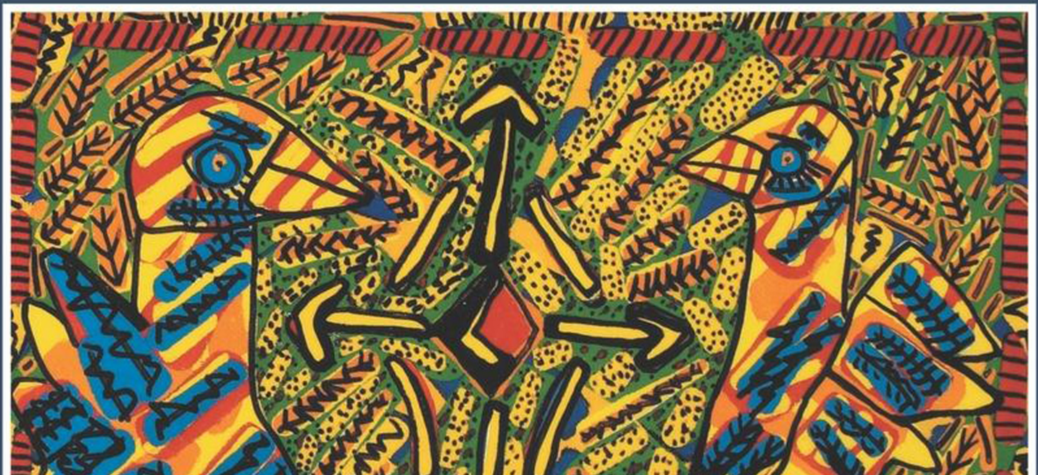
Social Foraging Theory

LUC-ALAIN GIRALDEAU
AND
THOMAS CARACO



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Social Foraging Theory

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To my parents, Germaine Levac and Aimé Giraldeau, who so often told me, *"Reste à l'école."* I did. And to my children, Félix and Ophélie, to whom I will say the same.—L.-A.G.

Contents

Preface

The sciences do not try to explain, they hardly even try to interpret, they mainly make models.
(John von Neumann)

When we decided to write this book, we wanted to offer readers a set of ideas they could apply to research on the foraging economies of social organisms. The result is a book that consists mainly of new models or reviews of older models; together they constitute a *Social Foraging Theory.* Our focus on modeling, rather than an emphasis on empirical results, reflects the somewhat disorganized way social foraging has been studied. Compared to conventional foraging theory, which concerns the behavior of independent individuals, the analysis of social foraging has lacked unifying themes, clear recognition of the problems that define social foraging, and consistent interaction between theory and experiments. So, we developed models that provide a thematic framework for the behavioral ecology of social foraging. The models collectively delineate a series of problems that span the theory as well as suggest quantitative methods for further development and application of the theory.

For most models discussed in the book, we include a "Summary Box" listing the particular model's distinguishing assumptions and main predictions. These boxes provide essential elements of the models for readers interested in concise statements of predictions to test. At the end of some chapters, we add a "Math Box," which either explores a general concept or provides a model's derivation for those readers interested in formal details. We hope these two devices will provide individual readers some options that make the book more useful.

Hassell and May (1985; see Ives 1995) observe that population ecologists cannot ignore behavior completely in the formulation of population-growth models, but behavioral ecologists can remain unconcerned about the population-level consequences of the phenomena they study. An original impetus in North America for studying behavioral ecology was an interest in exploring mechanisms underlying community structure. "Scaling up" from individual behavior to population dynamics remains a significant but elusive objective (e.g., Murdoch and Oaten 1975; Parker 1985; Schoener 1986; Green 1989; Goss-Custard et al. 1995; Sutherland 1996). We suspect that social foraging can provide some initial steps toward linking behavior to population-level patterns. So, where appropriate, we indicate implications of our models for population ecology.

The models we discuss in this book deal with groups of interacting foragers. At a general level, each model can be categorized as asking one of the two central questions of social foraging theory:

1. Given a particular set of ecological conditions, what can we predict about the size of foraging groups?
2. Given a foraging group of G members, what can we predict about their exploitation of particular resources, as individuals and as a group?

The first chapter defines social foraging and specifies the methods we use. We organize the rest of the book into five parts. The parts are linked by unifying themes, but each part develops a different traditional approach to research on social foraging. Part One emphasizes the first central question. Chapter 2 envisions two individuals attempting to avert starvation and avoid predation, and models the economics of foraging solitarily versus foraging as a group. Chapter 3 assumes that the two foragers belong to the same group and models the decision whether or not to share food when the individual discovers a resource patch.

Chapter 4 models foraging group size when each member's direct fitness increases with the size of the group, at least when groups are small. We refer to this as an *aggregation economy*. We analyze equilibrium group size for different "rules of entry" and show how genetic relatedness among group members may increase or decrease the equilibrium group size, depending on the rule of entry.

Chapter 5 reviews models for the size of foraging groups when each member's fitness declines as group size increases. We refer to this case as a *dispersion economy*; the models include the well-known Ideal Free Distribution (IFD).

The next three parts elaborate models following from the second central question. Part Two (chapters 6 and 7) considers the interaction between producers and scroungers in a group of G foragers. We define producers as group members that search for food clumps, and feed only when they discover food. Scroungers do not find food but attempt to feed whenever a producer locates a clump. The amount of food consumed by any group member and, hence, any group member's probability of starving depend on the frequency of producer and scrounger among the G individuals. The focal problem is predicting the equilibrium frequencies of the two resource-exploitation roles.

Chapter 6 selectively reviews empirical studies of the producer-scrounger interaction and organizes the extensive terminology that has become associated with social parasitism. Chapter 6 also presents a deterministic model for the equilibrium frequency of producer and scrounger in a foraging group.

Chapter 7 analyzes two stochastic models of the producer-scrounger game and suggests that group cohesion and cooperation may constrain the incidence of scrounging.

Part Three contains only a single chapter, but the topics considered merit recognition as a separate set of social foraging models. Chapter 8 reviews models that parallel the most prominent models that conventional theory has developed for solitaries: patch residence time and dietary choice. Models for group members' patch residence times introduced some of the basic concepts for a social foraging theory, but those ideas have not yet been afforded the empirical attention they deserve.

In Part 4 we focus on phenotypic variation among members of a foraging group. We fix group size and treat phenotypic diversity from different perspectives. Chapter 9 reviews an ecological method for partitioning phenotypic diversity between its within-individual and among-individual components. We indicate how patterns in resource quality or abundance may govern the components of phenotypic diversity.

Chapter 10 analyzes the spread of a learned foraging trait among members of a group. When an individual acquires the trait, its rate of finding food clumps increases. When clumps are shared among group members, opportunities to learn the trait through individual experience decline as more group members acquire the trait. However, a naive individual has more opportunity to acquire a trait by observing others as a trait becomes more common. Hence the advance of a learned trait, and phenotypic variation based on the presence or absence of the trait, may exhibit complex, frequency-dependent dynamics.

Chapter 11 models a group's phenotypic variation economically. We compare three types of groups: specialists on a preferred resource, generalists, and specialists that each search for a different resource (the skill pool). We show how the interaction of within-individual and between-individual constraints influences which group's members have the greatest chance of survival.

In Part Five, we conclude with a brief chapter, chapter 12, that synthesizes the book's recurring themes. We hope the book helps readers discover, or rediscover, some attractive directions for research.

Acknowledgments

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Parts of this manuscript were written while L.-A.G. was on sabbatical leave at Université Paris-XIII and McGill University. L.-A.G. thanks these institutions, and especially Jaap Kalff, for their hospitality. L.-A.G. and T.C. acknowledge financial support from Canadian and American taxpayers through research grants awarded by the Natural Sciences and Engineering Research Council (Canada), le Fonds pour la Formation des Chercheurs et l'Aide à la Recherche (Québec), and the National Science Foundation (USA). The various drafts of each chapter were transported across the Canada-USA border many times by our countries' valiant postal services. Given the number of delayed deliveries and occasional lost chapters, we are certain that a good number of postal workers of both countries have become assiduous readers of our work. We thank them for their interest. We thank the Montréal artist Michel Pimparé for allowing us to place one of his works (entitled *Jeux* [Games]) on the cover of our book. We also thank Alice Calaprice and Sam Elworthy of PUP for their excellent work. Finally, L.-.A.G. wishes to thank Dominique Proulx most warmly for her constant, often needed encouragement over the extended period of book writing and editing.

Montréal, Québec, Canada
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Social Foraging Theory

1 Social Foraging Theory: Definitions, Concepts, and Methods

1.1 What Is Social Foraging?

Social Foraging Requires Economic Interdependence of Payoffs

In this book we develop models where the functional consequence of an individual's foraging behavior depends on both the individual's own actions and the behavior of other foragers. We refer to the set of questions we analyze as "social foraging," defined by the concurrent economic interdependence among different individuals' payoffs or penalties. For the most part we restrict attention to effects of conspecifics' foraging decisions on individual survival, but several chapters will conclude with an examination of how predators' social foraging can have community-level consequences. We differentiate our subject from conventional (individual) foraging theory, reviewed by Pyke (1984), Stephens and Krebs (1986), and Schoener (1987). We emphasize that discriminating solitary versus social foraging involves more than extending previously analyzed questions to groups of foragers; economic interdependence implies a more fundamental biological difference (Maynard Smith 1984).

To make the point that social and conventional foraging are distinct, we can select a problem that has been well studied by conventional foraging theory and then identify the added complexity required by a social perspective. The classic prey-choice model specifies a predator's attack probabilities for different prey types upon sequential encounters (see Stephens and Krebs 1986). Typically, one associates a specific net rate of energy intake with the choices available to the solitary forager. That is, we could find the model predator's net rate of intake for a series of rational prey-selection strategies, e.g., take all prey as encountered versus take only the most profitable prey.

Now consider the same problem but allow two or more predators to exploit the same clump of prey. What now is the strategy that maximizes net intake rate? The answer is: it depends (see chapter 8 for details). The payoff obtained from any prey-selection strategy depends on the strategy adopted by the individual's competitors. So, taking only the best prey type will generate one intake rate if the competitors also do the same, but a different rate if the competitors take all prey types encountered instead. That is, economic interdependence means that the reward for a foraging policy depends simultaneously on all competitors' behavior. Furthermore, interdependent payoffs require that game theory replace the simple optimality models of conventional foraging theory, so that predictions follow from evolutionarily stable strategies (see below).

We recognize that the word "social" is semantically ambiguous. Indeed, its connotations can be rather diverse. For example, some researchers restrict use of the term "social" to organisms exhibiting a certain amount of familial dependence, those bearing elaborate behavioral displays, or those living within demographically structured groups. Others, however, use the term more liberally to include any animal that spends a good part of its life in groups, even if these groups are open, unstructured, and temporary. We use the word "social" in its broadest sense to mean any set of individuals that can be linked by identifiable, mutual relationships. Our criterion for social foraging simply requires that two or more individuals concurrently influence each other's energetic gains and losses. However, our simple definition merits a brief comment to clarify its range of application.

Social Foraging Does Not Require "Social" Organisms

Traditionally, some animal groups have been denied the status of social, often being referred to as mere aggregations. We contend that social foraging theory may apply whether animals are recognized as "social" or not. Both proximate and ultimate (or functional) distinctions have been proposed to separate true social groups (i.e., collections of social animals) from aggregations (collections of nonsocial animals). Ethologists tended to distinguish social groups from aggregations on the basis of the proximate causes of group formation. Social groups were viewed as the result of a genuine attraction between individuals, while aggregations were merely statistical coincidences of animals, often around a common resource: "Not all aggregations of animals however are social. When, on a summer night, hundreds of insects gather round our lamp, these insects need not be social. They may have arrived one by one, and their gathering just here may be clearly accidental; they gather because each of them is attracted by the lamp" (Tinbergen 1964, 1). Ecologists, for their part, have proposed a distinction at the ultimate, or functional, level. They discriminate social groups from aggregations because social groups are composed of individuals that derive specific evolutionary advantages from the presence of others while members of aggregations do not: "Intrinsic gregariousness has evolved to provide such concrete advantages . . . as the procurement of food. . . . In practice it may not be easy to distinguish social groups (in which individuals derive benefits by virtue of their presence with others) from aggregations" (Morse 1980, 271–272).

The ecologist's functional distinction between social groups and aggregations can be important when one is interested in the evolutionary origin of sociality. However, neither proximate nor functional distinction limits the application of social foraging theory. The essential property of social foraging is the interdependence of individuals' benefits and costs, whether foragers are attracted to one another or to the same food resource, and whether they mainly derive antipredatory or foraging benefits from their group membership.

The generality of our approach to social foraging can be illustrated with an example. Lions (*Panthera leo*) lead an apparently more complex social existence than do, say, pigeons (*Columba livia*). Lionesses live in permanent, structured social units composed of genetically related individuals that together raise and defend young as well as hunt prey (Schaller 1972; Bertram 1978; Packer 1986; Heinsohn and Packer 1995). Pigeons, on the other hand, form loose breeding colonies of probably unrelated individuals (Goodwin 1954) that do not forage in permanent, structured groups (Lefebvre and Giraldeau 1984). Instead, pigeons have individualized itineraries over a number of foraging stations, forming at each an open flock characterized by changing membership over the course of a day (Lefebvre and Giraldeau 1984; Lefebvre 1986). Despite the extensive differences between lion and pigeon sociality, we hold that the same economic approach of social foraging theory can help predict and explain the functional significance of both species' feeding-group sizes (Clark and Mangel 1984, 1986; Pulliam and Caraco 1984). For both lions (Caraco and Wolf 1975; Giraldeau and Gillis 1988; Packer 1986; Clark 1987) and pigeons (Lefebvre 1983), the amount of food available to an individual likely depends on the number of foragers within the group. It is this interdependence, coupled with the hypothesis that both organisms must forage efficiently to survive and reproduce, that allows the different foragers' equilibrium group size to be predicted by a single social foraging model. Therefore, even though the social life of lions and pigeons differ markedly, similar functional analyses unite them conceptually as social foragers. Emphasis on the distinctions, whether proximate or functional, between social groups and aggregations has obscured the apparent similarity of foraging decisions made by both types of organisms.

Social Foraging Is Not the Study of the Origin of Foraging Groups

It is often argued that animals such as small fish (Pitcher 1986), birds (Lazarus 1972), or primates (Wrangham 1986) may have become gregarious in response to predation. For certain other animals, such as lions, some experts argue convincingly that foraging benefits do not account for the origin of sociality (Packer et al. 1990). We can reasonably conclude that the evolutionary origins of some animals' group-feeding habits lie outside of their foraging economies. Should we exclude such species from studies of social foraging? We think not. The economic interdependence of group members' foraging behavior that defines the issues of social foraging neither requires nor precludes particular origins of sociality. Failing to discriminate between the evolutionary origins of sociality and contemporary functions of foraging groups as objects of study can confuse the issues of social foraging (as we define it). One may argue how effectively food, predation, or both explain sociality's origins. However, social foraging analyses, unlike those pertaining to the origin of sociality, do not treat antipredatory and energetic benefits as competing hypotheses. A model for social foraging in a contemporary environment will more likely emphasize how the two types of benefits may interact to govern some currency of fitness (e.g., Houston et al. 1993).

Several of our models take the probability of surviving as the currency of fitness. In general, we can write the probability of surviving some specified time interval as the product of the probability of avoiding starvation and the independent probability of avoiding predation. This approach combines the two sources of mortality into a single currency (e.g., Pulliam et al. 1982; Mangel and Clark 1986; McNamara and Houston 1986; Newman 1991). When decreases in starvation imply increases in predation, we can profitably use this approach to investigate social foragers' compromises between food and safety (e.g., Caraco et al. 1980a; Elgar 1986a; Newman and Caraco 1989; Abrahams and Dill 1989; Rayor and Uetz 1990; Houston et al. 1993).

Not every social foraging model will require analysis of a trade-off between foraging gains and avoiding predators. Suppose that all strategic options yield exactly the same hazard of predation; then it may be safe to ignore effects of predators (see Lindström 1989). When appropriate or convenient, one might choose to incorporate antipredatory requirements as constraints in a model for social foraging. Concern about antipredatory behavior seems to appear more frequently when group foraging is considered, possibly because predation is so often cited in discussion of sociality's origins. It is important to emphasize that predation is not more of a problem for group foragers (Martindale 1982; Edwards 1983; Lima et al. 1985; Mangel and Clark 1986; Stephens and Krebs 1986). In fact, one could turn the standard view around and suggest that since groups may provide reduced predation hazard, the foraging of animals in groups is less likely to be constrained by predators than is solitary foraging. Social foraging theory, then, focuses on contemporary adaptive function and says little about origins of sociality.

1.2 Concepts and Methods of Social Foraging Theory

There are at least two currently popular methods used to generate hypotheses about the functional significance of behavior. One, the comparative method, involves accumulating information about several populations or several species and then correlating ecological conditions with the populations' or species' attributes (e.g., Crook 1965; Altmann 1974; Jarman 1982; Clutton-Brock and Harvey 1984; Harvey and Pagel 1991). For instance, in their study of avian kleptoparasitism, Brockmann and Barnard (1979) review all published instances of the behavior to draw conclusions concerning the ecological circumstances that promote its evolution. The alternative method employs optimization techniques to formulate specific, often quantitative hypotheses about behavior (e.g., Pyke 1984; Parker 1984a; Mangel and Clark 1988). For instance, Vickery et al. (1991) and Caraco and Giraldeau (1991) both develop foraging games designed to analyze the economics of kleptoparasitic behavior, to predict the ecological circumstances under which the behavior is maintained. We favor the latter method because it has been particularly successful in predicting the behavior of solitary foragers (reviewed by Stephens and Krebs 1986), and has guided research programs across a broad spectrum of questions in behavioral ecology (Grafen 1991). The use of optimization methods in evolutionary ecology has been criticized at times (e.g., Cohen 1976; Gould and Lewontin 1979; Lande 1982; Gray 1987; Hines 1987). Most, if not all, of these criticisms have been answered reasonably and rigorously; rather than repeat the general arguments, we refer the reader to an appropriate literature (Maynard Smith 1978; Oster and Wilson 1978; Mayr 1983; Krebs and Davies 1984; Stephens and Krebs 1986; Schoener 1987). We shall, however, specify the game-theoretical concepts we apply to model the behavior of social foragers.

Optimization Models in Social Foraging Theory

The mathematical methods used in conventional models of adaptive foraging seldom can serve social foraging theory, where the efficiency of a particular behavioral strategy depends, by definition, on the frequencies of feasible strategies among an individual's competitors. Questions in social foraging theory still concern the adaptive significance of individual behavior, but the models rely on game-theoretical equilibria and the concept of an evolutionarily stable strategy (ESS) (Maynard Smith 1982; Parker 1984a; Hines 1987).

An evolutionarily stable behavior possesses both optimality and stability properties (Parker 1984a; Vincent and Brown 1984). An ESS combines these attributes because an ESS must qualify as a Nash equilibrium (e.g., Hines 1980; Thomas 1985). A Nash equilibrium is a set of strategies, one for each player, such that no player can improve its payoff by changing strategy when the other players continue using their Nash equilibrium strategies (e.g., Riley 1979; Caraco and Pulliam 1984; Parker and Sutherland 1986). So, an ESS maximizes a player's expected payoff in the sense that no other feasible strategy does better against an ESS than the ESS itself. Readers not inclined toward an optimality-based interpretation of an ESS may find comfort in Hines's (1987) discussion of a polymorphic evolutionarily stable strategy.

An ESS also has, of course, a stability property following from the Nash equilibrium concept. Depending on one's detailed characterization of the game (see below), stability may imply dynamics resistant to invasion by a rare alternative strategy or combination of strategies, or stability may refer to the consequences an individual incurs when deviating unilaterally from an ESS (Parker 1984a; Vincent and Brown 1984; Brown and Vincent 1987; Hines 1987).

It is worth noting that game theory may also be applied to problems where conspecifics differ in their ability to sequester resources (i.e., an asymmetric game), as well as to questions concerning interactions between species (e.g., Parker and Sutherland 1986). So we adopt a game theory approach, because with or without the full analysis of an ESS, it can help us investigate asymmetric competitive interactions, including circumstances where a social forager makes "the best of a bad job" (e.g., Parker 1984a; Caraco et al. 1989).

Phenotypic, Rather than Genetic, Focus

As mentioned in the preceding paragraph, the term "ESS" currently is used in several senses; Hines (1987) summarizes the theory. The definition and existence of an ESS, as well as the criteria for stability, can vary according to several properties of the model population or group. Strategies may be equivalent to alleles or assumed to be modified by the environment. The population may have a finite or infinite size (e.g., Riley 1979; Vickery 1987; M. Schaffer 1988; Nishimura and Stephens 1997). Interactions may or may not involve repeated play (e.g., Axelrod and Hamilton 1981). Only one or several different strategies deviating from a candidate ESS may occur simultaneously (e.g., Boyd and Lorberbaum 1987; Brown and Vincent 1987; Farrell and Ware 1989; Lorberbaum 1994). Each of these differences, and several more, has theoretical significance, but we cannot consider them all. In applying game theory to social foraging we adopt Hines's (1987) suggestion and look for the "practical relevance of the (ESS) concept to actual biological phenomena."

Some approaches to ESS theory use frequency-dependent payoffs to generate the dynamics of a system of competing alleles (e.g., Taylor and Jonker 1978; Hines 1980). Change in gene frequencies is the essence of evolution, but reducing complex social behavior to simple genotypes, as for instance, in Brockmann et al.'s (1979) field study of digging and entry in golden digger wasps (*Sphex icheumeneus*) we find generally too restrictive. We want to appreciate not only behavioral diversity due to attributes such as size, age, and sex, but also the important strategic variation due to learning. Our predictive models therefore focus on phenotypes. Like most behavioral ecologists, we rely on what Grafen (1991) calls the "phenotypic gambit." Most of our models invoke the original definition of an ESS (Maynard Smith 1982; see Parker 1984a; Houston and McNamara 1988), which essentially ignores genetic constraints once the set of possible phenotypes has been established (see below). Genetic and phenotypic models of a particular behavior should be viewed as complementary analyses. They often lead to identical conclusions (e.g., Aoki 1984; Michod 1984; Thomas 1985; Maynard Smith 1988; Moran 1992; Weissing 1996), and each approach has its advantages. Essentially, we assume in most cases that selection has enhanced learning capacities and decision-making rules that allow an individual to vary its behavior efficiently across a range of environmental and social conditions (Dawkins 1980; Barnard 1984a; Pulliam and Caraco 1984; Cosmides and Tooby 1987; León 1993).

Although we do not consider the intergenerational dynamics of gene frequencies, we do examine how learning can govern the frequencies of various phenotypes within a cohesive group. Social foragers must often experience a great deal of spatial and temporal variation in both resource characteristics and competitive interactions. If natural selection favors some form of phenotypic plasticity in such an environment (Via and Lande 1985; Fagan 1987a; West-Eberhard 1989; Lessells 1991; Houston and McNamara 1992; Moran 1992), a significant fraction of the variability in foraging behavior might be acquired through learning (e.g., Norton-Griffiths 1967; Krebs 1973; Werner and Sherry 1987). The acquisition of behavioral traits is usually the domain of learning psychologists, but behavioral ecologists recently have appreciated the importance of the process in terms of the problems faced by solitary foragers (e.g., Krebs et al. 1978; Pulliam 1980; Kamil 1983; Shettleworth 1984; Stephens and Krebs 1986). But learning from experience necessarily proceeds differently in a social context, where learning itself can generate polymorphisms in a manner analogous to frequency-dependent selection (Giraldeau 1984, 1997).

Terminological Clarifications

In this subsection we associate some behavioral terms with the game-theoretic concepts we use to solve our models. The same behavioral term can, of course, mean different things to different authors. For example, cooperation can mean a genetically determined attribute (e.g., Nowak and May 1992), a small set of phenotypically plastic behaviors (e.g., Pulliam et al. 1982; Noë 1990), or a broad class of phenomena ranging from mutualism to traits favored under group selection (e.g., Mesterton-Gibbons and Dugatkin 1997; see Brown 1983; Dugatkin 1997). Therefore, we want to specify the meaning of the behavioral terms we use in modeling social foraging. We use the definitions we assign consistently, and intend no criticism of alternative terminologies.

To begin, we view the difference between observable behavior and a foraging strategy as similar to the distinction between "territory and map"; the latter is an idealized guide to the former. As stated above, a strategic model for social foraging usually takes the form of a game, where each competitor pursues its own objective (e.g., increasing its consumption of discovered food). The game's solution predicts how the different players' often conflicting, but sometimes coincident, objectives can be resolved. However, models in two of the book's chapters are simpler; they assume a single strategic objective can predict social foraging behavior. Taking an example from chapter 4, suppose an individual increases its inclusive fitness by economically joining or avoiding a group of relatives. That is, we assume a single decision-maker takes an action rendering the sum of fitness effects on self and effects on relatives (weighted by degree of relatedness) positive. Then three possibilities can be favored under Hamilton's Rule (Hamilton 1964; Grafen 1984). If effects on both self and relatives are positive, we term the behavior a *mutualism*, without the need for special reference to kinship (see below). If the effect on self is negative but the effect on relatives is positive (and of greater absolute value), we term the actor's behavior *kin-directed altruism*. If the effect on self is positive and the effect on relatives is nonpositive (and, if negative, of lesser absolute value), we term the behavior *selfish*, again requiring no special reference to kin. We consider both mutualism and kin-directed altruism special cases of what we call *unconditional cooperation*. That is, the decision-maker's action promotes the fitness of other individuals, and natural selection can maintain the trait without it being conditioned on either an immediate or delayed response-in-kind by those other individuals (below we define *conditional cooperation*). The behavior defined as selfish does not, of course, qualify as cooperation, although it can be favored by Hamilton's Rule.

The other type of model where we require only a single strategic objective assumes that members of the same foraging group work essentially as a team (see Oster and Wilson 1978, 302). The models of chapter 11 suppose that group members begin the day in the same physiological condition, and then divide each food clump they discover equally. Consequently, a single currency assesses each group member's expected benefit obtained from using feasible patch-exploitation strategies. Our treatment of a group as a team resembles several other dynamic-optimization models of social foraging (Clark 1987; Mangel 1990; Székely et al. 1991). The terminology we use in chapter 11 differs little from conventional foraging theory (see Mangel and Clark 1988) and needs no explanation here.

Some of our models assume a game between two players, and others assume an N-player game. All of our applications of game theory assume uninformed play (see Bram and Mattli 1993). This means that each player chooses an action once per play of the game without knowledge of (or communication concerning) the action any other player is about to take. This is a common assumption in behavioral ecology; for alternatives, see Maynard Smith and Parker (1976), Pulliam and Caraco (1984), or Noë (1990).

Most of our models take the form of a symmetric game. Symmetry implies competitive equivalence of the players, so that each has the same payoff (or penalty) function. So, symmetry means that an individual's payoff or penalty is specified completely by the combination of interacting strategies, without reference to any other phenotypic attribute of this individual. In a few instances we consider a competitive asymmetry due to aggressive dominance. Nearly all of our game-theory models are discrete. That means each player's action on any single play of a game belongs to a finite set (as opposed, for example, to a War of Attrition that affords players a continuous set of alternative strategies); the number of elements in the set equals the number of possible pure strategies (see below). Consequently, the payoffs or penalties for two-player games can be arrayed in matrix form. For clarity and simplicity, the majority of our matrix games have only two pure strategies. Following Parker (1984a), we first identify a class of behaviors associated with social foraging. Then the model lets one action represent the presence of the class of behaviors, and lets the alternative action represent its absence.

Some of our models consider only a single round of play. But certain models' payoffs or penalties may conform to a Prisoner's Dilemma (e.g., Axelrod and Hamilton 1981; Nowak and Sigmund 1992; Mowbray 1997; Nishimura and Stephens 1997); when this occurs we consider the consequences of probabilistically repeated play. As pointed out by Mesterton-Gibbons and Dugatkin (1997), the distinction between single and repeated interaction of the same individuals, and between behaviors associated with single versus repeated play, should depend on a logical temporal scaling. Most of our models define the duration of a round of play as a foraging period τ time units long (see Newman and Caraco 1989). At the end of a foraging period, each player aquires some benefit or pays some cost, and then a new round of play may commence. Hence our temporal scaling of play mimics physiological and environmental constraints on the timing of foraging. More importantly, assuming repeated play of the same individuals helps focus attention on the fundamental significance of population spatial structure for the economics of individual interactions (Houston 1993; Ferriere and Michod 1996; Caraco et al. 1997; Levin et al. 1997).

In our applications of game theory, a strategy is a rule for using feasible actions; see discussion in Vincent and Grantham (1981) or Weissing (1996). In general, an individual's strategy may assign positive probability to two (or more) different actions and may be conditioned on environmental variables (e.g., food density) and/or the behavior of another player. Most of our models predict "pure" strategies, a solution with a single action. As mentioned above, we invoke the well-known Tit-for-Tat strategy (TFT) (Axelrod and Hamilton 1981) when the game qualifies as a probabilistically iterated Prisoner's Dilemma.

Next consider some concepts we apply in solving our game-theory models. The familiar notion of an evolutionarily stable strategy (ESS) envisions introduction of a single, rare strategy (which deviates from the ESS) into a population where all other individuals use the ESS. The stability property of an ESS requires that the rare, deviating strategy be disfavored. Recall that we require that an ESS qualify as a Nash equilibrium to the specified game (Parker and Sutherland 1986; Recer et al. 1987; Weissing 1996). A Nash equilibrium for a two-player game implies that neither player is tempted to change its strategy (hence behavior) as long as the other player continues to use its same strategy. For N players, no individual is tempted to change strategy as long as all others continue with their Nash-equilibrium strategies. If a player is not tempted to change strategy, it is because the individual cannot increase its payoff (or decrease its penalty) by altering its behavior (Vincent and Grantham 1981). As a convenience, we describe a Nash equilibrium as stable if unilateral deviation reduces that individual's payoff. We may describe a Nash equilibrium as neutrally stable if unilateral deviation has no effect on the individual's payoff. Not every Nash equilibrium qualifies as an ESS, but any ESS in our models will have the Nash-equilibrium property. Math Box 1.1 at the end of this chapter illustrates the application of the Nash equilibrium concept to solve first a discrete game, and then a continuous game.

Above we defined unconditional cooperation to include both kin-directed altruism (a cost to the actor benefits relatives) and mutualism (both individuals, whether related or not, benefit). A number of studies focus on nonrelated individuals, seeking only to increase their own payoff, that may be penalized if they fail to cooperate mutualistically (Caraco and Brown 1986; Mesterton-Gibbons 1991; Mesterton-Gibbons and Dugatkin 1992; see Clements and Stephens 1995). So, mutualism may occur with appreciable frequency among social foragers, when a Nash solution to a foraging game produces a mutualistic interaction. To discriminate between unconditional cooperation and our applications of the iterated Prisoner's Dilemma, we use the term *conditional cooperation* for the latter, where cooperation arises conditionally on simultaneous (conditional mutualism) or delayed (reciprocal altruism) reciprocation of behavior (see Summary Box 1.1).

While a Nash solution requires that an individual's unilateral deviation in strategy cannot be rewarded, a Pareto optimal solution allows that an individual might deviate and so increase its payoff, but only by reducing at least one other player's payoff (e.g., Vincent and Grantham 1981). So, Pareto

SUMMARY BOX 1.1 A SIMPLE TERMINOLOGY FOR CLASSES OF BEHAVIORS THAT MAY OCCUR AMONG SOCIAL FORAGERS

I. Selfish behavior
II. Cooperative behavior
  A. Group-selected altruism
  B. Unconditional cooperation
    1. Kin-directed altruism
    2. Mutualism
  C. Conditional cooperation
    1. Conditional mutualism
    2. Reciprocal altruism

Any behavior favored by natural selection results from a fundamentally competitive process. But we use the term "selfish behavior" when the actor increases its payoff and, as a consequence, decreases the payoff to one or more individuals (related or unrelated to the actor).

Cooperation implies that an action increases the payoff to one or more other individuals; the actor's payoff may increase or decrease. The actor cooperates unconditionally if the benefit to relatives is sufficiently large, or if the actor benefits via mutualism. The actor cooperates conditionally when the economics of cooperative behavior require a response in-kind; some form of social organization fostering repeated interactions of the same individuals is assumed. The cooperator may benefit from this response immediately (conditional mutualism; the standard Prisoner's Dilemma) or later (reciprocal altruism).

optimal solutions to a game assume that players mutually coordinate their strategies to advance each individual's payoff; hence Pareto optimality helps us identify consequences (but not always the ecological causes) of mutual cooperation. Of course, an advantage to cooperation between nonrelatives requires that mutual cooperators acquire a greater payoff than individuals lacking such cooperation (Axelrod and Hamilton 1981; Pulliam et al. 1982; Caraco and Brown 1986; Yamamura and Tsuji 1987; Mesterton-Gibbons 1991; Mowbray 1997; Nishimura and Stephens 1997).

Suppose two players have the choice between a cooperative and a noncooperative behavior, as in the Prisoner's Dilemma. Ordinarily, Pareto optimality identifies a continuous solution set, strategy pairs where the two players' payoffs satisfy the Pareto optimal condition (see Math Box 1.2). The Pareto-optimal solution set has the interesting property that increasing one player's payoff necessarily decreases the other player's payoff (Oster and Wilson 1978; Vincent and Grantham 1981). Hence, mutually cooperative players might have to "negotiate" a particular Pareto solution (Caraco and Pulliam 1984; Noë 1990). For a symmetric game, a Nash solution qualifying as an ESS implies that the competitively equivalent players receive the same expected payoff. Hence equality of expected payoffs, over some biologically relevant timescale (Nowak and Sigmund 1994; Mesterton-Gibbons and Dugatkin 1997), should also apply to models of mutual cooperation. Following Axelrod and Hamilton (1981), the most common application of the Prisoner's Dilemma in evolutionary biology assumes equivalent players and focuses on equality of expected payoffs at each round of repeated play.

Consider a single round of play when two equivalent individuals' payoff matrices conform to the Prisoner's Dilemma (defined in Math Box 1.2). Each player chooses either to cooperate or defect during that round of play. Defect is the more rewarding response to both cooperate and itself. Then pure defect is an ESS, and a player will always be tempted to defect against cooperation. But mutual cooperation rewards each player more than does mutual defection; hence the dilemma. The game serves as a reasonable metaphor for asking questions about possible cooperative interactions between nonrelatives (see Dugatkin 1997). Pure cooperation is a Pareto optimal solution for a single round of play; cooperation yields a greater reward than does the Nash equilibrium strategy, but cooperation is unstable against defection.

One escape from the dilemma assumes probabilistically repeated play and the Tit-for-Tat (TFT) strategy (Axelrod and Hamilton 1981; Mesterton-Gibbons 1991). TFT cooperates in the initial round of play and thereafter behaves as its opponent last did, until play is terminated. If the expected duration of the interaction between the same two players is sufficiently large, TFT is a Nash solution to the iterated game and an ESS (see Maynard Smith 1984 or Math Box 1.2). TFT is a reactive strategy; continued cooperation by a TFT strategist is conditional upon cooperation of the other player. Hence we refer to any behavior associated with the TFT strategy as *conditional cooperation.* That is, the decision-maker's action promotes the fitness of other individuals, but selection can maintain the trait only when it is conditioned on an immediate or delayed response-in-kind by the other individuals. For convenience, we use the term *conditional mutualism* when mutual cooperators benefit simultaneously, as in the (standard) iterated Prisoner's Dilemma. We use the term *reciprocal altruism* when nonrelated players alternate between altruist and recipient roles, so that the response-in-kind is delayed (see Noë 1990). For completeness we note that reciprocal altruism, as we define it, is not a solution to the standard iterated Prisoner's Dilemma (cf. Mesterton-Gibbons and Dugatkin 1997).

Conditional cooperation may or may not occur commonly among social foragers (see Dugatkin et al. 1992; Clements and Stephens 1995). But conditional cooperation can be quite interesting because its predictions often differ from behavior predicted in its absence. As we stated previously, perhaps the most important insight from TFT's stability is the significance of a social environment and a spatial grain in a population that together permit or promote repeated interaction between the same individuals. Recent evolutionary theory suggests that natural selection should relax genetic constraints on strategic behavior (e.g., Hammerstein 1996; Weissing 1996). In that light, our emphasis on phenotypic plasticity and economic decision-making invokes the iterated Prisoner's Dilemma as a general metaphor for ecological conditions that may favor repeated interactions and conditional cooperation. Summary Box 1.1 collects our behavioral terminology.

1.3 Interactions among Social Foragers

Having defined social foraging in terms of economic interdependence, and introduced both concepts and methods of social foraging theory, we now point out the general properties of questions analyzed in this book. Problems in social foraging require detailed assumptions about the process of searching for food. At least some group members must attempt to find food, but certain individuals may try to avoid the cost of searching (Barnard and Sibly 1981). Among the active searchers, different foragers may focus their effort on different resources (Giraldeau 1984). Furthermore, the probability density of the time taken to locate a patch of a particular resource can depend on both the number of individuals searching for that resource and the way their efficiencies interact (Ekman and Rosander 1987; Caraco et al. 1995). Most models of foraging processes, social or not, either neglect or deemphasize the often inherently random nature of food discovery. In contrast, we treat searching for (or capturing) food as stochastic, hypothesizing that the economics of social foraging commonly depend on the dynamics of food discovery. Math Box 1.3 provides examples of the tools we use to characterize the probabilistic processes of food discovery.

The next set of important assumptions in social foraging theory concerns the allocation of discovered food among group members. Food may be actively shared, divided equally among competitively equivalent foragers, or allocated asymmetrically according to dominance status (Caraco and Giraldeau 1991; Ranta et al. 1993; Ruxton et al. 1995). Differences in the way social foragers search for food, and patterns in the way they divide discovered food, together suggest a simple introduction to the economic interactions we model.

We can categorize any social forager as one of three types according to its food-searching behavior (following Vickery et al. 1991): producers, scroungers, and opportunists. Producers search their environment for food clumps (or divisible prey). When a producer discovers food, it can prevent other producers from usurping any of the resource but may elect to let them feed. Scroungers do not search for food directly. Instead, they attend to other foragers' clump discoveries and aggressively or stealthfully sequester some food at each clump found by either a producer or an opportunist. Opportunists both search for food directly and attempt to obtain food at clumps located by producers or other opportunists. An opportunist then simultaneously searches both as a producer and a scrounger but may be less efficient than either more specialized forager (Vickery et al. 1991). It is important to note that the same categories can be applied to individuals that switch among strategies. Hence, at any one time an individual may play one of the following: producer, scrounger, or opportunist. During the duration of that play of the game, it behaves according to the rules of the alternative it chose.

Producer versus Producer

Suppose two producers forage in close proximity. When one finds a clump, it might choose to share the food with the other producer, perhaps giving a "food call" to attract the other forager (chapter 3). Food-sharing might arise as a consequence of kinship (McNamara et al. 1994; Emlen 1995), conditional cooperation (Caraco and Brown 1986; Mesterton-Gibbons 1991), the danger of predation when feeding alone (Newman and Caraco 1989), or a mutualism (Stephens et al. 1995). More generally, consider a group of $(G - 1)$ producers that share food mutualistically. Their choice of admitting or repelling another producer presents the problem of equilibrium group size under a group-controlled entry rule (chapter 4; Giraldeau and Caraco 1993; Higashi and Yamamura 1993).

Producer versus Scrounger

Social foraging theory includes the producer-scrounger interaction (Part 2; Barnard and Sibly 1981; Giraldeau et al. 1990), which has been applied to a diversity of questions in population biology (Parker 1984b). In a large enough group, a rare scrounger can have an economic advantage over producers since the scrounger feeds at each clump found. However, scroungers require at least some producers to feed. Hence, we may anticipate an equilibrium mix of producers and scroungers (Vickery et al. 1991) unless the "cost of scrounging" is large enough to eliminate the latter (Caraco and Giraldeau 1991).

Producer versus Opportunist

For simplicity, suppose a group of two contains one producer and one opportunist (chapter 2). Both foragers search for food, but only the opportunist feeds at each clump discovered. Greater dominance status of the opportunist might produce this situation; the same result might arise when the producer finds resources much faster than does the opportunist. Symmetric competition will not likely maintain this interaction (Pulliam and Caraco 1984).

Opportunist versus Opportunist

Now each forager searches for food, and each acquires some food at every clump discovered. Groups of opportunists are sometimes termed an "information-sharing system" (chapter 6; Clark and Mangel 1984; but see Vickery et al. 1991). The problem of comparing solitary versus social foraging is often framed as an interaction of opportunists; two foragers, dividing each clump found, may survive better than each of two solitaries. Similarly, more sophisticated questions about equilibrium group size under a free-entry rule (Clark and Mangel 1986; Giraldeau and Caraco 1993; Higashi and Yamamura 1993) can be viewed as an interaction among opportunists (chapter 4).

Suppressing the importance of the searching process, while extending the spatio-temporal scale of the analysis, leads to questions about the ideal free distribution of competitors across resource patches (chapter 5; Fretwell 1972; Rosenzweig 1981; Sutherland and Parker 1985; Krivan 1996) and its various modifications. If different opportunists search for different resources, each individual searches as a specialist and feeds as a generalist. Hence the problem of the skill pool economy (Giraldeau 1984) is an interaction among opportunists (chapter 11).

Scrounger versus Opportunist

Only the opportunists discover food, and all group members feed at each clump. Each individual should achieve a greater foraging rate as the frequency of opportunists in the group increases. But the scrounger-opportunist group can persist due to knowledge limitation (chapter 10; Giraldeau et al. 1994b). That is, when some group members have acquired a skill needed to make a given resource available, other foragers may have few opportunities to learn the skill (and become a producer). In this case, social foraging constrains the group members' collective capacity to increase their economic efficiency.

Some other problems in social foraging are drawn directly from questions in conventional foraging theory. These include diet choice as a group member and patch residence time when resources deplete (chapter 9).

1.4 Concluding Remarks

Readers may have noticed recurring themes in our view of social foraging theory. It may be useful to collect these themes here, since we return to them in the chapters that follow. We stress the importance of the mutual dependence of individuals' payoffs and penalties. Economic interdependence may occur during the search for food, during the division of food following its discovery, or during both. These interdependencies define social foraging and set it apart from conventional foraging theory.

Another important theme is our view of foraging as a stochastic rather than deterministic process. Stochastic models take into account effects that reward variance exerts on a forager's survival, and more realistically depict the inherent uncertainty of foraging processes. They easily permit inclusion of predation hazard in our theory. So, survival probabilities and risk sensitivity are important themes that run through the book's chapters.

We also emphasize the importance of distinguishing between cooperative and noncooperative solutions to social foraging games. When appropriate, we investigate whether cooperative solutions, whether conditional or unconditional, occur and explore the biological circumstances under which we expect them to arise.

Math Box 1.1 Concepts from Game Theory

Here we review the idea of an evolutionarily stable strategy (ESS), in a form familiar to behavioral ecologists (Parker 1984a). We also review the related, but more general, concept of a Nash equilibrium (Vincent and Grantham 1981; Weissing 1996). We organize the presentation by first describing the structure and solution of a discrete game, and then doing the same for a continuous game. For convenience, we restrict this discussion to symmetric, two-player games. For further technical development, see Hines (1987) or Mesterton-Gibbons (1992).

A Discrete Game

Suppose an interaction, a contest, between two foragers (1 and 2) alters each individual's survival in a manner depending on the behavioral "choice" each makes. Each player selects an action from a set of S behaviors. S is a positive integer ($S \geq 2$), so the game is discrete rather than continuous.

The S^2 feasible behavioral combinations imply well-defined consequences, arrayed for player i ($i = 1, 2$) in an $S \times S$ matrix. We might express the consequences as survival probabilities, mortality probabilities, or another currency of fitness. For survival we let m_i represent player i's *payoff* matrix. For mortality or an energetic shortfall while foraging, we let M_i represent player i's *penalty* matrix. In a symmetric game the players are competitively equivalent, implying that they have the same payoff (penalty) matrix. So, $m_1 = m_2 = m$, and $M_1 = M_2 = M$. The majority of our models calculate probabilities of insuffícent energy intake, so here we discuss only penalty matrices M, with elements M_{rc} ($r = 1,2,\ldots,S; c = 1,2,\ldots,S$). Hence, the inequalities associated with an ESS will have the direction opposite that of the more familiar payoff-matrix formulation. But the distinction should be readily apparent, and this discussion parallels the analysis of our models.

Associated with the penalty matrix M, let π_i represent a strategy of player i ($i = 1, 2$). π_i is a column vector with S elements π_{ik} ($k = 1, 2, \ldots, S$). π_{ik} is the probability that player i chooses action k when the foragers interact. Hence, $0 \leq \pi_{ik} \leq 1$, and

$$\sum_{k=1}^{S} \pi_{ik} = 1.$$

Math Box 1.1 (*cont.*)

π_i is a pure strategy if a single element is unity, so that the other elements are 0. π_i is mixed if two or more $\pi_{ik} > 0$.

To motivate our models, let $w_i(\pi_i, \pi_j)$ represent the probability that player i fails to meet its energetic requirement when i has strategy π_i and player j has strategy π_j. The expected penalty w_i depends bilinearly on the strategies

$$w_i(\pi_i, \pi_j) = \pi_i^T M \pi_j, \tag{1.1.1}$$

where π_i is transposed. Each model player attempts to decrease its expected penalty and avoid an energetic failure.

An ESS

Suppose a strategy $\tilde{\pi}$ is an ESS for the game defined by penalty matrix M. If members of an infinite population use $\tilde{\pi}$, no single rare alternative can be favored (e.g., Parker 1984a). Then, for any feasible $\tilde{\pi} \neq \pi$, either

$$w(\tilde{\pi}, \tilde{\pi}) < w(\pi, \tilde{\pi}) \tag{1.1.2}$$

or

$$w(\tilde{\pi}, \tilde{\pi}) = w(\pi, \tilde{\pi}) \text{ and } w(\tilde{\pi}, \pi) < w(\pi, \pi). \tag{1.1.3}$$

When condition (1.1.2) holds, the stability of $\tilde{\pi}$ is clear. $\tilde{\pi}$ responds better to itself than does any rare alternative, since $\tilde{\pi}$ minimizes a player's expected penalty when the opponent uses $\tilde{\pi}$. When condition (1.1.3) holds, adopting $\pi \neq \tilde{\pi}$ against the ESS does not imply a greater penalty, according to the first part of the condition. But $\tilde{\pi}$ implies a lower expected penalty against π than the alternative π does against itself, according to the second part of condition (1.1.3). Hence, use of π must, on average, result in a greater expected penalty than does use of $\tilde{\pi}$, so $\tilde{\pi}$ remains an ESS. $\tilde{\pi}$ may be a pure or mixed ESS; all members of a population attain the same expected penalty, $w(\tilde{\pi}, \tilde{\pi})$, when all adopt the ESS.

Parker (1984a) discusses the "conditional ESS," a set of environmentally determined strategies. Put simply, variation in environmental circumstances (e.g., food density, predation hazard) leads individuals to adjust their behavior accordingly.

Nash Equilibria

Suppose the strategy pair $(\hat{\pi}_1, \hat{\pi}_2)$ is a Nash equilibrium for the game defined by penalty matrix M. As pointed out in Section 1.2, $(\hat{\pi}_1, \hat{\pi}_2)$

Math Box 1.1 (*cont.*)

specifies a strategy pair where neither player is tempted to deviate (i.e., alter its strategy) unilaterally. In terms of our example M, neither forager can reduce its chance of an energetic shortfall by changing its strategy as long as the other player continues to use its Nash strategy. This property does not require equality of expected penalties (consider an asymmetric interaction). But in symmetric games the players may have identical Nash strategies, implying they have the same expected penalties. In this case the common Nash strategy qualifies as an ESS; $\hat{\pi}_1 = \hat{\pi}_2 = \tilde{\pi}$, and

$$w_1(\hat{\pi}_1, \hat{\pi}_2) = w_2(\hat{\pi}_2, \hat{\pi}_1) = w(\tilde{\pi}, \tilde{\pi}). \qquad (1.1.4)$$

Every symmetric two-player game with $S = 2$ (a 2×2 matrix) has at least one Nash solution satisfying an ESS condition (either 1.1.2 or 1.1.3). Larger matrices ($S > 2$) may not have an ESS, but if they do, it will be a Nash equilibrium (Haigh 1975).

Diagonal Dominance

The simplest way to locate an ESS for a symmetric discrete game is to identify diagonally dominant columns (Haigh 1975). For the penalty matrix M, the M_{kk} ($k = 1, 2, \ldots, S$) are the entries on the main diagonal. Each M_{kk} quantifies how well an action responds to itself. Suppose

$$M_{kk} < M_{rk} \text{ for } 1 \leq r \leq S, r \neq k. \qquad (1.1.5)$$

Then the kth column of M is *diagonally dominant*. That is, M_{kk} is the minimal chance of an energetic failure when the other player uses the kth behavior. Since the kth behavior is the best response to itself, a pure strategy employing only behavior k is an ESS by condition (1.1.3.) Furthermore, the kth action cannot be part of another, mixed ESS for the same game. Since M has S columns, there can be as many as S pure ESS's (Haigh 1975).

If $S = 2$ and neither column exhibits diagonal dominance, the ESS (see above) may be pure or mixed. If a 2×2 matrix lacks diagonal dominance, the ESS has the form (e.g., Oster and Wilson 1978; Caraco and Pulliam 1984):

$$(\tilde{\pi}_{i1}, \tilde{\pi}_{i2}) = (M_{12} - M_{22}, M_{21} - M_{11}) / (M_{12} + M_{21} - M_{11} - M_{22}). \qquad (1.1.6)$$

The last expression applies in three cases:

1. If $M_{11} = M_{21}$ and $M_{12} < M_{22}$, then ($\tilde{\pi}_{i1} = 1, \tilde{\pi}_{i2} = 0$) solves (1.1.6), and is a pure ESS by condition (1.1.3).