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# Optimal Forager against Ideal Free Distributed Prey

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ABSTRACT: The introduced dispersal-foraging game is a combination of prey habitat selection between two patch types and optimal-foraging approaches. Prey's patch preference and forager behavior determine the prey's survival rate. The forager's energy gain depends on local prey density in both types of exhaustible patches and on leaving time. We introduce two game-solution concepts. The static solution combines the ideal free distribution of the prey with optimal-foraging theory. The dynamical solution is given by a game dynamics describing the behavioral changes of prey and forager. We show (1) that each stable equilibrium dynamical solution is always a static solution, but not conversely; (2) that at an equilibrium dynamical solution, the forager can stabilize prey mixed patch use strategy in cases where ideal free distribution theory predicts that prey will use only one patch type; and (3) that when the equilibrium dynamical solution is unstable at fixed prey density, stable behavior cycles occur where neither forager nor prey keep a fixed behavior.

*Keywords*: dispersal-foraging game, game dynamics, ideal free distribution, optimal foraging.

## Introduction

Although the foraging strategy of prey under predation risk is well studied (e.g., Brown and Kotler 2004), the predator's role is not as thoroughly investigated (Lima 2002). This is in spite of the fact that predation is an interaction between quite counterinterested species: prey and predator. We consider an optimal foraging predator (or forager) and a prey dispersing among patches. In order to guarantee that competition for food between prey does not mask the effect of predation, we assume that this food competition can be neglected. Our aim is to introduce a game, along with an appropriate solution concept, for this ecological situation. We combine optimal-foraging theory with the ideal free distribution (IFD), considering one forager individual and its one prey species dispersing in two different patch types.

We start from two basic optimal-foraging models. In the prey-choice model (Charnov 1976*a*), the forager chooses among prey with different handling times and the zero-one rule holds (when the more profitable prey is abundant, the forager ignores the other prey type; when the first type is less abundant, the forager uses both prey types). This model is strictly based on the idea of Holling functional response (Holling 1959): the handling times of different prey have a crucial effect on the number of killed prey. In the patch-use model (Charnov 1976*b*), the forager chooses the leaving time from an exhausted patch, and Charnov's marginal-value theorem is valid (the forager leaves the patch when its energy intake rate once in the patch matches its energy intake rate from all patches). In this model, the leaving time (which is the analog of the handling time in the first Charnov model) is a strategy of the forager, and so the functional response is slightly generalized, as it now depends on the patch-leaving times as well as on the density of prey. These two models combine to form a single optimal-foraging model (Stephens and Krebs 1986; McNamara et al. 1993) whose theory is mainly built on Holling type II functional response (Stephens and Krebs 1986). At first glance, the zero-one rule and Charnov's marginal-value theorem appear quite different. However, our basic intuition is that both are consequences of one basic rule (see "Forager's Rule of Time Average Based on Nash Equilibrium"; McNamara 1982).

The IFD aims to understand species distribution in several patches under the assumption that moving between patches is time and energy free (Fretwell and Lucas 1969; Křivan et al. 2008). The IFD is characterized as a distribution where individual fitnesses in all occupied patches are equal and at least as high as those in any unoccupied patch (e.g., Abrams et al. 2007). Although originally the IFD considered species' fitness on the basis of the resource levels in each patch, we assume that prey fitness is determined

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by predation risk in the different types of patches (e.g., Cressman et al. 2004). In these models, the stability of the IFD is determined by concavity or convexity. Specifically, if the functional response at current prey density is concave (e.g., either Holling II or Holling III with high prey density), then the prey use only one patch type. If the functional response is convex (Holling III with small prey density), the prey use both types of patches (see, e.g., Cressman and Garay 2009).

In our model, the optimal forager is pitted against the prey's optimal distribution. Since the predator and its prey have counteracting interests, game theory is required to find the common optimal behavior (Cressman and Garay 2011). Optimal-foraging theory and the IFD are based on the assumption that the other species (i.e., prey and forager, respectively) has fixed behavior. In the natural union of these models, we seek a solution of this game so that both models hold at the same time. This solution is strictly based on the assumption that only one player can change its behavior at a time (see "Static-Solution Concepts Based on the Nash Paradigm").

However, the forager and its prey can adjust their behaviors to the opponent's current strategy immediately (e.g., Katz et al. 2010, 2013; Juliana et al. 2011). In other words, in biology we cannot assume that only one player changes its strategy while the other player's strategy is fixed. It may seem unimportant whether it is only one or both players who can change strategy at a given time. But mathematically, these cases are quite different, as we see below. From the biomathematical perspective, it is then reasonable to describe the changing behaviors of players by a game dynamics in which players change strategy according to an opponent's strategy either one at a time or simultaneously (see "Dynamic-Solution Concepts Based on Game Dynamics"). Using behavior dynamics has three theoretical consequences. First, from a game-theoretical point of view, the game solution concept of Nash is slightly generalized.

Second, from the biological point of view, behavioral cycles are possible in game dynamics, whereas static solutions can predict only equilibrium outcomes. For instance, in the classical battle-of-the-sexes game (Hofbauer and Sigmund 1998), behavioral cycles occur when the Nash equilibrium (NE) is a mixed strategy. That behavioral cycles based on changing population densities have an important role in the study of species' coexistence among patches is also well known by many researchers (a partial list: Fryxell and Lundberg 1994, 1998; Abrams and Matsuda 2004; Cressman et al. 2004; Abrams et al. 2007; Abrams 2010; Cressman and Křivan 2013). The novelty of our article is the introduction of a new game between the optimal forager and its dispersing prey in a short enough timescale that changes in prey density can be ignored (as is assumed in optimal-foraging theory). The behavioral cycles that we find at fixed density generalize those in cellular-automata models of spatial predator-prey dynamics (e.g., Molina et al. 2013) when the interaction is local and the system is not well mixed.

Finally, the dynamic-solution concept predicts that the forager can stabilize prey mixed patch use in cases where the static-solution concept (given by standard IFD theory under the assumption that the forager does not change its fixed mixed patch preference) predicts that prey use only one patch. The reasoning is as follows; if prey use only one type of patch, then an optimal forager, by changing its behavior, will use only this type, too. Thus, prey survival rate is maximal in the other patch type, and so the prey can use this patch type as a "refuge." Thus, the prey will use the second patch type as well (see "Results: Comparison of the Two Solution Concepts"). This line of reasoning suggests using experiments and/or field observations to check which game-theoretic solution concept (i.e., static or dynamic) is valid.

In the next section, we introduce a mechanistic prey dispersal and predator enter-and-leave game, called the dispersal-foraging game (DFG). The two sections after the DFG is introduced study its two solution concepts. We then compare these solution concepts in "Results" before the final discussion.

## Dispersal-Foraging Game

To build the DFG model among different types of patches, the possible behaviors (i.e., strategies) of both the forager and its prey must be described, as well as the effects that these behavioral choices have on individual fitnesses (i.e., payoffs). These concepts are based on the system habitat and the foraging-time duration.

### *Habitat*

Consider a system that consists of two types of patches, with $y_1$ ($y_2$) the number of patches of type $A_1$ ($A_2$). We assume that different types of patches are well mixed (in particular, the different types are not geographically segregated), and so, by a random walk, the forager encounters a random series of patches with relative frequencies $d_1 = y_1/(y_1 + y_2)$ and $d_2 = y_2/(y_1 + y_2)$ for the two types. The reader may think of the prey occupying two host plant species that are scattered randomly in a forest (i.e., each plant is then a patch). The patch types then determine different ecological conditions for the foraging process.

### *Foraging-Time Duration*

Foraging-time duration is denoted by $T$. This time interval $T$ is considerably shorter than the reproduction time of prey. Furthermore, the forager is certain to survive but can visit only a small percentage of the $y_1 + y_2$ patches. In fact, $T$ is short enough that the strategic decisions taken by the forager and the prey have constant fitness consequences throughout this time interval (i.e., the consequences are independent of when the decisions occur). More details of this are given in the following discussion of behaviors and payoffs. We emphasize that this time independence is the basic condition needed for the derivation of the payoff functions.

### *Prey Behavior*

To satisfy Charnov's assumption that the forager's energy gain from a given patch is an increasing function of time spent there, we assume that prey do not flee to other patches during forager attacks. Before the forager arrives, prey occupy the patches. Let $x$ denote the total number of prey and $s$ be the average patch-preference strategy of the whole prey population (i.e., $sx$ and $(1-s)x$ prey are in patches of type $A_1$ and $A_2$, respectively). For simplicity, assume that the local prey density $x_1$ in each type $A_1$ patch is the same (i.e., $x_1 = sx/y_1$) and that the prey density in each type $A_2$ patch is exactly $x_2 = (1-s)x/y_2$. In particular, we do not consider random prey distribution within a given patch type (e.g., Iwasa et al. 1981; Stewart-Oaten 1982).

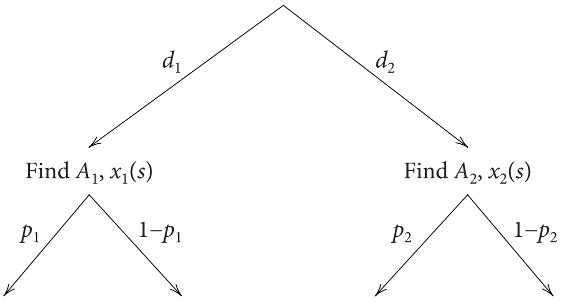
Thus, the prey strategy, characterized by the choice $0 \leq s \leq 1$, is straightforward. The same cannot be said for the forager. To emphasize the game-theoretic aspect of our model, we make simplifying assumptions on its possible behaviors in the next subsection.

### *Forager Behavior*

The foraging process involves several steps. In the first step, the forager spends time $\tau_0$ finding a patch at an energy cost $c$. We assume that the forager does not visit the same patch twice in time period $T$ and that the patch encounter probabilities do not depend on the foraging strategy (i.e., $d_1$ and $d_2$ are constant encounter probabilities with patch $A_1$ and $A_2$, respectively).

Following the standard assumption in classical optimal-foraging theory (e.g., Stephens and Krebs 1986, p. 17), assume that, on finding a patch, the forager immediately recognizes the patch type. The forager then makes two conditional decisions: whether to enter the recognized patch and how long to stay in the chosen patch. (1) For the "enter" strategy, let $p_i \in [0, 1]$ $(i = 1, 2)$ denote the probability of entering an encountered $A_i$ patch (Charnov 1976*a*, 1976*b*). (2) For the "leave" strategy, let $\tau_i \geq 0$ $(i = 1, 2)$ denote the time period spent by the forager once an $A_i$ patch is entered (Charnov 1976*b*).

We now have the possible behaviors of the forager and its prey and are in a position to determine the forager's fitness by finding its expected energy intake during time $T$. Specifically, the prey population has strategy $s \in [0, 1]$ and the forager's strategy is $(p, \tau)$, where $p := (p_1, p_2) \in [0, 1] \times [0, 1]$ and $\tau := (\tau_1, \tau_2) \in [0, T] \times [0, T]$. These are indicated in the dispersal-foraging game tree of figure 1. This tree also



| Activities | Use $A_1$ | Not Use $A_1$ | Use $A_2$ | Not Use $A_2$ |
|---|---|---|---|---|
| Probability | $d_1p_1$ | $d_1(1-p_1)$ | $d_2p_2$ | $d_2(1-p_2)$ |
| Time duration | $\tau_0+\tau_1$ | $\tau_0$ | $\tau_0+\tau_2$ | $\tau_0$ |
| Energy intake | $g_1(x_1(s), \tau_1) - c$ | $-c$ | $g_2(x_2(s), \tau_2) - c$ | $-c$ |

**Figure 1:** With fixed strategies of the "players," the tree of the game contains all information to calculate the payoff of the forager. At the first level, $d_i$ denotes the probability that forager finds patch $A_i$, where the local density of prey $x_i(s)$ depends on the average patch preference ($s$) of the whole prey population. At the second level, $p_i$ denotes the "enter" strategy of forager into patch $A_i$. This tree generates the activity distribution of forager. Each endpoint of the tree corresponds to one activity. One observer can collect the probability of each activity, the time duration of each activity (depending on the forager's leaving strategy $\tau_i$), and the energy intake of each activity. On the basis of this information, we can calculate the strategy-dependent functional response and so the net energy intake rate of forager.

includes the information necessary to calculate fitness (see also Cressman et al. [2014], who develop a general method based on such decision trees).

### *Payoff Function for Forager*

Since optimal-foraging theory postulates that the forager maximizes its average net energy intake per unit time (Turelli et al. 1982), forager payoff is taken as this intake rate. When the forager enters an $A_i$ patch, the net energy gain from the prey, $g_i(x_i, \tau_i)$, depends on the local prey density $x_i$ there and the amount of time $\tau_i$ that the forager spends in this patch. Biologically reasonable properties of this function are that it is increasing in both $x_i$ and $\tau_i$ and that $g_i(x_i, 0) = g_i(0, \tau_i) = 0$ (Stephens and Krebs 1986).

For fixed behavior and encounter probabilities, figure 1 provides the activity distribution. For example, if the forager encounters an $A_1$ patch and enters it, this activity occurs with probability $d_1p_1$, and so on. Since we assume that the players' strategies $s \in [0, 1]$, $p_i \in [0, 1]$, $\tau_i \geq 0$, the parameters $d_i$ and $x$, and the gain functions $g_i$ $(i = 1, 2)$ do not change during time $T$, the expected time duration $E(\tau)$ of an activity chosen at random is given by

$$E(\tau) = \tau_0 + d_1p_1\tau_1 + d_2p_2\tau_2. \tag{1}$$

The corresponding calculation of the expected energy intake of an activity chosen at random simplifies to

$$E(G) = d_1p_1g_1(s, x, \tau_1) + d_2p_2g_2(s, x, \tau_2) - c, \tag{2}$$

where $c$ is the fixed energy cost of finding a patch. On the basis of our basic condition that encounter (and thus activity) probabilities do not change during $T$, Garay and Móri (2010), using Wald's (1944) equality, show that the forager's expected payoff function is

$$\Psi(s;\ p, \tau) := \frac{E(G)}{E(\tau)} = \frac{d_1p_1g_1(s,x,\tau_1) + d_2p_2g_2(s,x,\tau_2) - c}{\tau_0 + d_1p_1\tau_1 + d_2p_2\tau_2} \tag{3}$$

(see "Derivation of Functional Response" in the appendix, available online). This is the average net energy intake rate of a randomly chosen activity (i.e., the average net energy intake per average time duration of one activity). We emphasize that the basic condition holds under the assumptions of our patch model (i.e., no further simplifying assumptions are needed), since the probability of finding a patch does not depend on the forager's strategy and the forager never visits the same patch twice. Hence, the proportions of patch types among visited and nonvisited patches are the same and are also unchanged during $T$. We note that if the energy unit is defined as the energy gain from one prey and the cost $c$ is negligible, then $\Psi$ is a functional response.

Clearly, staying longer in a given patch increases the food gain from this patch type and also increases the expected time duration $E(\tau)$, even though it decreases the number of searches during $T$. The main point is that, from equations (1) and (2), staying longer can change $E(G)$ and $E(\tau)$ simultaneously, and so it is unclear whether such a choice is to the forager's benefit. Similar qualitative effects result from changing other strategies as well (even the prey strategy!).

### *Payoff Functions for Prey*

While the forager is trying to optimize its intake rate, prey want to avoid being killed. For simplicity, assume that prey are killed only by the forager (i.e., without the forager, each prey is certain to survive in a given patch). If we further assume that individual prey fitnesses in the two patch types differ only through their interactions with the forager, then the payoff of an individual prey can be measured by its survival probability (Garay and Varga 2011). To this end, let $\alpha$ be the forager's energy intake when one prey is killed. (Here we ignore the possibility that there may also be an energy cost of foraging, which is often assumed to increase linearly with respect to time spent in the patch; Stephens and Krebs 1986.) Thus, $g_i(s, x, \tau_i)/\alpha$ gives the average number of prey killed in an encountered $A_i$ patch. Moreover, by another application of Wald's equality, the expected number of prey killed per unit time in $A_i$ patches is

$$\frac{d_1p_1}{\tau_0 + d_1p_1\tau_1 + d_2p_2\tau_2}\frac{g_1(s,x,\tau_1)}{\alpha},$$

and so the individual survival rate of prey in an $A_i$ patch (i.e., their payoff) is

$$\begin{aligned} \chi_1(s, x;\ p, \tau) &= 1 - \frac{d_1p_1}{\tau_0 + d_1p_1\tau_1 + d_2p_2\tau_2}\frac{g_1(s,x,\tau_1)}{(\alpha xs/y_1)}, \\ \chi_2(s, x;\ p, \tau) &= 1 - \frac{d_2p_2}{\tau_0 + d_1p_1\tau_1 + d_2p_2\tau_2}\frac{g_2(s,x,\tau_2)}{[\alpha x(1-s)/y_2]}. \end{aligned} \tag{4}$$

It is important to point out here that there is an essential difference between prey and forager payoff functions, $\chi_i$ and $\Psi$, respectively. Specifically, whereas the forager's payoff does not depend on another forager's strategy, and so the forager optimizes its behavior, given prey strategy $s$, the survival rate of a given prey type depends on the strategies used by other prey; that is, for the prey, we have a population game (Broom and Rychtar 2013).

The above prey and predator behaviors, together with their payoff functions, define the DFG as a union of the IFD and Charnov's two models of optimal-foraging theory. The assumptions underlying the DFG and these components are identical. More precisely, if we fix the predator behavior, then we get back the IFD from the DFG, and if we fix the prey behavior, we get back the optimal-foraging model from the DFG. Now the theoretical problem arises, What is the solution concept for the DFG? We investigate two possibilities in the next two sections: respectively, when prey and their predator cannot change their strategies at the same time and when these strategies change simultaneously.

## Static-Solution Concepts Based on the Nash Paradigm

The Nash equilibrium (NE) is a solution concept for games involving two (or more) players, in which no player can gain by changing his own strategy while the other player keeps his strategy fixed. Following the Nash paradigm, let us assume that either only prey or only the forager can change its strategy at a particular time. Then, the strategy pair $s^*$ and $(p^*, \tau^*)$ is a static solution if conditions (5) and (6) hold.

### *Solution for Prey*

With forager strategy fixed at $(p^*, \tau^*)$, the prey are engaged in a single-species habitat-selection game (Cressman et al. 2004). As stated in the introduction, $s^*$ is an IFD (as introduced by Fretwell and Lucas [1969] before its connection with evolutionary game theory was recognized) if (1) prey payoffs in all occupied patches are the same and (2) this payoff is at least as high as that in any unoccupied patch. That is,

$$\chi_i(s^*, x, p^*, \tau^*) \geq \chi_j(s^*, x, p^*, \tau^*) \tag{5}$$

for all $i, j$ whenever a patch of type $A_i$ is occupied. With predator strategy fixed at $(p^*, \tau^*)$, condition (5) is equivalent to $s^*$ being an NE of the prey habitat-selection game, as shown by Cressman and Křivan (2006). That is, an IFD $s^*$ is an NE.

When the IFD definition is applied to our two-patch model, prey may use both patch types at the IFD if the survival rate is the same in both. In general, however, equality in survival rate of prey does not imply that the forager's gains from different patches are also equal. For instance, the prey patch preference does not take into account varying searching costs of the forager in different patches.

### *Solution for Forager*

When prey strategy is fixed at $s^*$, the predator is faced with an optimization problem, since its payoff depends only on its own strategy. The NE is then the classical optimization solution $(p^*, \tau^*)$ (Stephens and Krebs 1986), called the optimal-foraging strategy. That is, for any other strategy $(p, \tau)$, we have

$$\Psi(s^*;\ p^*, \tau^*) \geq \Psi(s^*;\ p, \tau). \tag{6}$$

The static-solution concept that combines conditions (5) and (6) seems natural, since it simply unifies, under the Nash paradigm, the IFD concept from the prey habitat-selection game with the forager optimal-foraging strategy.

In the appendix, "Dynamical Characterization of Static Solution of the DFG" provides insight into the stability properties of the static-solution IFD concept for the prey. We find that if both gain functions are convex in $s$ (like Holling III at small prey density), then there is a unique mixed IFD and it is an evolutionarily stable strategy (ESS). Thus, prey use both patch types. On the other hand, if both gain functions are concave in $s$ (like Holling II), then there is at least one IFD that is also an ESS, with all prey using only one patch type. There may also be a mixed IFD, but this cannot be an ESS, since it is not stable.

For the remainder of this section, we further examine the static-solution concept for the forager.

### *Forager's Rule of Time Average Based on Nash Equilibrium*

Let us consider the problem as generally as possible in the context of optimal-foraging theory. Denote by $\sigma_1 \in S_1$ and $\sigma_2 \in S_2$ the strategy choices of two players. In our case, player 1 (the forager) has a multidimensional strategy set $S_1$, and player 2 is the prey. The forager optimizes its energy intake rate. Formally, to define this rate, we have to consider two functions: $T(\sigma_1, \sigma_2)$ is the average time duration, and $G(\sigma_1, \sigma_2)$ is the average energy intake when the players use the strategy pair $(\sigma_1, \sigma_2)$. The payoff function of the forager is then $\Gamma_1(\sigma_1, \sigma_2) := G(\sigma_1, \sigma_2)/T(\sigma_1, \sigma_2)$. Since we concentrate here on the NE behavior of the forager, the payoff function $\Gamma_2$ for the second player can be arbitrary and its strategy fixed at $\sigma_2^*$. If the optimal-foraging behavior $\sigma_1^*$ is unique (e.g., the inequality in eq. [6] is strict), then the forager's payoff decreases whenever its strategy changes, while the other player's strategy is fixed (formally, $\Gamma_1(\sigma_1^*, \sigma_2^*) > \Gamma_1(\sigma_1, \sigma_2^*)$ for $\sigma_1 \neq \sigma_1^*$). In game-theoretic terms, $(\sigma_1^*, \sigma_2^*)$ is a strict NE with respect to the behavior of player 1.

If the forager changes its strategy, there are two consequences: intake changes by $\mathrm{DG}(\sigma_1) := G(\sigma_1, \sigma_2^*) - G(\sigma_1^*, \sigma_2^*)$, and time duration changes by $\mathrm{DT}(\sigma_1) := T(\sigma_1, \sigma_2^*) - T(\sigma_1^*, \sigma_2^*)$, simultaneously. In "Rule of Time Average for Forager in the appendix, an elementary proof shows that $(\sigma_1^*, \sigma_2^*)$ is a strict NE (with respect to forager behavior) if and only if

$$\mathrm{DG}(\sigma_1)T(\sigma_1^*, \sigma_2^*) < \mathrm{DT}(\sigma_1)G(\sigma_1^*, \sigma_2^*) \tag{7}$$

for any other forager strategy $\sigma_1$. In particular, if there is no difference in time duration between strategies $\sigma_1$ and $\sigma_1^*$ (i.e., $\mathrm{DT}(\sigma_1) = 0$), then the energy intake must be higher at the strict NE. We note that equation (7) is a version of McNamara's (1982, p. 274) potential function: "the expected future gain on a patch minus the expected loss due to lost time: time which could be spent on other patches foraging at mean rate." From equation (7), we have two rules.

"+*Rule of time average*." If the forager's strategy change increases the time duration (i.e., $\mathrm{DT}(\sigma_1) > 0$), then the average intake rate $G(\sigma_1^*, \sigma_2^*)/T(\sigma_1^*, \sigma_2^*)$ at the NE is greater than the ratio of the change in intake to the change in time duration. Formally,

$$\frac{G(\sigma_1^*,\sigma_2^*)}{T(\sigma_1^*,\sigma_2^*)} > \frac{\mathrm{DG}(\sigma_1)}{\mathrm{DT}(\sigma_1)} \tag{8}$$

for all $\sigma_1$ with $\mathrm{DT}(\sigma_1) > 0$.

"−*Rule of time average*." If the forager's strategy change decreases the time duration (i.e., $\mathrm{DT}(\sigma_1) < 0$), then the average intake rate $G(\sigma_1^*,\sigma_2^*)/T(\sigma_1^*,\sigma_2^*)$ at the NE is less than the ratio of the change in intake to the change in time duration. Formally,

$$\frac{G(\sigma_1^*,\sigma_2^*)}{T(\sigma_1^*,\sigma_2^*)} < \frac{\mathrm{DG}(\sigma_1)}{\mathrm{DT}(\sigma_1)} \tag{9}$$

for all $\sigma_1$ with $\mathrm{DT}(\sigma_1) < 0$.

In the following two remarks, we show that the zero-one rule and Charnov's marginal-value theorem are valid at the forager's NE ($p^*$, $\tau^*$) of the dispersal-foraging game. These results follow from considering NE behavior with respect to $p^*$ and $\tau^*$, respectively, assuming that prey behavior is fixed at the NE strategy $s^*$.

*Remark 1 (Zero-One Rule).* If the forager encounters an $A_i$-type patch, it is faced with the question, Use or do not use this patch? That is, it must decide on $p_i^*$. If it does use the patch, it spends time $\tau_i^*$ there. A straightforward calculation shows that changing its strategy to $p_i$ results in $\mathrm{DG}(p_i, \tau_i^*)/\mathrm{DT}(p_i, \tau_i^*) = g_i(s^*, x, \tau_i^*)/\tau_i^*$. Since this is independent of the choice of $p_i$, the rule of time average (eq. [8]) yields

$$p_i^* = 1 \text{ if } \frac{g_i(s^*,x_i,\tau_i^*)}{\tau_i^*} > \Psi(s^*,p^*,\tau^*). \tag{10}$$

That is, an encountered patch $A_i$ is used with probability 1 if the resultant energy intake rate once in this patch is greater than the forager energy intake rate from all patches. Similarly, $p_i^* = 0$ if the inequality in equation (10) is reversed. This is the well-known zero-one rule (Charnov 1976*a*) that a given patch type is either always entered when encountered or never entered.

*Remark 2 (Marginal-Value Theorem).* Consider a forager who has spent $\tau_i$ in an $A_i$ patch (thus $p_i^* = 1$) and has collected energy $g_i(s^*, x, \tau_i)$ from it. Now the forager's question is, Leave this patch or not? If the forager spends extra time in this used patch, an easy calculation shows that $\mathrm{DT} = d_i\Delta\tau_i$ and $\mathrm{DG} = d_i[g_i(s^*, x, \tau_i + \Delta\tau_i) - g_i(s^*, x, \tau_i)]$. Using equation (8), we find that the forager does not leave if $(g_i(s^*, x, \tau_i + \Delta\tau_i) - g_i(s^*, x, \tau_i))/(\Delta\tau_i) > \Psi(s^*; p^*, \tau^*)$, which implies Charnov's well-known marginal-value theorem:

$$\frac{d}{d\tau_i} g_i(s^*, x, \tau_i^*) = \Psi(s^*; p^*, \tau^*) \tag{11}$$

(Charnov 1976*b*). That is, the forager leaves the patch at that time when its energy intake rate once in the patch matches its energy intake rate from all patches.

## Dynamic-Solution Concept Based on Game Dynamics

The above static-solution concept (see also "Dynamical Characterization of Static Solution of the DFG" in the appendix) is based on the assumption that only one player can change its strategy at a time. There are three problems with this approach. The first is that it assumes that there is a separation of timescales between behavioral changes by prey compared to those by the predator. In biology, there is no general reason for ruling out that these counterinterested agents change their strategies on the same timescale. Second, random perturbation cannot be excluded in biology, and so no "player" keeps its strategy unchanged. Third, forager and prey can adjust their behaviors to the opponent's current strategy immediately (see, e.g., Katz et al. 2010, 2013; Juliana et al. 2011). Hence, solutions given by the Nash paradigm have to be examined to see whether they correspond to the expected outcome of the real biological system. This situation can be treated by a game dynamics that describes the behavior changes of prey and forager, leading to the following concept.

*Game-dynamics solution concept: a strategy pair (or a behavior cycle) is a dynamic solution if it is locally asymptotically stable with respect to a game dynamics describing the behavior changes of prey and forager*. Since the DFG is a mixture of evolutionary and classical games, we must combine two different types of game dynamics. For the prey species we use the replicator dynamics (Hofbauer and Sigmund 1998; Garay 2003), whereby the proportion of prey in a given patch increases if and only if prey have higher payoff in this patch:

$$\dot{s} = s(1 - s)[\chi_1(s, x; p, \tau) - \chi_2(s, x; p, \tau)]. \tag{12}$$

From "Dynamical Characterization of Static Solution of the DFG," in the appendix, an IFD $s^*$ will be stable with respect to equation (12) at fixed $(p, \tau)$ if and only if it is an ESS of the prey habitat-selection game.

Second, we focus on the dynamic stability of the forager's NE behavior, when the prey strategy is fixed at $s$. Since there is only one forager, the classical adaptive dynamics cannot be applied (specifically, adaptive dynamics is based on either population structure [Dieckmann and Law 1996; Vincent and Brown 2005] or relative advantage [Hofbauer and Sigmund 1998]). For this reason, we use the following partial adaptive dynamics (Garay 2002), which moves the foraging strategy in the direction of higher predator payoff:

$$\dot{p}_1 = p_1(1-p_1)\frac{\partial\Psi(s,p_1,p_2,\tau_1,\tau_2)}{\partial p_1}, \tag{13}$$

$$\dot{p}_2 = p_2(1-p_2)\frac{\partial\Psi(s,p_1,p_2,\tau_1,\tau_2)}{\partial p_2}, \tag{14}$$

$$\dot{\tau}_1 = \tau_1\frac{\partial\Psi(s,p_1,p_{2,}\tau_1,\tau_2)}{\partial \tau_1}, \tag{15}$$

$$\dot{\tau}_2 = \tau_2\frac{\partial\Psi(s,p_1,p_2,\tau_1,\tau_2)}{\partial \tau_2}. \tag{16}$$

In "Dynamical Characterization of Static Solution of the DFG," in the appendix, we show that optimal-foraging behavior $(p^*, \tau^*)$ at fixed $s$ corresponds exactly to a locally asymptotically stable rest point under this predator dynamics.

However, it is important to emphasize that the above combined predator-prey dynamics describes the way the counterinterested "players" (prey population and forager) simultaneously change their strategies according to the opponents' current strategies. The game-dynamics solution is then a locally asymptotically stable rest point $(s^*, p^*, \tau^*)$ of equations (12)–(16). In cases where such a rest point does not exist but a stable behavior cycle emerges, this cycle is also considered a solution to the game dynamics.

## Results: Comparison of the Two Solution Concepts

To compare the static- and dynamic-solution concepts, we concentrate on the situation when both patches are used by prey and by forager. That is, we assume that $p_1 = p_2 = 1$ and consider the rest points $(s^*, \tau_1^*, \tau_2^*)$ of equations (12), (15), and (16) with $0 < s^* < 1$, and $\tau_1^*, \tau_2^*$ both positive. The combined dynamics is then

$$\begin{aligned}\dot{s} &= s(1-s)[\chi_1 - \chi_2],\\ \dot{\tau}_1 &= \frac{\tau_1 d_1}{E(\tau)}\left(\frac{d}{d\tau_1}g_1 - \Psi\right),\\ \dot{\tau}_2 &= \frac{\tau_2 d_2}{E(\tau)}\left(\frac{d}{d\tau_2}g_2 - \Psi\right).\end{aligned} \tag{17}$$

It is clear that, if $(s^*, \tau_1^*, \tau_2^*)$ is a dynamic solution of the DFG, then $s^*$ a static solution for the prey (i.e., it satisfies inequality [5] because $\chi_1 = \chi_2$ at $(s^*, \tau_1^*, \tau_2^*)$). However, as we see in the next two sections, which use Holling type III and II functional responses, with respect to prey density in each patch type, the converse is not true. These results rely on the convexity/concavity of the gain $g_i(x_i(s), \tau_i)$ in patch $i$ as a function of patch density $x_i(s)$ and as a function of patch-leaving time $\tau_i$.

As a partial summary of the results we obtain, if $g_i(x_i(s), \tau_i)$ is convex in $x_i(s)$ at $s^*$ and locally concave in $\tau_1$ and $\tau_2$ at $(\tau_1^*, \tau_2^*)$, then $s^*$ is stable (i.e., an ESS) for the prey dynamics (eq. [12]) and $(\tau_1^*, \tau_2^*)$ is stable for the predator adaptive dynamics (eqq. [15], [16]). Global concavity in $\tau_1$ and $\tau_2$ implies that $(\tau_1^*, \tau_2^*)$ is the optimal-foraging behavior when prey strategy is fixed at $s^*$. On the other hand, if $g_i(x_i(s), \tau_i)$ is concave in $x_i(s)$, then $s^*$ is unstable for the prey dynamics (eq. [12]). These dynamic-stability results assume that only one player changes its strategy at a time, whereas the dynamic-solution concept allows both predator and prey to change strategies at the same time. The consequences of this are examined in the next two subsections.

### *Holling III Gain Functions*

If the energy gain $g_i(x_i(s), \tau_i)$ is a convex function of patch density $x_i(s)$ for $i = 1, 2$, as occurs for Holling III functional responses when prey density in patch type $i$ is low, then prey payoff is a decreasing function of its density in each patch (i.e., $g_i(x_i(s), \tau_i)/x_i(s)$ is an increasing function of $x_i(s)$). In this case, Fretwell and Lucas (1969) show that there will be a unique IFD. In fact, Cressman and Křivan (2006) prove that this IFD is an ESS. Intuitively, if the forager's strategy does not change, then the stability of the prey rest point is guaranteed by the following: if the local prey density decreases in patch $A_1$ and increases in patch $A_2$, then the individual survival rate in patch $A_1$ increases and that in patch $A_2$ decreases, and vice versa. In other words, if a prey individual moves to the other patch, then its survival rate decreases. The IFD is then a stable equilibrium of the prey dynamics (eq. [12]) for fixed patch-leaving times $\tau_1$ and $\tau_2$ of the predator. For high prey density in both patch types, this is no longer the case, as we see in the next subsection, on Holling II gain functions.

For the predator dynamics, we have an optimization problem in the patch-leaving times $\tau_1$ and $\tau_2$ (see "Dynamical Characterization of Static Solution of the DFG," in the appendix). Since both leaving times $\tau_1^*$ and $\tau_2^*$ are positive, local asymptotic stability with respect to perturbations in the predator population (i.e., stability under the predator dynamics of eqq. [15], [16]) is equivalent to the predator gain functions $g_i(x_i(s), \tau_i)$ in both patches being concave in the leaving times at the equilibrium $(s^*, \tau_1^*, \tau_2^*)$ (i.e., $g_i(x_i(s), \tau_i)$

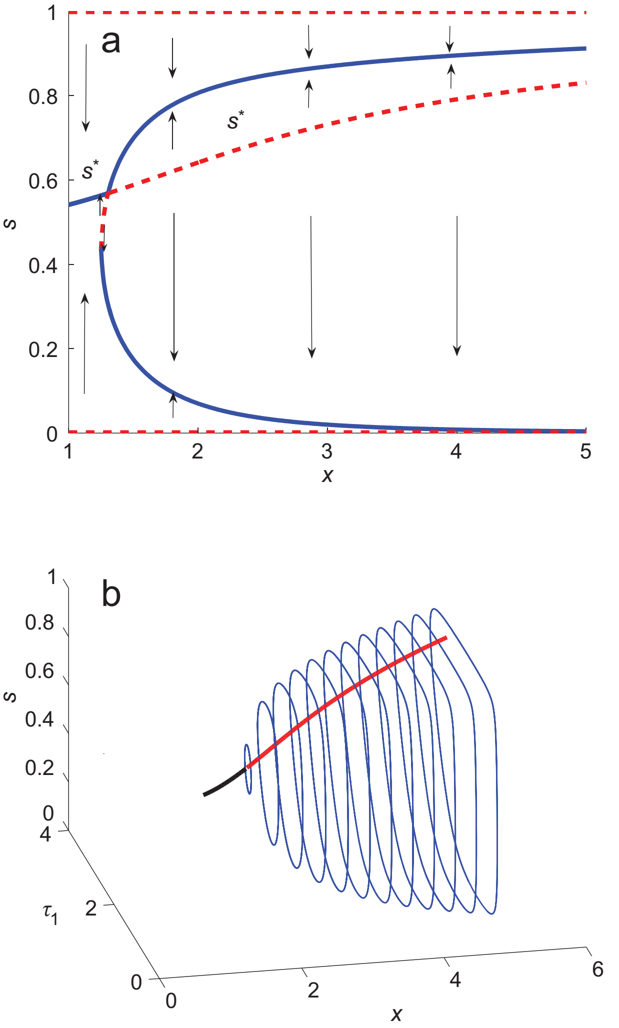


**Figure 2:** Trajectories of the game dynamics for typical Holling III gain functions of the form $g_i(x_i, \tau_i) = a_i x_i^2 \tau_i / (x_i^2 + a_i x_i \tau_i + a_i)$, where $a_1 = 0.3$ and $a_2 = 0.5$. *a*, Prey replicator dynamics, with predator strategy fixed at $(\tau_1^*, \tau_2^*)$, as a function of $x$. The interior equilibrium $s^*$ is globally stable until $x = 1.3$ (solid blue curve) and then becomes unstable for $x > 1.3$ (dashed red curve), in which case the prey evolve to different mixed equilibria of equation (12) (i.e., the solid blue curves) that are locally asymptotically stable but do not correspond to rest points of dynamical system (17). *b*, For $x < 1.66$, trajectories of equation (17) approach the equilibrium $(s^*, \tau_1^*, \tau_2^*)$ on the solid black curve with mixed NE $s^*$. For larger $x$, the trajectories approach a stable limit cycle (i.e., one of the solid blue curves) and the equilibrium $(s^*, \tau_1^*, \tau_2^*)$ is unstable (indicated by one of the points on the solid red curve). Thus, for intermediate values of $x$ (i.e., $1.3 < x < 1.66$), $(s^*, \tau_1^*, \tau_2^*)$ is stable even though $s^*$ is an unstable NE of the prey habitat-selection game. Other parameters: $y_1 = y_2 = 1$, $\alpha = 0.5$, $\tau_0 = 0.4$, $d_1 = d_2 = 1/2$, and $c = 0$.

is locally concave in $\tau_i$ for $i = 1, 2$). Conversely, if these gain functions are globally concave in patch-leaving time, then a stable rest point of the predator dynamics corresponds to optimal-foraging behavior.

Gain functions of the form $g_i(x_i, \tau_i) = a_i x_i^2 \tau_i / (x_i^2 + a_i x_i \tau_i + a_i)$ with $a_i$ positive are typical Holling III functional responses in prey density $x_i$ (i.e., convex in the local prey density $x_i$ when $x_i$ is small, becoming concave for larger $x_i$) that increase to the saturated consumption level of $a_i \tau_i$ at high prey density. They are also globally concave in leaving time $\tau_i$, with all prey consumed if the predator stays in this patch type sufficiently long. Thus, if $(s^*, \tau_1^*, \tau_2^*)$ is a rest point of the dynamical system (17), then the prey NE $s^*$ is an ESS for small values of $x$ but not an ESS for large values of $x$ when the forager strategy is fixed at $(\tau_1^*, \tau_2^*)$, as shown in figure 2*a*. In fact, for the parameters chosen in this figure, there are two interior ESSs (blue curves) for large $x$. These, however, are not associated with equilibria of the DFG, since the equilibrium forager strategy corresponding to these values of $s$ is not $(\tau_1^*, \tau_2^*)$.

There is consistency with these NE results and the stability of $(s^*, \tau_1^*, \tau_2^*)$ under equation (17), in that the game-dynamics solution is a stable equilibrium for small values of $x$ and a stable limit cycle for large $x$ (fig. 2*b*). That is, this bifurcation diagram is qualitatively what is expected, in that the static-solution concept $(s^*, \tau_1^*, \tau_2^*)$ is locally asymptotically stable for small $x$ and unstable for large $x$. However, the transition value of $x$ from stability to instability of $s^*$ (found numerically to be $x = 1.3$ in fig. 2*a*) is different from the transition value of $x = 1.66$ from stability to instability of $(s^*, \tau_1^*, \tau_2^*)$ in figure 2*b*. Specifically, for intermediate total population size $x$, we find that $(s^*, \tau_1^*, \tau_2^*)$ is stable under equation (17) even though the static prey solution would be unstable without the stabilizing effect of the forager's behavior. In these cases, there is a discrepancy between the static-solution concept and the game-dynamics solution.

Observe that, in cases where stable behavior cycles emerge as the game-dynamics solution, neither prey nor forager keep a fixed behavior; instead, each replies to the actual behavior of the other. Furthermore, as can be shown numerically, the average prey behavior over one behavioral cycle is different from the equilibrium value $s^*$, an outcome that contrasts with known results (Hofbauer and Sigmund 1998) for population density cycles in predator-prey interactions based on Lotka-Volterra models and for the behavioral cycles of the classical battle-of-the-sexes game.

### *Holling II Gain Functions*

Now suppose that prey payoff is an increasing function of its density in each type of patch (e.g., $g_i(x_i(s), \tau_i)$ are concave functions of $x_i(s)$ for $i = 1, 2$, as occurs for Holling II functional responses). Then prey survival in patch type $i$ is at a maximum if all prey are in this patch. Thus, there is at least one IFD with all prey in the same patch type, and this is also an ESS (see "Dynamical Characterization of Static Solution of the DFG" in the appendix). There may also be a second ESS with all prey in the other patch type. In this latter case, there will be a third IFD with prey in both patch types (corresponding to $A_i$), but this will not be an ESS since, intuitively, concavity means that, at this IFD, if a prey moves to the other patch, then its survival rate increases. That is, although the IFD with prey in both patch types is an NE, it is not stable with respect to perturbations in the prey population (i.e., it is not stable under the prey dynamics of eq. [12]). This phenomenon is discussed by Fretwell and Lucas (1969) and raises the question whether such an $s^*$ should be considered an IFD (see "Dynamical Characterization of Static Solution of the DFG" in the appendix).

Gain functions of the form $g_i(x_i, \tau_i) = a_i x_i \tau_i / (x_i + a_i \tau_i + 1)$ with $a_i$ positive are typical Holling II functional responses in prey density $x_i$ (i.e., globally concave in $x_i$) that increase to the saturated consumption level of $a_i \tau_i$ at high prey density. Thus, if $(s^*, \tau_1^*, \tau_2^*)$ is a rest point of the dynamical system (17), then the prey NE $s^*$ is not an ESS when the forager strategy is fixed at $(\tau_1^*, \tau_2^*)$ (see fig. 3*a*). In fact, for the parameters chosen in this figure, there are two ESSs, both of which have all prey in one patch type. On the other hand, as in "Holling III Gain Functions," these gain functions are globally concave in leaving time $\tau_i$, with all prey consumed if the predator stays in this patch type sufficiently long. That is, $(\tau_1^*, \tau_2^*)$ is a stable rest point of the predator dynamics when prey strategy is fixed at $s^*$.

From the above discussion, we expect $(s^*, \tau_1^*, \tau_2^*)$ to be unstable under equation (17). However, as seen in figure 3*b*, $(s^*, \tau_1^*, \tau_2^*)$ is in fact stable under equation (17) (i.e., it is a game-dynamics solution) for large total population size $x$. This example shows more clearly than figure 2 that a game-dynamics equilibrium solution may not be a stable static solution for the prey population (i.e., $s^*$ may not be stable for eq. [12]). We can say that forager behavior stabilizes the mixed prey distributions, since if the forager's strategies are fixed then the prey population will use only one patch.

## Discussion

The dispersal-foraging game (DFG) is the union of optimal-foraging theory and the IFD, where a prey's payoff function is its survival rate and the forager's payoff is the number of prey killed per unit time. We studied two different solution concepts for the DFG. The static NE concept is an equilibrium $(s^*, \tau_1^*, \tau_2^*)$ that is a straightforward union of requirements that $s^*$ be an IFD of the prey habitat-selection game and that, at this IFD, the predator adopts its optimal-foraging behavior. The dynamic concept looks for a stable solution of the game dynamics (either an asymptotically stable rest point or a stable cycle of eq. [17]). A fundamental difference between these static- and dynamic-solution concepts is that the Nash assumption (i.e., only one player can change its strategy at a time) implicitly precludes the possibility of behavior cyclic solutions.

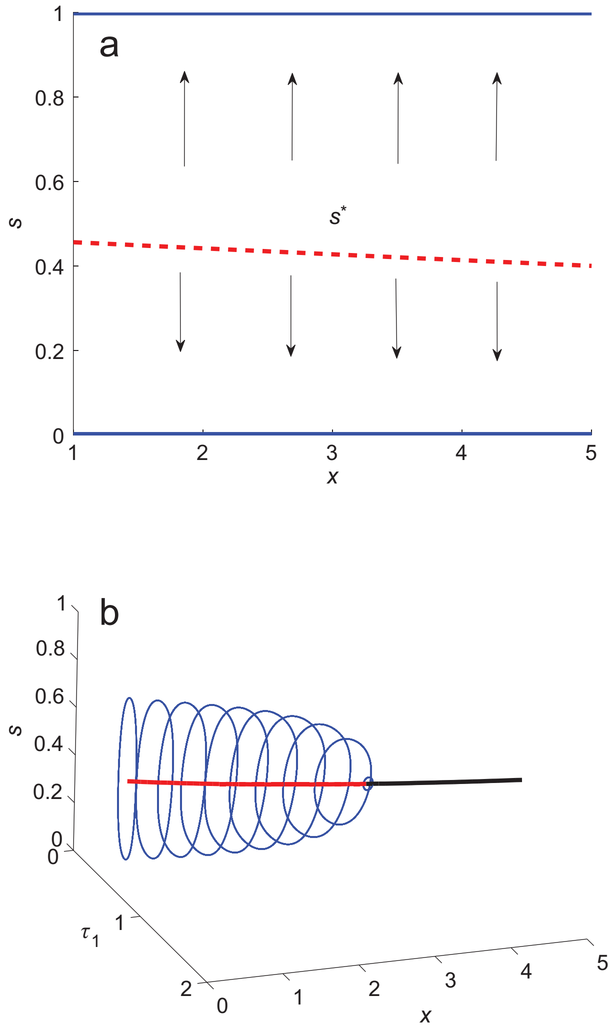


**Figure 3:** Trajectories of the game dynamics for typical Holling II gain functions of the form $g_i(x_i, \tau_i) = a_i x_i \tau_i / (x_i + a_i \tau_i + 1)$, where $a_1 = 0.9$ and $a_2 = 0.8$. *a*, Prey dynamics, with predator strategy fixed at $(\tau_1^*, \tau_2^*)$, as a function of $x$. The interior equilibrium $s^*$ is unstable (dashed red curve), and the prey evolve to all be in one patch (i.e., the blue lines that are locally asymptotically stable). *b*, Bifurcation diagram with respect to total prey population size $x$ for the game dynamics of equation (17). For small values of $x$, trajectories of equation (17) approach a stable limit cycle (i.e., one of the solid blue curves). In particular, the equilibrium $(s^*, \tau_1^*, \tau_2^*)$ on the dotted red curve with mixed NE $s^*$ is not stable (which is consistent with the instability of $s^*$ for the static prey solution concept in *a*). On the other hand, for larger values of $x$, trajectories of equation (17) approach the stable equilibrium $(s^*, \tau_1^*, \tau_2^*)$ on the solid black curve, a result that is unexpected from the static-solution concept. Other parameters: $y_1 = y_2 = 1$, $\alpha = 0.8$, $\tau_0 = 0.4$, $d_1 = d_2 = 1/2$, and $c = 0$.

The game-theoretic NE condition is especially important when applied to the predator's behavior. Specifically, we showed how this leads to the rule of time averages: the optimal predator behavior involves those activities that ensure larger time average intake than the time average of all activities. Both the zero-one rule and Charnov's marginal-value theorem of optimal-foraging theory then follow directly from our rule of time averages. Furthermore, since the static solution is a rest point of the combined predator-prey game dynamics, there are cases when both solution concepts give the same prediction; that is, when the NE is locally asymptotically stable with respect to the game dynamics.

However, we have also shown that the two solution concepts can be quite different. As an important example, when both gain functions are concave in patch prey density (like Holling II), the static solution predicts that prey use only one patch type, whereas the game-dynamics solution predicts mixed habitat use (see fig. 3*b*, where the combined dynamics leads to either a stable equilibrium or a stable limit cycle). The intuitive reason for this outcome is that, when prey use only one patch type, the forager consequently also concentrates on this patch. This leads to the other patch becoming a prey "refuge" because of the forager's behavior, and so prey start to use this patch as well. Similar discrepancies between the two solution concepts arise for Holling III gain functions (see fig. 2). In practice, the dynamical solution can guarantee that the prey use both patch types more often than classical approaches based on the IFD.

We also emphasize that the behavioral cycles we observe in our models based on prey IFD and predator optimal foraging occur at fixed density. This shows not only that we should expect cycling in predator-prey population sizes over long periods of time but also that game-theoretic reasoning predicts that individual behavior often cycles over short time intervals when population size can be assumed to be fixed. Our observations illustrate that total prey density displays a " behavior bifurcation effect" in the sense that by increasing density, stable behavior equilibrium becomes stable behavior cycles (fig. 3), or vice versa (fig. 2). This phenomenon is parallel to the "paradox of enrichment" known in population ecology (Rosenzweig 1971), where increasing the carrying capacity of prey causes a bifurcation. It should also be noted that, although the bifurcations from stable equilibrium behavior to stable cyclic behavior that we observed use total prey density as the bifurcation parameter, bifurcations occur in other model parameters as well.

We recall some biological considerations and examples that serve to justify our dynamic-solution concept. First, we agree with Lima (2002, p. 74) that "some failures of standard optimal diet theory" (Sih and Christensen 2001) and standard IFD theory (e.g., Julliar 2000) "might be explicable in terms of a predator-prey game." The dynamic concept provides new insights into these prey-predator systems, where prey behavior and the forager's strategies together determine a high killing rate and neither optimal-foraging theory nor the IFD fit the observations. These issues also arise in applied ecology. Specifically, it is generally acknowledged that optimal-foraging theory and the IFD are important for biological control of pests (Mills and Wajnberg 2008). The utilization of phytoseiid predatory mites as biological control agents is widespread (Vila and Cabello 2014). However, the dispersion of spider mites (e.g., *Tetranychus urticae*) between patches is not an IFD, since reproductive success varies between habitats (Julliar 2000). At the same time, predatory mites of the Phytoseiidae (Acari) have not adapted to optimal foraging (Konakandla 2006; Gontijo et al. 2010; Maeda 2010; van der Hammen et al. 2012). In the following two examples, the above pest-predator system exists with habitat heterogeneity. First, in the United States, apple orchards in Utah, whose total ground vegetation cover was at least 50%, had predatory mite populations that sufficed to keep pest mites below their damaging levels (Alston 1994). Second, spider mites (*Tetranychus kanzawai*) in deciduous fruit tree orchards in Japan usually overwinter on ground vegetation. In the spring, they first increase their populations on the vegetation and then move onto fruit trees. The predator *Phytoseiulus persimilis*, released onto ground cover, may eliminate spider mites before they migrate onto fruit trees (Takahashi et al. 1998; Takafuji and Amano 2001). In similar situations, whether game theory leads to a deeper understanding of predation, especially whether stable behavior cycles should occur when optimal-foraging theory and/or the IFD does not predict observed behavior, can be tested by field trials.

Finally, Holling II functional responses are very common in nature (e.g., Hassell et al. 1976), and so the shape of the gain function used in figure 3 is quite realistic. In this case, prey use only one patch type at a classic IFD/ESS, whereas the forager can stabilize the prey's mixed habitat use at the game-dynamics solution. The existence of such examples is a strong argument to justify the dynamic-solution concept.

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Example of a prey species, *Tetranychus urticae* Koch (Acari: Tetranychidae), using mixed habitat under the predation pressure by *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae), that has importance in applied ecology (e.g. the biological control of pests). In the photo, an adult predator captures an adult prey. Photograph by Tomás Cabello.