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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. It is hoped that the model developed is a simplified representation of reality, one that provides insight into the structure and function of often complex systems (Jeuken 1969). Of the many models applied to ecological problems, the principle of optimization, borrowed from economics, has received considerable use (Rapport and Turner 1977). In optimization models, a goal variable (currency) is maximized using some cost-benefit function. Our 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 optimum or fine-tuned responses to environmental contexts. The currency here is Darwinian fitness and the goal, its maximization. The methodology and problems associated with the application of optimality theory to ecological problems has received extensive treatment in several reviews (Cody 1974; Maynard Smith 1978; Oster and Wilson 1978; Oster and Rocklin 1979; Lewontin 1979). Despite some criticism of it (see Rapport and Turner 1977), many workers feel that "optimization models have been, and are likely to remain, the principle conceptual framework for thinking about evolutionary trends at the phenotypic level" (Oster et al. 1980).

The species optimization criteria most often used in ecology are best applied to cases in which the performance of an individual is independent of (is not affected by nor has an affect 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 the modeling effort. This review is intended to provide ecologists both with the necessary background and incentive to use the evolutionary game theory construct in place of species optimization where appropriate.

The biological variant of game theory originated with Maynard Smith and Price (1973) and the reader should consult Maynard Smith's recent (1982) book 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 areas that are not detailed in his treatment: 1) the links between classical and evolutionary game theory; 2) the application of evolutionary game theory to ecological problems; and 3) 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 the relationships herein. 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 a local population competitive phenomenon. Both within species and between species competition are dealt with. 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 diffeence in the outcomes of these two methods of analysis are far from trivial. Finally we consider other applications to which 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 exhibited 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 form 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 greater, being of considerable importance to economics and business (e.g., Selten 1973; Marschak and Selten 1974; Friedman 1977; McDonald 1975; Schotter and Schwödiauer 1980), the social sciences and politics (e.g., Riker 1962; De Swaan 1973; Brams 1975), the military (e.g., Aumann and Maschler 1966), social psychology (e.g., Bartos 1967; Goffman 1969; Rapoport et al. 1976), and most recently to evolutionary biology (e.g., Hamilton 1967; Trivers 1971; Maynard Smith and Price 1973; Maynard Smith 1982). Nevertheless, the terminology used in parlor games and the theory of games is similar. The decision-makers are termed "players" and the objective function of optimization theory is the "payoff function" which assigns a value or measure of success received from playing a particular "strategy" (specification of how a player will act in all potential situations). The "game" then is a collection of rules known to all players which determines what each player can possibly do and the outcome of the use of particular choices or strategies.

Game theory was originally developed by von Neumann and Morgenstern (1944) as a mathematical tool for the social sciences. Its classical aim was to provide insight into the problem of rational (conscious) decision-making in interpersonal conflicts (See Luce and Raiffa (1957) for a discussion). This involved the mathematically intricate task of dealing simultaneously with the strategical planning of at least two players, each of them trying to obtain the best possible payoff for his personal interest. In classical game theory, a player's payoff is measured subjectively and is defined by personal value judgements of what success is. In contrast neo-Darwinian analysis of this type of contest replaces the subjective notion of success with an objective criterion. Here, the player's payoff is measured as its change in expected Darwinian fitness resulting from playing a particular strategy in a game. 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. By decision we here refer 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 parallel between the ways in which neo-Darwinists and classical game theorists analyze conflicts is in the attention given to individual success and not to the success of groups or aggregates of individuals. This criterion is of course, especially important to biological applications of the theory, since the theory of natural selection emphasizes contributions to the reproductive success of individuals rather than to populations or other higher categories. In both the neo-Darwinian and classical game theory one cannot use simple optimization criteria in identifying a successful strategy: the payoff maximum changes with the relative frequencies of use of different strategies in the population or group of players. How then is a solution to a contest reached? In the classical "non cooperative game," the Nash Equilibrium Point (Nash 1951) is used as the basic solution concept. Evolutionary game theory is based on the structure of non-cooperative game theory. This is because cooperative game theory does not emphasize strategic solutions and often considers payoffs to groups of individuals, whereas non-cooperative game theory includes both cooperative and non cooperative contexts in which the solution is based on benefits to individual players (See for example Harsanyi and Selten 1980)). 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 to the classical game). 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, attention was drawn to other quantities—especially to the concept of the worst possible outcome. The so-called "maximin philosophy" (sometimes referred to as the minimax) was based on the idea that a player should choose that strategy which maximizes among the worst possible outcomes. Since the work of Nash (1951), the maximin principle has not been central to classical game theory, though some workers still apply it in limited contexts (e.g., Rapoport 1980). This fact has not been recognized in some of the comparisons biologists make between classical game theory and evolutionary game theory. Maynard Smith (1976), for example, placed too much emphasis on the differences between the 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 (Selten 1980; Hammerstein 1981). The Evolutionarily Stable Strategy as defined by Maynard Smith and Price (1973) for pairwise animal conflicts has the property that a population of individuals adopting the strategy I is stable against invasion by initially rare mutants adopting other strategies J. For I to be an ESS, the expected payoff in fitness E of I played against itself must either be greater than that of any other strategy J played against I

$$E\ (I,I) > E\ (J,I)$$

or 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:

$$E\ (I,J) > E\ (J,J).$$

(This ESS-condition is based on the assumption of random pairing of conflict partners). A successful strategy (trait) from the standpoint of Darwinian fitness must therefore, not only be well adapted to its environment, but also must be adaptive with respect to potential competition with conspecifics and perhaps even with heterospecifics. The success of this trait depends critically 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 particularly developed by Lewontin (1961), Lloyd (1977) and Slatkin (1979). Within this theoretical framework, one can look for population states in a trait that are in a dynamically stable equilibrium under selection. The ESS solution approximates such states.

It is unreasonable to expect that ultimately ESS theory should be converted to a branch of population genetics. It has been developed to provide insight into the evolution of phenotypes in the more complex ecological situations without detailed knowledge of the genetic system underlying the traits. One only assumes that enough genetic variability exists for natural selection to work on. For computational simplicity, in fact, ESS analyses are usually based on asexual inheritance. As such the ESS is defined as the phenotype toward which members of a species population would evolve given parthenogenetic (haploid) inheritance. Where sexual inheritance (diploid) has been incorporated into the ESS model, similar results have been obtained to those achieved with the haploid model for the two strategy game involving unselected players (Gadgill et al, 1980; Hines 1980; Maynard Smith 1981; Treisman 1981). There is a problem, however, with polymorphic populations exhibiting more than two strategies. Gadgill et al. (1980) 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 (Slatkin 1979; B. Charlesworth in Lloyd 1977). The ESS solution, then can be reliably applied to most ecological contexts involving frequency dependent selection.

THE NATURE OF A GAME: CLASSICAL GAME THEORY

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 still sketch the major goals and methodology of classical (non-cooperative) game theory.

Consider the famous classical paradigm about which more than 2000 papers have been published within the social sciences. We shall introduce this game, known as "The Prisoner's Dilemma" (Luce and Raiffa 1957), by first giving its most popular interpretation and, then, defining its formal structure. The interpretation reads as follows. Two persons are arrested because they can be proven to have committed a minor crime which is generally punished with a 1 year prison sentence. However, they are also suspected to be guilty of a major crime for which they would be charged an additional 9 years. Insubstantial evidence exists for conviction on this latter offense and a confession is essential to the prosecution's case. The district attorney offers the following deal to obtain the needed confession. If only one of the prisoners confesses that both have committed the major crime, this witness will be free immediately (i.e., will serve no time in prison), whereas his partner in the crimes will have to pay the penalty of a 10 year prison term. If both confess, they will be forgiven the minor crime but not the major one so each will serve a 9 year term. Clearly, if neither individual confesses, both will have to serve only the penalty for having committed the minor crime (i.e., a 1 year prison term). Note that 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 non-cooperative game theory does not attempt to describe or predict actual human behaviour 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 calculation power and consistent preferences, should best pursue his interests.

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

1. Who are the player's 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, 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 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 given that player 2 chooses to "deny". One could then ask how player 1 would have to act in order to maximize his payoff. According to the payoff matrix (Fig. 1), he would clearly have to "confess", since 10 is more than 9. To "confess" is therefore called player 1's best reply strategy against deny. Furthermore, if it were given that the opponent chooses to "confess", player 1's best reply strategy would also be to "confess". Since the game

		STRATEGIES OF PLAYER 2	
		CONFESS	DENY
STRATEGIES OF PLAYER 1	CONFESS	1 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 years saved from serving the maximum penalty of 10 years prison for the respective individual playing the strategy indicated in the cell against the strategy exhibited by the other player.

is symmetrical (i.e., players are merely distinguished as 1 or 2 for our convenience) the same argument holds for player 2. From this 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, a rational solution of this game can, then, only be that both opponents "confess", since otherwise they would receive lower payoffs (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 rational behavior would be 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 and Selten (1980) 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 the 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. It is that if each player expects his opponent to behave according to the rational solution, neither should have the incentive to deviate from this solution by playing another strategy. 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 (Nash 1951). Note that the Prisoner's Dilemma Game shown in Fig. 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 which has three equilibrium pairs.

Game of Chicken

The "Game of Chicken" (e.g., Brams 1975) is a very simple model of a sport that was especially fashionable among american teenagers in the fifties. In this game (frequently played by Riechert), two persons steer their bicycles (or cars) towards one another at top speeds. If we ignore the more complex strategic features of "timing" which 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 first swerves 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 zero since no money is lost or gained; if one player only swerves, the one who does pays $10 (receives a negative payoff of -10) and the one who does not receives $10 (a positive payoff of +10).

The Game of Chicken is presented in matrix form in Fig.2. Player 1's best reply strategies are indicated by arrows 1 and 3; 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 that decision which yields the highest payoff against a given strategy of one's opponent. The points at which two arrows meet are necessarily equilibrium points. In the Game of Chicken these are : A, "swerve" (player 1) - "not swerve" (player 2) and B, "swerve" (player 1) - "not swerve" (player 2). 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 is so because the individuals would not know who should act as player 1 or 2. The two equilibrium points identified by the arrow technique are not symmetric and hence cannot be rational solutions. Has the game of Chicken really no symmetric equilibrium point and thus no rational solution? Classical game theorists believe that there should

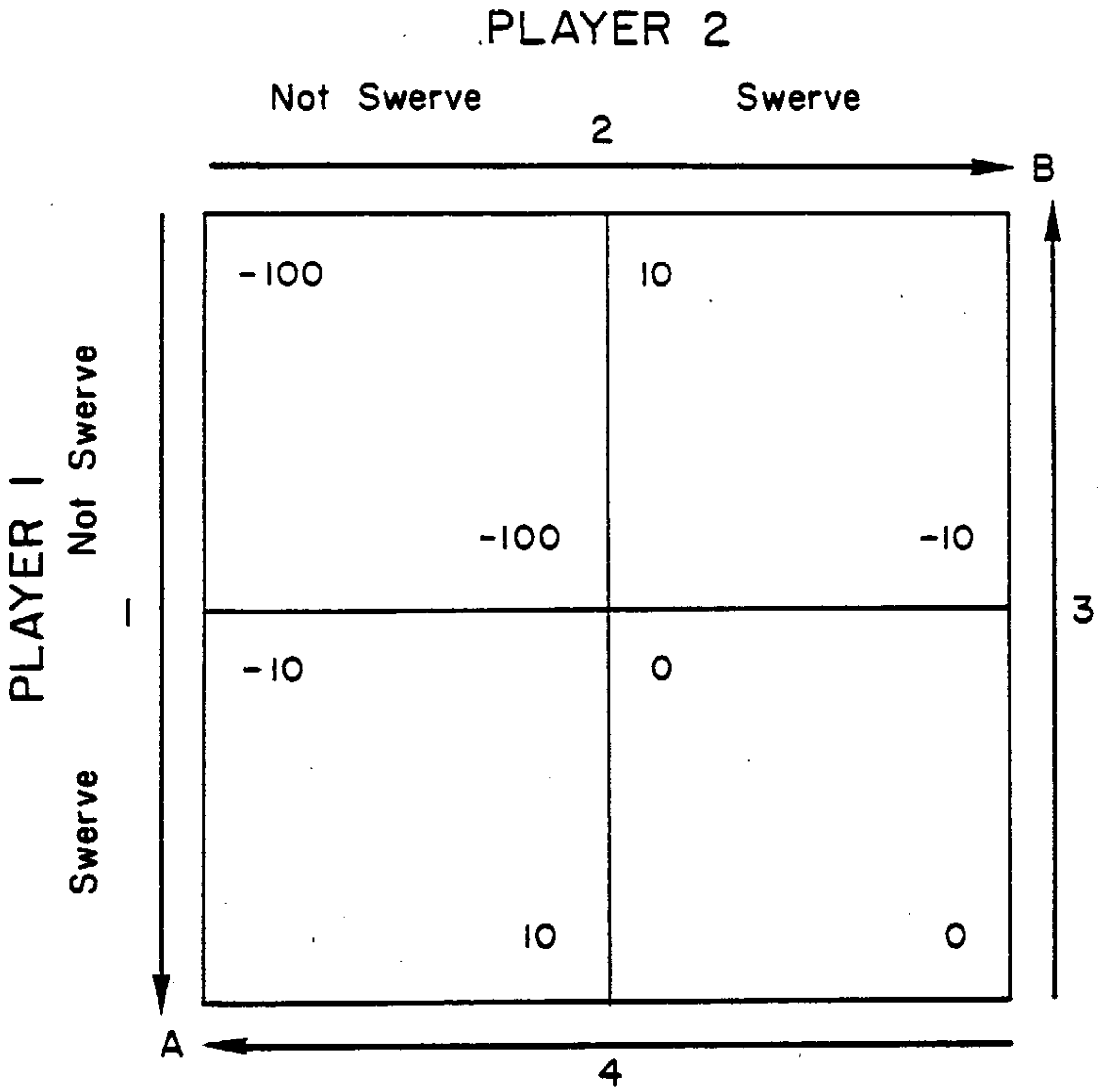

Figure 2. Game of Chicken. The arrows indicate best reply strategies. Arrow 1 for example indicates that player 1's best reply to "not swerve" is "swerve". Arrow 4 indicates that player 2's best reply to "swerve" is "not swerve". Equilibrium pairs of pure strategies correspond to points at which arrows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

A) player 1 "swerve" - player 2 "not swerve";

B) player 2 "swerve" - player 1 "not swerve".

STRATEGY J: PROBABILITIES

		3/4 Not Swerve	1/4 Swerve
STRATEGY I: PROBABILITIES	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 expected (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 2/5 and 3/5 respectively. The opponent's strategy J is to play "not swerve" and "swerve" with probabilities 3/4 and 1/4 respectively. The expected payoff to I if played against J is defined as the sum of all four entries. Therefore,

$E(I, J) = -100\cdot\frac{2}{5}\cdot\frac{3}{4} + 10\cdot\frac{2}{5}\cdot\frac{1}{4} - 10\cdot\frac{3}{5}\cdot\frac{3}{4} = -33.5$.

be a rational solution to most conflicts. They thus 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 strategy set of "mixed strategies" is taken into consideration. A mixed strategy is a specification of probabilities with which each pure strategy will be exhibited by a player in a particular game, as for example: "swerve" with probability 0.2 and "do not swerve" with probability 0.8. Note here, that the original pure strategies 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, we denote his expected payoff by E(I,J). Within the context of Bayesian decision theory, the player wishes to optimize E(I,J). The expected payoff E(I,J) is defined as a probibility-weighted sum of the payoffs a player would receive in each cell of the matrix shown in Fig. 2:

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

where I_i = the probability that an I-player exhibits the i-th pure strategy, J_j = the probability that a J-player exhibits the j-th pure strategy, n = the number of pure strategies, and a_{ij} = 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 extended to mixed strategies, a strategy I is called a best reply to another strategy J, if it satisfies the inequality

$$(2) \qquad E(I,J) \geq E(K,J)$$

for all strategies K. Furthermore, I is called an equilibrium strategy if I is a best reply to I. The fundamental characterizing property of 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 means that if I is an equilibrium strategy (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(not swerve, I) = E(swerve, I). Let p = the probability that an I-player does not swerve. From Figure 2 then

$E(\text{not swerve}, I) = -100p + 10(1-p)$,

$E(\text{swerve}, I) = -10p + 0(1-p)$,

which implies $p = 1/10$ and $1-p = 9/10$. The equilibrium strategy for the Game of Chicken is thus to "swerve" with a probability of 9/10 and "not swerve" with a probability of 1/10. 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, the Hawk-Dove Game of Maynard Smith and Price (1973). The structure of this game is well known and a good review of the general game and its modifications is available in Maynard Smith (1982). Our interest is in a simple ecological example which though analysable as a two individual or pairwise contest might be extended to the n-person context characteristic of most ecological applications. We thus use as our example plant competition for water in desert plants. This is intended mainly as a didactical example. Arguments similar to the ones developed here, however, might be applied to the analysis of fragmented phenotypes in clonal plants discussed in Noble et al. (1979). Let's assume that desert plants compete for water (something that is subject to some debate: Gulmon et al. 1979). Three sources of water are available to these plants: 0-20 cm, 20-100 cm and greater than 100 cm in depth (Solbrig et al 1977). The lateral root systems of plants utilize water at or near the surface (i.e., for our purposes that available within 1 m of the surface), while underground sources of water are exploited by the elongated tap roots. The efficient utilization of one water source (surface or underground) precludes use of the other in the desert ecosystem (Solbrig et al. 1977). Hence desert plants tend to specialize on one or the other of the two root systems. Succulents, for instance, specialize on the lateral root system and the utilization of surface water, while other species are true phreatophytes in that they tap only underground water (Robinson 1957). Ludwig, however, in Solbrig et al. (1977) states that most perennial shrub species have the potential for either extensive lateral or tap root development. It is this group of plants that we wish to deal with in our example.

Pairwise Interactions

In our basic "Root Game", we are analysing the individual shrub's "decision" to either emphasize development of the lateral or tap root component of its water (and nutrient) procurement system. Although admittedly, an individual plant usually competes with more than one neighboring individual, we model only 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—quantities of water obtained/unit time. We assume, however, that these payoffs show the following relationship to changes in Darwinian fitness: quantities of water and dissolved nutrients taken up are proportional to reproductive output. The average amount of water uptake/unit time by a lateral root system in the absence of a competing nearest neighbor is defined as "S" for surface water (0-1 m depth). Likewise, "U" denotes the expected quantity of water obtained by the tap root 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—that two neighboring plants using the lateral root system each receive one half of the available surface water. No such competitive effect is included in the basic model for the tap root system, since it is assumed that this source of water, once located, 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 tap root, there is no competition for water since once found, there is an adequate supply. We assume, however, that the distribution of underground water is patchy and hence not as "spatially" reliable as surface water. For this initial analysis, we must also assume that both players in the game make the decision as to which root system to emphasize at the same time—perhaps they are colonizers following a frost or fire kill in a local area.

Fig. 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 (arrow configuration) is that of the Prisoner's Dilemma Game already discussed. Indeed, if we add the best reply arrows to Fig. 1, exactly the same picture emerges. If shrubs were rational thinking beings, they would thus have to develop only lateral roots in this context. If, however, $U > S/2$, the best reply strategies are different ones. The reader may easily find how to change the arrows in Fig. 4. Arrow 1 no longer points upwards but downwards and arrow 2 points now to the right. The best reply structure is now identical to the Game of Chicken (Fig. 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 $\underline{I}$, if they were rational, since $\underline{I}$ is by definition a best reply to itself.

EVOLUTIONARILY STABLE STRATEGIES It is clearly not of direct biological interest to argue which root systems shrubs should develop as rational beings. In fact, however,

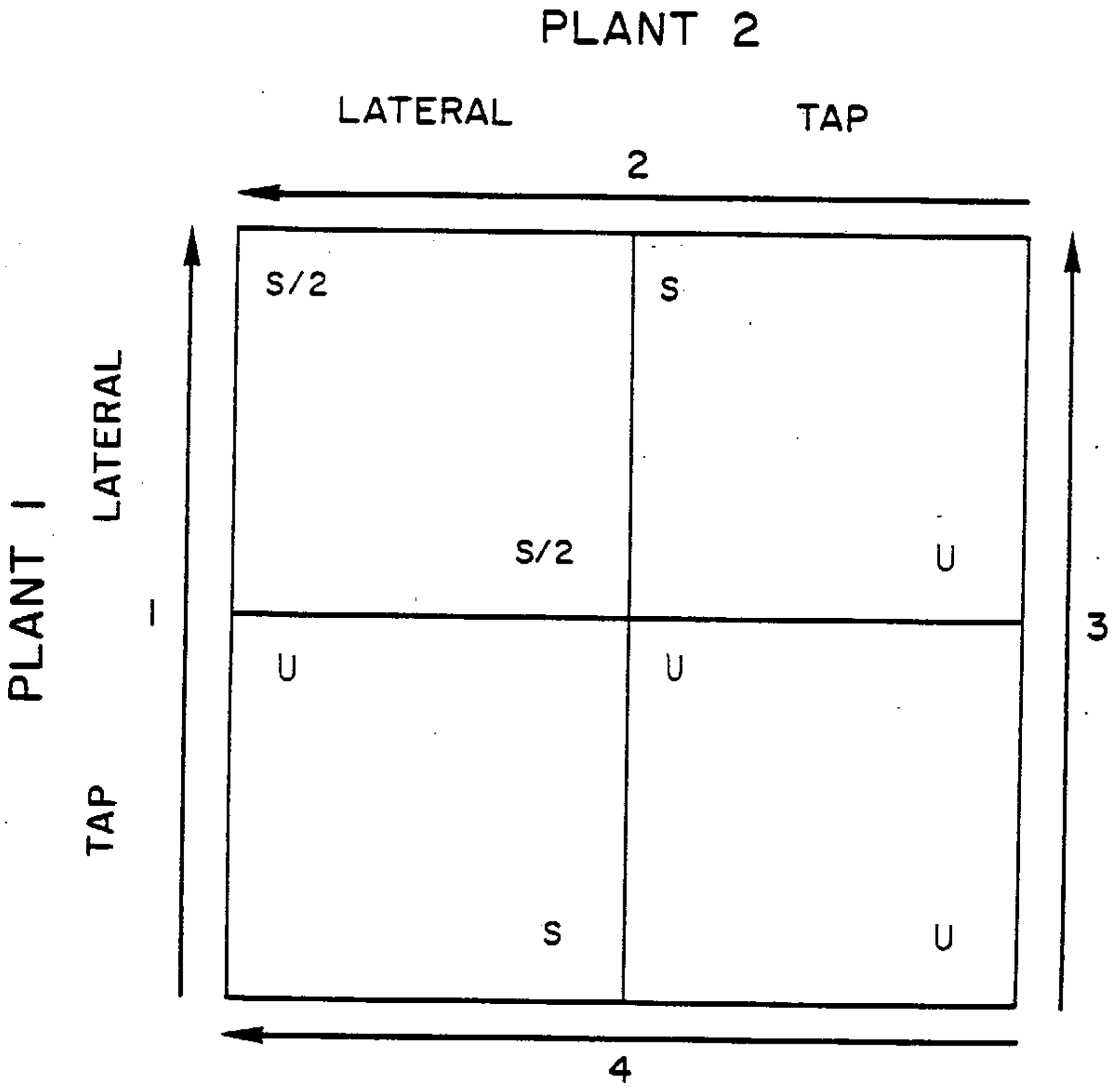

Figure 4. Root Game. The arrows indicate best reply strategies when U < S/2, where U = supply of underground water and S = quantity of surface water available to a lateral root. Note similarity in best reply structure to Prisoner's Dilemma Game.

the outcome of frequency dependent selection operating on phenotypic traits corresponds reasonably well to what rationality would suggest. Let's 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 (phenotypes) should one expect to find in a population as long-term outcomes of natural selection, given that game-like conflict occurs among members of the population generation after generation. When 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 higher expected fitness than I in this population of I-playing shrubs. If all strategies of the Root Game are considered as potential mutant strategies, this means that I must necessarily be a best reply to I. The term best reply is here considered as in game theory: $E(I,I) \geq E(J,I)$ for all strategies J. Remember that this is the central property of classical game theory also. The 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 strateges (I,I) is a symmetric (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 in that if another strategy J is as successful as I in the population of I players, 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, which satisfies the following two conditions (i) and (ii).

(i) Equilibrium Property

I is a best reply to I: $E(I,I) \geq E(J,I)$ 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 the original formulations by Maynard Smith and Price (1973) and Maynard Smith (1974). The identification of the two conditions as a game theoretic equilibrium and an additional stability property respectively is attributed to Selten (1980) and Hammerstein (1983a, b) and is used in Hammerstein (1981), Hammerstein and Parker (1982). This identification is an important one since it reveals that the main property (i) of an ESS is equivalent to that which characterizes a symmetrical Nash Equilibrium Point of classical game theory.

The calculations of an ESS for the Root Game with the parameter values of $U < S/2$ is easy. We do not need any further algebra, since the arrows in Fig. 4 tell us that the strategy "lateral" is the only best reply to itself: $E(\text{lateral, lateral}) > E(J,\text{lateral})$ 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 $U > S/2$, there exists no pure strategy which is a best reply to itself, since the arrows are arranged as in the Game of Chicken (Fig. 2). However, as pointed out earlier, a 2 X 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 which is to build a lateral root system with positive probability p and a tap root system with positive probability $1-p$. The characteristic property of I is then that both "lateral" and "tap" are best replies to I: $E(\text{lateral}, I) = E(\text{tap},I) = E(I,I)$. From $E(\text{lateral}, I) = p\,S/2 + (1-p)S$ 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:

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

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

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

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

and the expected payoff to J of playing against itself:

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

After some calculations, one gets:

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

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 either simultaneously negative or positive. We have thus demonstrated for the case of $U > S/2$ that it is an evolutionarily stable strategy to build lateral root system with a probability of $p = 2(1-U/S)$.

The Root Game has thus 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 to expand the lateral system with a probability of $p = 2(1-U/S)$ and to emphasize the tap system with probability 1-p. This need not be the case in other evolutionary games. In some cases there may be no ESS at all and in others there may be several ESS's, 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 and Cannings (1976) and Haig (1975) for examples of the treatment of the subject.

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

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

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

where q denotes the probability with which J builds a lateral root. We calculate the maximum by deriving E(J,J) with respect to q. This yields the expression

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

which is zero for $q = 1 - U/S$. The maximum water uptake per individual would thus be achieved if the modelled shrub population developed a lateral root with probability $1 - U/S$. On the other hand, the ESS probability for emphasis on a lateral root system would be 1 if $U < S/2$ and $2(1-U/S)$ if $U > S/2$. This means that for a wide range of parameter values, ESS analysis of the problem predicts that twice as many plants would emphasize tap roots in a local population than predicted by optimization criteria (Fig. 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 payoff E(J,J) predicted for the species

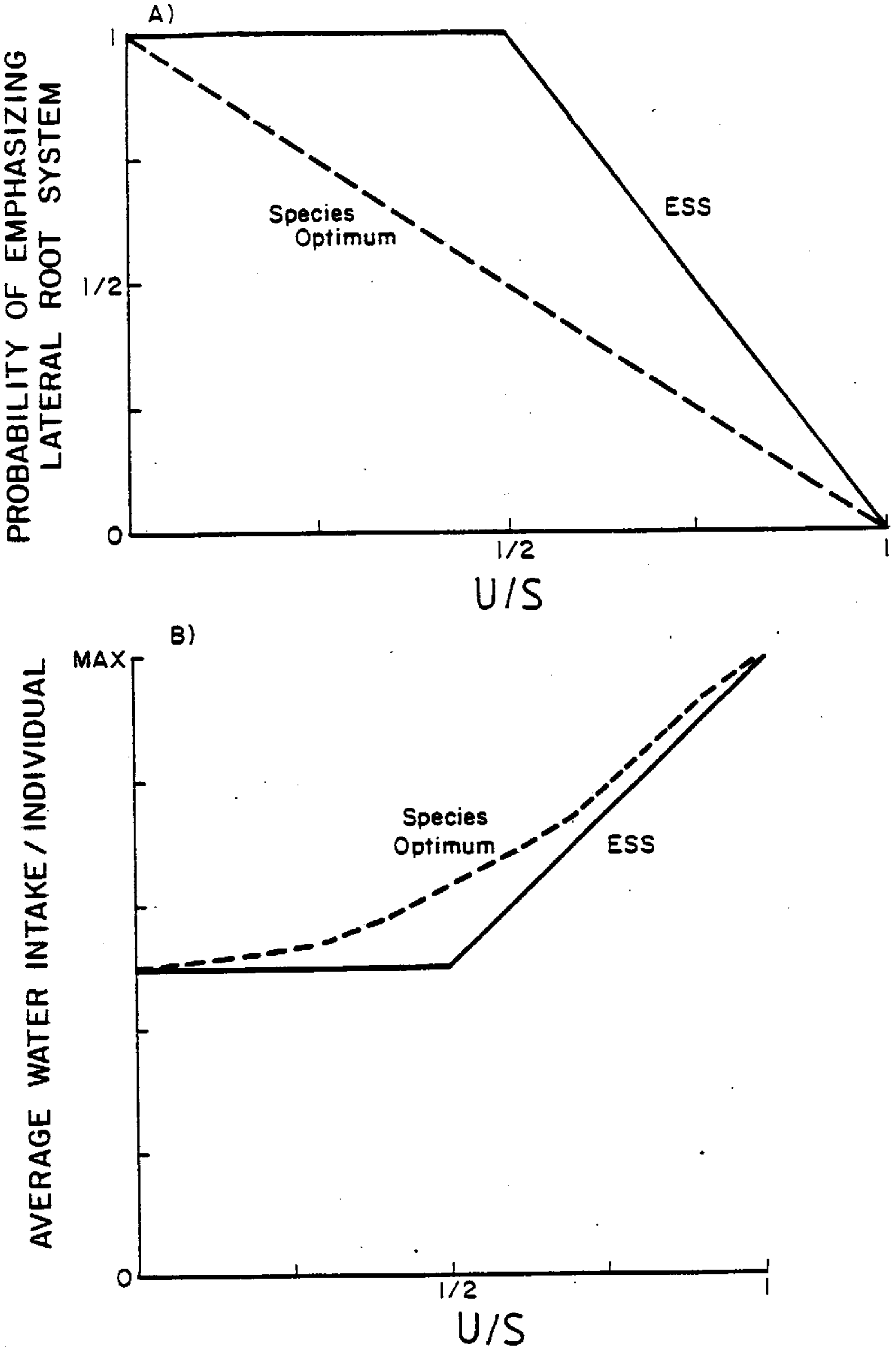

Figure 5. Comparison of predictions of ESS versus species optimum analyses of hypothetical root competitive system over range of environmental contexts. a) proportion of phenotypes emphasizing lateral roots in the population as a function of the ratio of underground water to surface water. b) Comparison of predicted water uptake/individual as a function of 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.

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

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

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

ADDITIONAL EXAMPLES In the context of animal conflict, Maynard Smith and Price (1973) 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 "escalate" or a non-aggressive strategy, "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 "escalate".

The game becomes more complicated when the two players are assigned distinct roles, A and B, such as "owner" and "intruder" in territorial conflicts (Maynard Smith 1974, Maynard Smith and Parker 1976). The ESS is then to "escalate" in one role and to "display" in the other. Selten (1980) has demonstrated mathematically that if there is a role-difference which 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 (non fighting) 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 to locate the ESS's for the game. This is because in order to identify an ESS, all of the roles an individual potentially finds itself in during its life must be included in the analysis. The evolutionary game describing asymmetric contests is, in principle, a symmetric game. However, Hammerstein (1981, 1983b) has developed a method in which models of asymmetric contests can be decomposed into subgames in which asymmetric Nash equilibrium points become relevant to evolutionary game theory. This 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 non-aggressive in another role (B), despite the fact that role does not affect relative fighting ability or reward. These instances are called "uncorrelated asymmetries" and there has been considerable interest in trying to understand under what conditions correlated versus uncorrelated asymmetries may settle contests conventionally (Parker 1974, Hammerstein 1981, 1983b, Parker and Rubenstein 1981, Hammerstein and Parker, 1982). It appears as if in the more continuous strategy sets (e.g., finely tuned levels of aggression), only "commonsense" or correlated asymmetries are possible cues (e.g., owner wins 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 analyse the asymmetric contest is extremely important, since there are numerous biological examples of this contest structure. A few are of the uncorrelated type. Davies (1978) presents, for instance, evidence for an uncorrelated asymmetry that settles territorial disputes among male speckled wood butterflies. Males defend sunspots which they occupy while waiting for females during mating periods. The asymmetry is one of ownership versus non-ownership or firstcomer versus latecomer status. Davies found that the ownership status of individuals can be reversed experimentally with appropriate changes in the behavior of the contestants. Manipulations producing two owners further led to prolonged fights not observed when the ownership asymmetry was present. Note that there is some difference of opinion as to whether this contest situation represents an uncorrelated asymmetry, since time in sunspots increases the body temperature of the occupants, which may give firstcomers fighting advantages (Austad et al. 1979). Other examples of possible uncorrelated asymmetries include competition for access to females in parasitic hymenoptera (Wilson, 1961), for funnel-retreats in a colonial spider (Burgess 1976), and for foraging sites in the zebra spider (Jacques and Dill 1980). In the case of the social spiders, Burgess (1976) 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 merely initiated encroachment towards nearby retreat holders, creating a domino effect in changes of retreat ownership in the colony.

Most of our observations of asymmetric contests, however, are 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 (Riechert 1978a). 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 (1975, 1976, 1978a,b, 1979, 1981, 1982) provide data about both payoffs and strategic behavior. The quality of web-sites is known and varies both within and between populations. Two asymmetries exist in the terrritorial disputes of this spider: relative weight of the opponents and owernships status. These parameters have been shown to be the major determinants of contest structure and outcome (Riechert 1978b, 1979, 1982, in press). To date two kinds of games have been proposed as first approximations to these agonistic interactions (Maynard Smith 1982, Hammerstein 1981, 1983b). We have yet to deal with the complex sequential structure evident in these contests though. At the beginning of a contest, for instance, only the territory owner seems to "know" site quality. However, this information appears to have been obtained by the intruding spider by the end of the first bout of the contest (first series of actions leading to a retreat by one of the spiders). This information does not appear to be overtly transmitted by the owner (Maynard Smith and Riechert, in press). The available theoretic framework to deal with these complications would be an extensive representation of the game's sequential and information structure similar to that discussed for classical game theory in Selten (1975).

It is not possible to deal with the many contest models that have been developed along the lines of the Hawk-Dove game here. Rather we refer the reader to Maynard Smith's reviews (1979, 1982) for both discussions of the models and additional biological examples. (See also Dawkins 1980). In the present paper, it seems more important to emphasize the fact that there is a much wider range of applications of evolutionary game theory than the field of agonistic behavior. For example, the problem of parental investment in offspring can be conceived as a game in which the parents and often also the offspring are players (Maynard Smith 1977, Grafen and Sibly 1978, Parker and McNair 1978, McNair and Parker 1978, Parker 1979, Parker and McNair 1979, McNair and Parker 1979, Schuster and Sigmund 1980).

Another important application of evolutionary game theory is the problem of the evolution of cooperative behavior. Consider an example given by Pulliam et al. (1982) involving a winter feeding flock of yellow-eyed juncos (Junco phaeonotus), a subset of a local population. Risk of predaton 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 non-cooperative alternation of scanning and feeding by all individuals and b) scanning carried out by a few individuals while others continuously forage (cooperation). From empirical studies it was deduced that the actual behavior of the juncos is rather of the cooperative type. Because for each individual of the flock, it is more advantageous to "feed" and to let others "scan" than vice versa, we are confronted with a game-like situation.

Pulliam and his collaborators point out that the scanning game is not only played once but many times in the flock. From classical game theory, it is well known that repeated games between the same interacting individual (so called supergames; Luce and Raiffa 1957) may have to be played cooperatively by rational players, though the rational solution to a single such game would be to behave in a non-cooperative 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 is, however, only the case if there is sufficient uncertainty as to the number of repetitions. The biological recognition of this consequence of repeated games was first recognized by Trivers in his work on reciprocal altruism (1971). A number of workers have since contributed to our understanding of the phenomenon (Axelrod and Hamilton 1981, Eshel and Cavalli - Sforza 1982).

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 time. In this section, we show how the Root Model might be extended to permit analysis of the context with many players.

As in the pairwise analysis there exist two pure strategies, "lateral" and "tap", and the corresponding mixed strategies which assign probabilities to "lateral" and "tap". We make different assumptions about the level of competition individuals possessing tap versus lateral roots encounter: an individual shrub emphasizing the tap root competes with all members of its local population for a portion of water available in the local underground reservoir, while the individual with the expanded lateral system competes with only its nearest neighbors—assuming that the spacing is regular as indicated for many desert plants (e.g., Beals 1968; Barbour 1969; Woodell et al. 1969; Waisel 1971; Fonteyn and Mahall 1978; Moore and Bhadresa 1978).

Let us now reconsider the Root Game, adapting the model to non-pairwise 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 six corners. We propose that competition for surface water is local—that each shrub competing for surface water does so with a maximum of six 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 cases when all of its 6 neighbors also play "lateral". 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 tap roots.

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 tap root system depends on how many "tap root" players are present in the population. The availability of underground water is therefore represented as a linearly decreasing function of the proportion, q, of "tap root" players in the population. Water uptake by shrubs utilizing the tap root 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 (1982) and (1983)[a, b] 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 is expected change in fitness received by an individual playing the strategy J in a population of I players. As before, we consider two alternative pure strategies, "lateral" and "tap". Let's assume that the mixed strategy I consists of building a lateral root with probability I_1 and a tap root with probability $I_2 = 1 - I_1$. We define the game by first analysing the payoff function associated with the two special cases: $I_1 = 0$ (the pure strategy tap) and $I_1 = 1$ (the pure strategy lateral). The payoff to a shrub producing a lateral root in a I-playing population is $W(\text{lateral},I) = S_{min}(1 + n/6)$ with n equal to the expected number of tap root neighbours. Since I_2 is the probability that a neighbor emphasizes the tap system and there are 6 neighbors, we have $n = 6 I_2 = 6(1-I_1)$. Substituting this expression for n, and using the parameter $S = 2 S_{min}$ for the maximally possible water intake from the surface one gets:

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

We can obtain the expected payoff for the pure

strategy "tap" in a similar manner. According to our introductory statements, we have $W(\text{tap},I) = U(1-uq)$, where q = the proportion of tap roots in the population. In an I-playing population, this proportion is $q = I_2$, and thus

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

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

$$(12) \quad W(J,I) = J_1 W(\text{lateral},I) + J_2 W(\text{tap},I) = J_1 S(1-0.5I_1) + J_2(U(1-uI_2)).$$

ESS CONDITIONS The mathematical notion of the ESS given in the previous section applies only to pairwise interactions. We consider the generalization of the equilibrium condition (i) and the stability condition (ii) 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:

(j) Equilibrium Condition: $W(I,I) \geq W(J,I)$ for all strategies J.

The equilibrium condition is similar to that used in the pairwise interactions (i). 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 conditon (j) may not be the only adaptive strategy present in a population of I players: 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 $P_{I,J,\varepsilon}$ and let $W(J, P_{I,J,\varepsilon})$ and $W(I, P_{I,J,\varepsilon})$ denote the fitness of J and I respectively in population $P_{I,J,\varepsilon}$. With these definitions, the stability condition can now be formulated. An equilibrium strategy I is said to be stable against strategies which are also adaptive in the exact equilibrium population of I-players, if it has the following property:

(jj) For every strategy $J \neq I$ such that $W(J,I) = W(I,I)$, the inequality $W(I,P_{I,J,\varepsilon}) > W(J,P_{I,J,\varepsilon})$ 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 or tap roots. The water intake cannot be greater than $\max_{lat} = S$ for a lateral root and $\max_{tap} = U$ for a tap root. Conversely, the average water intake cannot be lower than $\min_{lat} = S/2$ at the surface and $\min_{tap} = U(1-u)$ at the underground water source. The pure strategy "lateral" is an ESS if $\min_{lat} > \max_{tap}$. In this case, no mixed ESS exists. Likewise, the pure strategy tap is an ESS if $\min_{tap} > \max_{lat}$. For these two strategies the inequality (j) holds in its strict form and condition (jj) 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 $W(I,I) \geq W(J,I)$ for all J. According to Hammerstein (1983b), this is equivalent to saying that I satisfies the following equation:

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

the characteristic property of best reply strategies again. Equation (13) simply implies that

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

Solving this equation (14) yields the mixed equilibrium strategy $I = (I_1,I_2)$ with

$$(15) \quad I_1 = \frac{S/U + u - 1}{u + 0.5\ S/U}$$

Note that 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 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 $(1-\varepsilon)I + \varepsilon J$, and in a population consisting of a fraction, $1-\varepsilon$ of I-players and a fraction ε of J-players, then the inequality expressed in the stability condition (jj) may be simplified as follows. Let $K = (1-\varepsilon)I + \varepsilon J$ be the strategy "build lateral roots with probability $(1-\varepsilon)I_1 + \varepsilon J_1$". The inequality in (jj) then is equivalent to

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

In order to show that the equilibrium strategy I satisfies (16) note that

$$(17) \quad W(I,K) - W(J,K) = (I_1 - J_1)(W(lat,K) - W(tap,K)).$$

Suppose first that $I_1 < J_1$. From this it follows that $K_1 > I_1$ and thus $W(lat,K) < W(tap,K)$. The expression in (17) is then positive as required. Conversely, if $I_1 > J_1$, the expression (17) is also positive, since this implies that $W(lat,K) > W(tap,K)$. Thus the strategy, I, defined in (15) is not only an equilibrium strategy, but also an ESS. Note that 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 (1930) 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., Hamilton 1967, Trivers and Hare 1976, Charnov et al. 1978, Charnov 1981, Maynard Smith 1980). Let us briefly show how sex ratio theory fits into the theoretical ESS framework outlined in this section. (See Maynard Smith (1982) for an explicit presentation). A strategy I is the relative proportion of males which the corresponding phenotypes would on the average produce. There is a continum 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's consider the payoffs. Because the main selective effect involved in 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 here the number of grandchildren 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 (notable exception = 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.

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

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

Hamilton and May (1977) 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 is expected to occur, even when the habitat is homogeneous, constant and saturated and when seed mortality during disperal is 'high'. They also show from inspection of various models that seed dispersal cannot be understood in terms of species-optimum utilization of resources. This is analogous to our result for the Root Game namely that the predicted ESS-water consumption is signficantly lower than that expected for species-optmial water consumption. Ellner and Shmida (1981) and Ellner (1982) also submit the seed dispersal problem to ESS analyses.

Another problem that is of a game theoretic nature concerns how animals distribute themselves over habitat patches in a variable environment. Parker (1970) considered this problem for male dungflies (Scatophaga stercoraria) seeking matings at cow pats ranging from fresh to less fresh. Since female dung flies are more likely to approach fresh cow pats than older cow pats, cow pats vary in quality to the males. According to the concept of the Ideal Free Distribution (Fretwell and Lucas 1970, Fretwell 1972), in the absence of active competition for sites, organisms should be distributed in such a way that fitnessess in different habitat patches is equalized. Parker (1970, 1974) found the distribution of male dung flies on the set of cow pats available to match the Ideal Free Distribution. A similar distribution of mallard ducks in feeding patches was noted by Harper (1982). The exhibition of an Ideal Free

Distribution can be consistent with game theoretic predictions if in particular the following conditions are met: 1) the species lacks the strategic means to defend habitat patches against occupation by conspecifics 2) that individuals can freely move between patches. Similar comments can be made about some foraging problems (e.g., Milinsky 1979).

In a many-player context, the decision between "digging" a burrow or "entering" an already existing burrw has been identified as a choice problem encountered by the digger wasp, Sphex ichneumoneus (Brockmann et al. 1979, Brockman and Dawkins 1979, Dawkins and Brockmann 1980). The strategy "enter" has associated with it a risk of encounter with a burrow owner which leads 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 which indicate that the model developed in Brockman et al. (1979) explains the data from only one population. The other apparently is not at an ESS.

Other many-player contexts that have been analysed as evolutionary games include "arms races" in nature (Parker 1979, Haig and Rose 1980, Maynard Smith 1982) and the effect of intraspecific competition on plant growth (Mirmirani and Oster 1978).

Competition Involving Two Or More Species

The general kind of model introduced in the previous section can be extended to cases involving simultaneously both intra- and interspecific competition. We will discuss the game-theoretic analysis of a two-species system along the conceptual lines proposed by Hammerstein (1983a), again using root competition in desert shrubs for illustration.

Suppose that two shrub species compete for water, and that both are able to emphasize either the lateral or the tap root systems. This is not to say, however, that both species have the same set of strategies. Neither strategies nor payoffs (in fitness) are considered comparable between species: each species is assumed to have a specific strategy set and measure of relative fitness. Therefore, the payoff in terms of fitness to an individual in population 1 will be W_1, and the payoff specific to an individual in population 2 will be termed W_2. Technically, the strategies "lateral" and "tap" should also be indexed in order to clarify to which population strategy set they belong. To avoid excessive use of indices in this case, however, we assume that it will always be clear from the context to which strategy set "tap" and "lateral" belong. The same convention holds for mixed strategies I, J, ,etc.

Unlike the one-species case, the between species analysis must take into consideration the relative numbers of individuals belonging to the respective species. 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 <u>relative abundance distribution</u>.

The model can now be outlined as follows. A strategy I for members of species 1 is a pair of probabilities $I = (I_1, I_2)$ with which "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 <u>interspecific strategy combination.</u> 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, allowance is made for the simultaneous occurrence of intra- and interspecific frequency-dependent fitness effects. 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 precisely defined as the Darwinian fitness of a single stategist in a community in which all members of a particular - population exhibit the strategy typical to that population.

Then for a given distribution $A = (x,y)$ of relative abundances, let $W_1(H, I, J, A)$ denote the payoff (change in fitness) to a single H-strategist in population 1 if the community plays the interspecific strategy combination (I,J). Furthermore, 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 chapter, these payoffs can be defined as follows for the root game:

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

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

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 and tap roots 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 tap root is emphasized. This explains how the fitnesses of "lateral" and "tap" relate to those defined in the previous section. Finally the payoff to a mixed strategy $H = (H_1, H_2)$ is again defined as the expected fitness associated with playing H:

(21) $W_i(H, I, J, A) = H_1 W_i(\text{lateral}, I, J. A) + H_2 W_i(\text{tap}, I, J, A)$.

ESS COMBINATIONS. The mathematical conditions for evolutionary stability in n-species models are detailed in Hammerstein (1983a). Reflected in the conditions is the idea first proposed by Maynard Smith and Price (1973) that, within a species, a strategy must be stable against invasion by mutant strategies that are sequentially encountered (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 at a given time in a community and that strategies must be stable against invasion by this single mutant. (This extension of the Maynard Smith and Price stability assumption is implicit in the coevolution arguments presented for competing species by Lawlor and Maynard Smith (1976)).

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" versus "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 no explicit assumptions are made as to the relationship existing between A and the strategies exhibited. Corresponding to these two types of models, there are two methods of analysing interspecific competition. Associated with the partial model is the "pragmatic" calculation of ESS's for all A's. Generalized conclusions about strategies independent of A must then be drawn from inspection of the list of ESS's obtained from the calculations. Note, however, that 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 simultaneously predict both strategies and relative species abundances. It is not sufficient to merely show which strategies would be evolutionarily stable for given species abundance distributions. In this "ambitious" method, one must also determine whether A would be generated by the strategies identified as stable. 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 requisite to successful completion of the full model analysis.

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

An interspecific strategy combination (I, J) is called evolutionarily stable (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.

Note that in the complete model, one must identify that strategy combination (I, J) and 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 analysing 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 versus the underground water source: species 1 being the better of the two species. In terms of our model parameters, this means that $S_1/U_1 > S_2/U_2$. We also assume that the difference in 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 analysed using techniques already presented in earlier sections. 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 the two species to differ in their efficiencies of water utilization at respective levels, however, the analogous equation for species 2 cannot be satisfied simultaneously. Either I or J must, therefore, be a pure strategy which emphasizes roots only at one resource level.

After some calculation we find that for given model parameters, there is exactly

Table 1. Evolutionarily stable strategy combinations for the two-species root game*

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

*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, 2 respectively, and u is a measure of the effect of tap root density on the underground water resource.

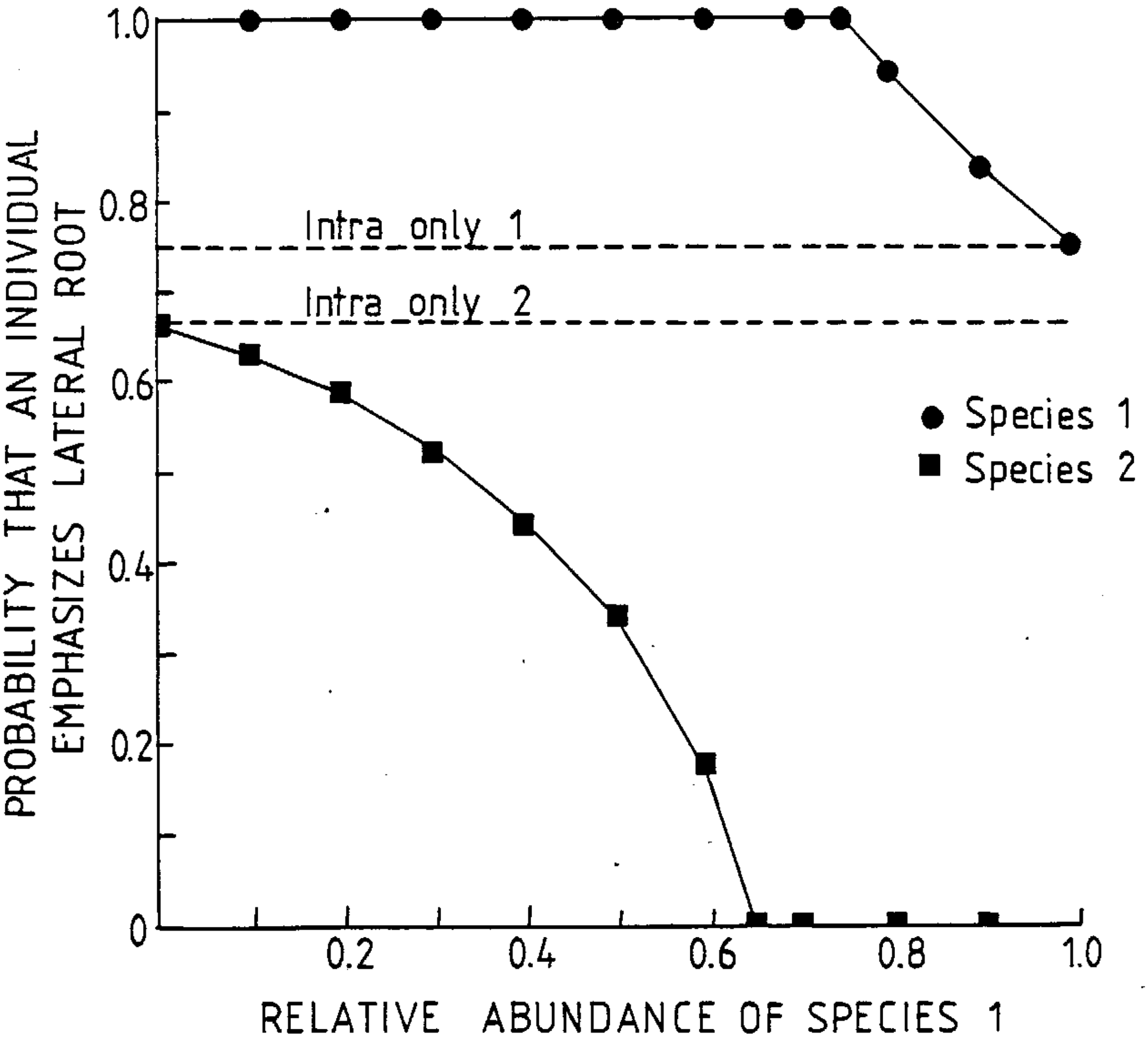

Figure 6. ESS-combinations in a two species Root Game as shown (solid lines). It is assumed that both within and between species frequency dependent selection are in operation. Dotted lined show ESS-probability of emphasizing lateral root system for each species in the absence of the other species. Parameter values used in the example: S_1/U_1 = 1.6, S_2/U_2 = 1.5, u = 0.

one ESS-combination for each distribution of relative abundance. An ESS-combination is of either of three types shown in Table 1. Note that all three types of ESS-combination share the following features:

a) Species 1 emphasizes the lateral system with a higher probability 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 they would do in playing an ESS in the absence of interspecific competition.

c) Both species do not simultaneously play mixed strategies.

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. Note, therefore, that in the absence of interspecific competition, each would evolve to a similar ESS, one that emphasizes lateral roots with a moderately high probability (i.e., dashed lines for respective species in Fig. 6). Intraspecific competition in this case effects the exhibition of some degree of tap root emphasis in both populations. The evolutionary outcome of interspecific frequency dependent effects is a strong divergence in root system emphasis in the two species (Fig. 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 that of 2 is a result of avoidance of between species competiton with 1. Slatkin (1979) emphasizes the significance of relative species 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 and Maynard Smith (1976). As in the root game above, their treatment also involved a two-species case and the partitioning of two distinct resources. However, the definition of evolutionary stability used by Maynard Smith and Lawlor in the paper is only proposed for a special type of model and does not refer explicitly to a game. It seems to be desirable to base the analysis on explicit games with many players.

Auslander et al. (1978) also analyzed a coevolution problem, in this case between a host and its parasite. The host larvae were assumed to either dwell "shallow" or "deep" in the ground, while developing; the parasite had identical choices. A pair of mixed strategies was identified which was evolutionarily stable in the game-theoretic sense. The pair of mixed strategies was, however, not found to be stable when the selection process was modeled as a dynamic system. This is because the authors used the term ESS as synonymous with the "Nash Equilibrium"; no reference to or test was made for the additional second criterion (jj: the stability property). Their "game theoretic solution" in fact, does not meet the second criterion and thus is not an ESS (See Hines 1981 and Hammerstein 1983 a).

The gregariousness of prey in the coevolution of predator-prey systems is another area to which game theory has been applied. In his "geometry for the selfish herd", Hamilton (1971) 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 (1981) extended Hamilton's ideas and emphasized their game-theoretic aspects.

CONCLUDING REMARKS

The population geneticist might be of the opinion that evolutionary game theory is merely a reformulation of the Theory of Frequency Dependent Selection. It is true that ESS-analyses lead to conclusions that could be reached through the framework of population genetics (e.g., Maynard Smith 1981, Eshel 1981), albeit with much greater effort. This is, in fact, the significant contribution ESS theory makes. 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 (1982) book Evolution and the Theory of Games, Lewontin (1982) attributes the success of the book to its avoidance of game theoretic apparatus. In this review, however, we have shown that a very close relationship exists between the solution concepts of the two theories. The apparatus of classical game theory is thus very relevant to biology and is more evident in Maynard Smith's book than Lewontin suggests.

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