, that an ESS may "instruct" a player to be aggressive in a given role (A) and nonaggressive in another role (B), despite the fact that role does not affect relative fighting ability or reward. These instances are called uncorrelated asymmetries; there has been considerable interest in trying to understand the conditions under which correlated vs uncorrelated asymmetries may settle contests conventionally (40, 42, 43, 80, 84). In the more continuous strategy sets such as those with finely tuned levels of aggression, it appears as if only "commonsense" or correlated asymmetries are possible—e.g. the owner or stronger opponent wins. On the other hand, the discrete strategy sets may lead to far less obvious conventions of settling disputes.

Being able to analyze the asymmetric contest is extremely important, since there are numerous biological examples of this contest structure. A few fall into the uncorrelated category. For instance, Davies (17) presents evidence for an uncorrelated asymmetry that settles territorial disputes among male speckled wood butterflies. Males defend sunspots that they occupy while waiting for females during mating periods. The asymmetry is one of ownership vs nonownership or firstcomer vs latecomer status. Davies found that the ownership status of individuals can be reversed experimentally, with appropriate changes in the behavior of the contestants resulting. Furthermore, manipulations producing two owners led to prolonged fights that were not observed when the ownership asymmetry was present. There is some difference of opinion as to whether this contest situation represents an uncorrelated asymmetry that may give firstcomers fighting advantages, since time in sunspots increases the body temperature of the occupants (3). Other examples of possible uncorrelated asymmetries include competition for access to females in parasitic Hymenoptera (112), for funnel retreats in a colonial spider (12), and for foraging sites in the zebra spider (48). In the case of the social spiders, Burgess (12) actually observed an "intruder wins rule" for occupation of disputed funnel retreats in a colony. Owners withdraw from the retreats upon encroachment by conspecifics and in turn encroach upon nearby retreat holders, creating a domino effect with successive changes of retreat ownership in the colony.

Most of our observations of asymmetric contests, however, are examples of the common sense or correlated type. One such case has been documented for the funnel web spider, *Agelenopsis aperta*, which competes for web sites and associated energy-based territories (90). The situation exhibited by *Agelenopsis aperta* represents a particular challenge to evolutionary game theory, since it has been possible to make quantitative measurements of many features relevant to functional ESS analyses. Riechert's extensive field studies (89–94, 96) provide data about both payoffs and strategic behavior. The quality of web sites is known and varies both within and between populations. Two asymmetries—the relative weight of the opponents and the ownership status—exist in the territorial disputes of this spider. These parameters are the major determinants of contest structure and outcome (91, 92, 94, 95). Two kinds of games have been proposed to date as first approximations of these agonistic interactions (40, 42, 66). However, we have yet to deal with the complex sequential structure evident in these contests. At the beginning of a contest, for instance, only the territory owner seems to "know" the site quality. By the end of the first bout of the contest (i.e. first series of actions leading to a retreat by one of the spiders), however, the intruding spider appears to have obtained this information, which does not appear to be overtly transmitted by the owner (69). The available theoretical framework that could deal with these complications is an extensive representation of the game's sequential and informational structure similar to that which Selten (102) discussed for classical game theory.

It is not possible to consider here the many contest models that have been developed along the lines of the Hawk-Dove game. Rather, we refer the reader to Maynard Smith's reviews [(63, 66); and with Slatkin (105)] for both discussions of the models and additional biological examples (see also 18). In the present paper, it seems more important to emphasize that evolutionary game theory can be applied to a much wider range of situations than simply agonistic behavior. For example, the problem of parental investment in offspring can be conceived as a game in which the parents, and often the offspring also, are players (33, 56, 57, 61, 81–83, 100).

Another important application of evolutionary game theory is to the problem of the evolution of cooperative behavior. Consider an example given by Pulliam et al (85) involving a winter feeding flock of juncos, a subset of a local population. The risk of predation by hawks and other large vertebrates is a major concern to these birds during foraging bouts. A solitary forager must, therefore, take time out from feeding to scan for predators. Within the foraging flock two alternatives are available to the birds: (*a*) the noncooperative alternation of scanning and feeding by all individuals and (*b*) the cooperative alternative of having a few individuals scan while others continuously forage. It was deduced from empirical studies that the actual behavior of the juncos is cooperative. Because it is more advantageous for each individual of the flock to feed and to let others scan, rather than vice versa, we have a game-like situation.

Pulliam and his collaborators point out that the scanning game is not played once, but many times, in the flock. From classical game theory, it is well known that repeated games between the same interacting individuals (so-called supergames; 55) may have to be played cooperatively by rational players, although the rational solution to a single such game would be to behave in a noncooperative fashion. The pairwise Prisoner's Dilemma Game outlined earlier takes this form if the game is played several times. The rational behavior in the repeated Prisoner's Dilemma Game is to deny rather than to confess. This outcome, however, only will occur if there is sufficient uncertainty concerning the number of repetitions. In his work on reciprocal altruism, Trivers (108) was the first to recognize the consequences of repeated games in a biological context. A number of workers have contributed to our understanding of the phenomenon since then (4, 25).

Games With Many Players

In many ecological contexts competitive effects are not limited to pairwise interactions. The success of one individual in a local population, for instance, may be dependent on how much food other members of its population have consumed per unit of time. In this section, we show how the Root Model might be extended to permit an analysis of the context where many players are involved.

As in the pairwise analysis, there are two pure strategies—lateral and tap—and the corresponding mixed strategies consisting of various probabilities assigned to each of them. We make different assumptions about the level of competition that individuals possessing tap vs those possessing lateral roots encounter: an individual shrub emphasizing the taproot competes with all members of its local population for a portion of the water available in the local underground reservoir, while the individual with the expanded lateral system competes only with its nearest neighbors—assuming that the spacing is regular, as indicated for many desert plants (e.g. 5, 7, 27, 73, 111, 113).

Let us now reconsider the Root Game, adapting the model to nonpairwise interactions. If our desert shrubs are spaced such that all individuals are equidistant from one another, then every individual finds itself in the center of a hexagon with a neighbor at each of the 6 corners. We propose that competition for surface water is local—i.e. that each shrub competing for surface water does so with a maximum of 6 other individuals. Let $S_{\min}$ equal the minimum amount of water a shrub adopting the lateral root strategy can obtain; a given lateral root player will receive $S_{\min}$ in those cases when all 6 of its neighbors also adopt the lateral strategy. If one of this shrub's neighbors plays tap, however, its payoff increases to $S_{\min} + S_{\min}/6$. The general equation for the amount of water available to shrubs emphasizing the lateral root system is then $S_{\min}(1 + n/6)$, where n denotes the number of neighbors emphasizing taproots.

At the level of the underground water reservoir, we assume that competition is more global and that the quantities of water available to shrubs emphasizing the taproot system depend on how many taproot players are present in the population. The availability of underground water is therefore represented as a linearly decreasing function of the proportion, q, of taproot players in the population. Water uptake by shrubs utilizing the taproot system is expressed as $U(1 - uq)$ where U denotes the maximum quantity of water a shrub with a major tap root might obtain under extremely low competition and u denotes the relationship between the number of competitors and water availability in the underground reservoir.

Unlike the pairwise models we have dealt with in previous examples, we cannot analyse the n-person game in payoff matrix form. Since neighbors interact with other neighbors, it is impossible to identify small groups of players that interact only among themselves. Hammerstein [in Maynard Smith (66) and in (41, 42)] has developed the methodology for dealing with evolutionary games consisting of large numbers of players. He replaces the payoff matrix with the payoff function $W(J,I)$, which represents the expected change in fitness received by an individual playing strategy J in a population of I players. As before, we consider two alternative pure strategies—lateral and tap. Let us assume that the mixed strategy I consists of building a lateral root with probability I_1 and a taproot with probability $I_2 = 1 - I_1$. We define the game by analyzing the payoff function associated with the two special cases first: $I_1 = 0$ (the pure tap strategy) and $I_1 = 1$ (the pure lateral strategy). The payoff to a shrub producing a lateral root in an I-playing population is $W(\text{lateral}, I) = S_{\min}(1 + n/6)$, with n equal to the expected number of taproot neighbors. Since I_2 is the probability that a neighbor emphasizes the tap system and there are 6 neighbors, we have $n = 6I_2 = 6(1 - I_1)$. Substituting this expression for n and using the parameter $S = 2S_{\min}$ for the maximally possible water intake from the surface, one gets:

$$W(\text{lateral}, I) = S(1 - 0.5I_1). \qquad 10.$$

We can obtain the expected payoff for the pure tap strategy in a similar manner. According to our introductory statements, we have $W(\text{tap},I) = U(1-uq)$. In an I-playing population, the proportion of taproots in the population $(q) = I_2$, and thus:

$$W(\text{tap}, I) = U(1-uI_2). \qquad 11.$$

From these derivations for the two extremes, we can define $W(J,I)$ for the mixed strategy J as:

$$W(J,I) = J_1W(\text{lateral}, I) + J_2W(\text{tap}, I) = J_1S(1 - 0.5I_1) + J_2\, U(1-uI_2) \qquad 12.$$

ESS CONDITIONS The mathematical notion of the ESS given in the previous section only applies to pairwise interactions. We will consider the generalizations of the equilibrium (*i*) and the stability (*ii*) conditions in turn here. An evolutionarily stable strategy must be adaptive in a population of individuals playing this strategy. A strategy I has this property if it is a best reply in the following sense:

(*iii*) Equilibrium Condition
$W(I,I) \geqslant W(J,I)$ for all strategies J.

The equilibrium condition is similar to that used for pairwise interactions. It differs in that the expected payoff W has a different meaning from the payoff E in (*i*). According to the definitions made above, $W(J,I)$ denotes the payoff for playing J in a population of I players, whereas $E(J,I)$ denotes the payoff for playing J against a single I player.

The stability condition is more difficult to extend to the infinite population game. Remember that an equilibrium strategy identified under condition (*iii*) may not be the only adaptive strategy present in a population of I players; other strategies, J, may also exist such that $W(J,I) = W(I,I)$. An I playing population is only stable against intrusion by an equally adaptive strategy J if the fitness of J is smaller than the fitness of I in a "disturbed" I population containing a small fraction ϵ of J-players. Let us denote this disturbed population by $P_{I,J,\epsilon}$ and let $W(J, P_{I,J,\epsilon})$ and $W(I, P_{I,J,\epsilon})$ denote the fitness in population $P_{I,J,\epsilon}$ of J and I, respectively. With these definitions, the stability condition can now be formulated. An equilibrium strategy *I* is said to be stable against strategies that are also adaptive in a given equilibrium population of *I*-players if it has the following property:

(*iv*) Stability Condition

> For every strategy $J \neq I$ such that $W(J,I) = W(I,I)$, the inequality $W(I,P_{I,J,\epsilon}) > W(J,P_{I,J,\epsilon})$ holds for sufficiently small values of ϵ.

In calculating the ESS for the *n*-person or infinite population Root Game, we have to remember that the model assumes that there are upper and lower limits to the amount of water an individual gains from developing lateral roots or taproots. The water intake cannot be greater than $\max_{lat} = S$ for a lateral root and $\max_{tap} = U$ for a taproot. Conversely, the average water intake cannot be any lower than $\min_{lat} = S/2$ at the surface and $\min_{tap} = U(1-u)$ at the underground water source. The pure lateral strategy is an ESS if $\min_{lat} > \max_{tap}$. In this case, no mixed ESS exists. Likewise, the pure tap strategy is an ESS if $\min_{tap} > \max_{lat}$. For these two strategies, the inequality (*iii*) holds in its strict form and condition (*iv*) need not be checked.

For the range of average payoffs in which $\min_{lat} < \max_{tap}$ and $\min_{tap} < \max_{lat}$, however, a mixed ESS exists. Suppose that *I* with $0 < I_1 < 1$ is a mixed strategy such that $W(I,I) \geqslant W(J,I)$ for all *J*. According to Hammerstein (42), this condition is equivalent to saying that *I* satisfies the following equation:

$$W(\text{tap}, I) = W(\text{lateral}, I), \qquad 13.$$

which again is the characteristic property of best reply strategies. This equation simply implies that:

$$S(1 - 0.5I_1) = U(1 - uI_2). \qquad 14.$$

Solving this last equation yields the mixed equilibrium strategy $I = (I_1, I_2)$, with

$$I_1 = \frac{S/U + u - 1}{u + 0.5\,S/U} \qquad 15.$$

Of course, any other strategy $J \neq I$ would be just as successful as *I* in a population playing *I* exclusively (i.e. $W(J,I) = W(I,I)$ for all strategies *J*). This result forces us to check whether the second ESS condition (*ii*) is satisfied. If we assume that there is no difference between the fitness of a strategy in a population playing the strategy $(1 - \epsilon)I + \epsilon J$, and in a population consisting of a fraction, $1-\epsilon$, of *I*-players and a fraction ϵ of *J*-players, then the inequality in the stability condition (*iv*) may be simplified as follows. Let $K = (1 - \epsilon)I + \epsilon J$ be the strategy to "build lateral roots with a probability $(1 - \epsilon)I_1 + \epsilon J_1$." The inequality in (*iv*) then is equivalent to:

$$W(I,K) > W(J,K). \qquad 16.$$

In order to show that the equilibrium strategy I satisfies Equation 16 note that:

$$W(I,K) - W(J,K) = (I_1 - J_1)\,[W(\text{lat},K) - W(\text{tap},K)]. \qquad 17.$$

Suppose first that $I_1 < J_1$. From this it follows that $K_1 > I_1$ and thus $W(\text{lat},K) < W(\text{tap},K)$. The expression in Equation 17 is positive then as required. Conversely, if $I_1 > J_1$, this expression is also positive, since this implies that $W(\text{lat},K) > W(\text{tap},K)$. Thus the strategy I defined in Equation 15 is not only an equilibrium strategy, but also an ESS, and I has properties similar to those obtained for the ESS in pairwise interactions.

ADDITIONAL EXAMPLES A classical problem to which evolutionary games with many players can be applied is that of sex ratios. Fisher (26) was the first to show that if the production of male and female offspring is equally costly, then females should produce both sexes at equal rates; his argument has received considerable attention (e.g. 14, 15, 37, 64, 109). Let us briefly show how sex ratio theory fits into the theoretical ESS framework outlined in this section. [See Maynard Smith (66) for an explicit presentation.] A strategy I is the relative proportion of males that the corresponding phenotypes would produce on the average. There is a continuum of such strategies ranging from $I = 0$ to $I = 1$. For example, in $I = 1/3$ male and female offspring are produced at a ratio of 1:3. Let us consider the payoffs. Because the main selective effect involved in the sex ratio does not show up in the F_1 but in the F_2 generation, the number of grandchildren must be used as the fitness measure in this game. Let the fitness function $W(I,J)$ denote the number of grandchildren that an I player has in a population of J players. The following equation for I is based on the assumption that every offspring has both a mother and a father (the notable exception is the haplodiploid Hymenoptera): $W(I,J) = N^2(1 - I + I(1-J)/J)$, where N is the total number of offspring a female can produce. In order to calculate an equilibrium strategy I for this infinite set of strategies, we can use the following condition:

$$[\partial\, W(H,I)/\partial\, H]_{H = I} = 0 \qquad 18.$$

It turns out that this condition is only satisfied for $I = 0.5$. This strategy I can also be shown to satisfy the stability condition (*iv*). We thus get the classical answer to the sex ratio problem: $I = 0.5$ is an ESS.

Hamilton & May (39) discuss an interesting ecological problem using a similar theoretical approach to that outlined in this many player section. They ask how offspring dispersal is affected by intraspecific competition. They find 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. By inspection of various models, they also show that seed dispersal cannot be understood in terms of species-optimum utilization of resources. This conclusion is analogous to our result for the Root Game—namely that the predicted ESS for water consumption is significantly lower than that expected for species-optimal water consumption. Ellner and Shmida (21, 22) also submit the seed dispersal problem to ESS analysis.

Another problem of a game theoretic nature concerns how animals distribute themselves over habitat patches in a variable environment. Parker (79) considered this problem for male dung flies *(Scatophaga stercoraria)* seeking matings at cowpats that ranged from fresh to less fresh. Since female dung flies are more likely to approach fresh cowpats than older ones, cowpats vary in quality to the males. According to the concept of the Ideal Free Distribution (28, 29), in the absence of active competition for sites, organisms should be distributed in such a way that the fitnesses in different habitat patches are equalized. Parker (79, 80) found that the distribution of male dung flies on the set of cowpats available matched the Ideal Free Distribution. Harper (44) noted a similar distribution of mallard ducks in feeding patches. The exhibition of an Ideal Free Distribution may be consistent with game theoretic predictions if the following conditions are met: (*a*) the species lacks the strategic means to defend habitat patches against occupation by conspecifics, (*b*) individuals can freely move between patches. Similar comments can be made about some foraging problems (e.g. 71).

In another many player context, the decision between "digging" a burrow or "entering" an already existing burrow has been identified as a choice encountered by the digger wasp, *Sphex ichneumoneus* (10, 11, 19). Associated with the enter strategy is a risk of encountering a burrow owner, leading to an agonistic bout. The ESS solution to the problem of whether to dig or to enter is a mixed one. The example is especially interesting because of the availability of data from two populations that indicate that the model developed in Brockmann et al (11) explains the data from only one population; the other apparently is not at an ESS. Other many-player contexts that have been analyzed as evolutionary games include "arms races" in nature (36, 66, 81) and the effect of intraspecific competition on plant growth (72).

Competition Involving Two or More Species

The general kind of model introduced in the previous section can be extended to cases simultaneously involving both intra- and interspecific competition. We discuss the game-theoretic analysis of a two-species system along the conceptual lines proposed by Hammerstein (42), again using root competition in desert shrubs as an illustration.

Suppose that two shrub species compete for water, both being able to emphasize either the lateral or the taproot systems. Neither strategies nor payoffs (in fitness) are considered comparable between species: Each species is assumed to have its own strategy set and measure of relative fitness. Therefore, the payoff in terms of fitness to an individual in population 1 will be termed W_1, and the payoff to an individual in population 2 will be W_2. Technically, the lateral and tap strategies should also be indexed in order to clarify the population strategy set to which they belong. To avoid excessive use of indices in this case, however, we assume that the strategy set to which tap and lateral belong will always be clear from the context. The same convention holds for mixed strategies I, J, etc.

Unlike the one-species case, the interspecific analysis must take the relative numbers of individuals belonging to the respective species into consideration. Let x denote the relative abundance of species 1, and y that of species 2. The distribution $A = (x,y)$ with $x + y = 1$, will be referred to as the relative-abundance distribution.

The model can now be outlined as follows. A strategy I for member of species 1 is a pair of probabilities $I = (I_1, I_2)$ that lateral and tap will be realized. A strategy $J = (J_1, J_2)$ for population 2 is defined analogously. A particular combination (I,J) of single strategies for each population will be called an interspecific strategy combination. The two-species system is said to play this combination when population 1 consists of I-strategists and population 2 consists of J-strategists. At this point, payoffs have to be introduced. In the present framework, an allowance is made for the simultaneous occurrence of frequency-dependent intra- and interspecific effects on fitness. The fitness of a given individual depends thus on the strategies being played in both populations. Furthermore, fitness is assumed to depend on the relative abundance of the species involved. As in the previous section, the notion of payoff can be defined as the Darwinian fitness of a single stategist in a community in which all members of a particular species population exhibit the strategy typical to that population.

Therefore, for a given distribution $A = (x,y)$ of relative abundances, let $W_1(H, I, J, A)$ denote the payoff to a single H strategist in population 1 if members of the community play the interspecific strategy combination (I,J). Also, let $W_2(K, I, J, A)$ denote the corresponding payoff to a single K strategist in the second population. Using similar arguments to those used in the previous section, these payoffs can be defined as follows for the root game:

$$W_i(\text{lateral}, I, J, A) = S_i\,[1-0.5(xI_1 + yJ_1)] \qquad 19.$$

$$W_i(\text{tap}, I, J, A) = U_i[1-u(xI_2 + yJ_2)], \qquad 20.$$

for $i = 1,2$. In order to understand these definitions, remember that, for example, I_1 and I_2 represent an I player's probabilities of emphasizing lateral roots and taproots, respectively. Therefore, the term $xI_1 + yJ_1$ represents the probability that a randomly chosen individual emphasizes the lateral root system. Correspondingly, the term $xI_2 + yJ_2$ stands for the complementary probability that the taproot is emphasized. These equations explain how the fitnesses associated with lateral and tap relate to those defined in the previous section. Finally, the payoff to a mixed strategy $H = (H_1H_2)$ is again defined as the expected fitness associated with playing H:

$$W_i(H, I, J, A) = H_1W_i(\text{lateral}, I, J, A) + H_2W_i(\text{tap}, I, J, A). \qquad 21.$$

ESS COMBINATIONS The mathematical conditions for evolutionary stability in n-species models are detailed in Hammerstein (41). Reflected in the conditions is the idea first proposed by Maynard Smith & Price (68) that, within a species, a strategy must be stable against invasion by mutant strategies that are encountered sequentially (i.e. one at a time). Hammerstein proposes that we extend this idea to the n-species context by assuming that only one mutant strategy is encountered in a community at a given time and that strategies must be stable against invasion by this single mutant. This extension of the Maynard Smith & Price stability assumption is also implicit in the coevolution arguments for competing species presented by Lawlor & Maynard Smith (50).

A conceptual remark concerning the distribution $A = (x,y)$ of relative species abundances must also be made before we are able to state the ESS conditions for the n-species games. "Complete" vs "partial" model analyses deal with A in different ways. In the complete model, assumptions about how A depends on the strategies played are included in the analysis, whereas in the partial model there are not. Corresponding to these two types of models, there are two methods of analyzing interspecific competition. "Pragmatic" calculation of ESS's for all A's is associated with the partial model. Generalized conclusions about strategies that are independent of A must then be drawn from inspecting the list of ESS's obtained from the calculations. However, if a specific biological example is being investigated, the species relative-abundance distribution, A, can be specified for the partial model and only one ESS calculation need be completed. In the complete model, one must attempt to predict both strategies and relative species abundances simultaneously. It is not sufficient to merely show which strategies would be evolutionarily stable for given species abundance distributions; one must also determine whether A would be generated by these strategies. In principle, the complete model approach will provide more information about a system than the partial analysis method. In practice, however, we rarely will have the kind of understanding of the dynamics of a particular system that is required for successful completion of the full model analysis.

We will use the partial two-species model in analyzing the Root Game. As such, ESS's must be identified with respect to given A's. If we fix a strategy J for population 2, but consider the full set of strategies for population 1, however, we will have reduced the game for population 1 to a single-species game that is "induced by J." This manipulation permits us to state the definition of an ESS combination *(I,J)* by means of the formal ESS conditions already introduced for the single species case.

An interspecific strategy combination *(I,J)* is called evolutionarily stable (i.e. is an ESS combination) with respect to a given *A* if it satisfies the following two conditions:

(*a*) *I* is an ESS for the single species game induced by *J*.
(*b*) *J* is an ESS for the single species game induced by *I*.

In the complete model, one must identify that strategy combination *(I,J)* and the associated abundance distribution *A* that satisfies (*a*) and (*b*) and the additional condition:

(*c*) *A* is ecologically stable, given *(I, J)*.

CHARACTER DIVERGENCE We are now equipped with the conceptual background necessary to analyze the two-species Root Game introduced above. In this game we assume that the two species in question differ slightly in the efficiency with which they exploit the surface water source vs the underground water source; species 1 is the more efficient one of the two species. In terms of our model parameters, this condition means that $S_1/U_1 > S_2/U_2$. We also assume that the difference in the surface and underground exploitation efficiencies of neither species is strong enough to favor a given root system, regardless of the root composition of the community: $S_1 > U_1 (1 - u)$ and $U_2 > S_2/2$.

The game can be analyzed using techniques that have already been presented. For example, if *(I, J)* is an ESS combination in which *I* is to play both lateral and tap with positive probabilities, then the equation $W_1(\text{lateral}, I, J, A) = W_1(\text{tap}, I, J, A)$ must hold. Because we assume that the two species differ in their efficiencies of water utilization at their respective levels, however, the analogous equation for species 2 cannot be satisfied simultaneously. Either *I* or *J* must, therefore, be a pure strategy that only emphasizes roots at one resource level.

After some calculation we find that, for given model parameters, there is exactly one ESS combination for each distribution of relative abundance. The ESS combination will be one of three types shown in Table 1. All three types of ESS combinations share the following features:

(*a*) Species 1 emphasizes the lateral system with a higher probablity than species 2 (remember here that $S_1/U_1 > S_2/U_2$).
(*b*) Species 1 plays lateral with a higher probability and species 2 plays lateral with a lower probability than either would in the absence of interspecific competition.
(*c*) Both species do not play mixed strategies simultaneously.

Table 1 Evolutionarily stable strategy combinations for the two-species root game[a]

Condition	Probability of emphasizing lateral root system	
	Species 1	Species 2
$1 - yu < R_2(1 - x/2)$	1	$\frac{R_2(1 - x/2) + uy - 1}{y(u + R_2/2)}$
$R_2(1 - x/2) < 1 - yu < R_1(1 - x/2)$	1	0
$R_1(1 - x/2) < 1 - yu$	$\frac{R_1 + u - 1}{x(u + R_1/2)}$	0

[a] Here, $R_i = S_i/U_i$ denotes the relative value of the surface water resource to species i. Furthermore, x and y are the relative abundances of species 1 and 2, respectively, and u is a measure of the effect of taproot density on the underground water resource.

We illustrate these points in Figure 6, which represents a numerical example of the analyses showing how the ESS combination varies with the distribution of relative species abundances. In this example, both species are assumed to be more efficient users of surface than of underground water, though 1 is slightly more efficient than 2. Therefore, in the absence of interspecific competition, each would evolve to a similar ESS that emphasizes lateral roots with a moderately high probability (i.e. the dashed lines for the respective species in Figure 6). Intraspecific competition in this case effects the exhibition of some degree of root emphasis in both populations. The evolutionary outcome of interspecific frequency-dependent effects is a strong divergence in root-system emphases in the two species (Figure 6). An ecological interpretation of the outcome of the ESS analysis is that the character divergence induced on 1 by species 2 is the result of release from intraspecific competition, whereas 2's results from the avoidance of interspecific competition with 1. Slatkin (104) emphasizes the significance of species relative abundances in coevolution. The results of our analyses also show that these abundances have a strong quantitative effect on the ESS root composition.

Other Models of Coevolution

The first attempt to extend ESS theory to the coevolution of competing species was undertaken by Lawlor & Maynard Smith (60). As in the Root Game above, their treatment involved a two-species case and the partitioning of two distinct resources. Maynard Smith & Lawlor, however, used a definition of evolutionary stability that is limited to a special type of model and does not refer explicitly to a game. Such analyses are best completed using explicit games with many players.

Auslander et al (2) also analyzed a coevolution problem, in this case between a host and its parasite. The host larvae were assumed to dwell either "shallow" or "deep" in the ground while developing; the parasite had identical choices.

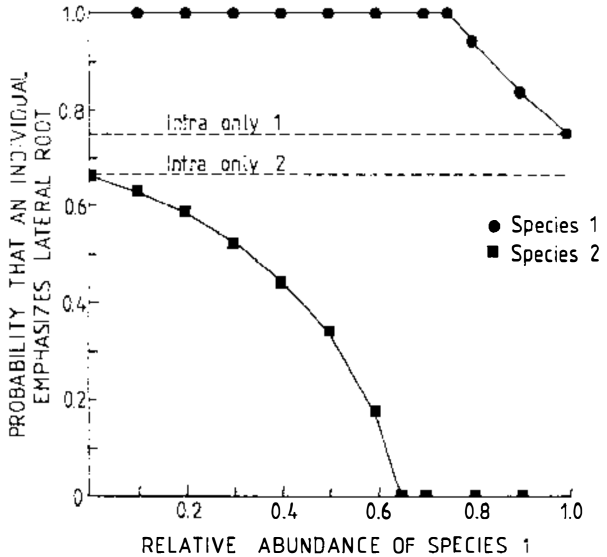


Figure 6 ESS-combinations in a two species Root Game as shown by the solid lines. It is assumed that both intra- and interspecific frequency-dependent selection are in operation. The dotted lines show the ESS-probability of emphasizing the lateral root system for each species in the absence of the other species. The parameter values used in the example are: $S_1/U_1 = 1.6$; $S_2/U_2 = 1.5$; $u = 0$.

They identified a pair of mixed strategies that were evolutionarily stable in the game-theoretic sense. They were not stable, however, when the selection process was modeled as a dynamic system, because the authors used the term ESS as synonymous with the Nash equilibrium point. They did not test for the additional second criterion (*iv*: the stability property). Their "game theoretic solution," in fact, does not meet the second criterion and thus is not an ESS (see 41, 47).

The gregariousness of prey in the coevolution of predator-prey systems is another area where game theory has been applied. In his "geometry for the selfish herd," Hamilton (38) pointed out that a single prey individual may be more likely to be captured alone than in a large herd, if predators select prey randomly from the first group of prey they meet. Eshel (23, 24) extended Hamilton's ideas and emphasized their game-theoretic aspects.

CONCLUDING REMARKS

The population geneticist might think that evolutionary game theory is merely a reformulation of the theory of frequency-dependent selection. While it is true that ESS analyses lead to conclusions that could be reached through the framework of population genetics (e.g., 24, 65), it would take a much greater effort. ESS theory's significant contribution is that it permits us to investigate complex systems which would be difficult, if not impossible, to delineate through more classical genetic methods of analysis.

We would like to make one further comment, in this case concerning the relationship between classical and evolutionary game theory. In a recent review of Maynard Smith's (66) book, *Evolution and the Theory of Games,* Lewontin (53) attributes the success of the book to its avoidance of a game-theoretic apparatus. In this review, however, we have shown that a very close relationship exists between the solution concepts of the two theories. Thus the apparatus of classical game theory is very relevant to biology and is more evident in Maynard Smith's book than Lewontin suggests.

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