Optimal Forager Against Ideal Free Distributed Prey

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Abstract. The introduced dispersal-foraging game is a combination of prey habitat selection among 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 that (a) each stable equilibrium dynamical solution is always a static solution, but not conversely; (b) 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; (c) when the equilibrium dynamical solution is unstable at fixed prey density, stable behavior cycles occur where neither forager nor prey keep a fixed behavior.

1 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 counter-interested species: prey and predator. We consider an optimal foraging predator (shortly 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 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 ideal free distribution (IFD), considering one forager individual and its one prey species dispersing in two different patch types.

We start from the following two basic optimal foraging models: In the prey-choose 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, then the forages 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 (forager leaves the patch at that time where 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 analogue of the handling time in the first Charnov model) is a strategy of forager and so the function response is slightly generalized as it now depends on the patch leaving times as well as 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 the first glance, the zero-one-rule and the Charnov's marginal value theorem appear quite different. However, our basic intuition is that both are consequences of one basic rule (see rule of time average in Section 3.1, cf. 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; Krivan 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 in any unoccupied patch (e.g. Abrams et al. 2007). Although originally the IFD considered species' fitness based on the resource levels in each patch, we assume prey fitness is determined 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 will use only one patch type. If the functional response is convex (Holling III with small prey density), the prey use both type 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 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 the static solution concept based on Nash Equilibrium (NE) in Section 3).

However, the forager and its prey can adjust their behaviors to the opponent's current strategy immediately (e.g. Juliana et al. 2011; Katz et al. 2010, 2013). 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 will see. 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 its opponent strategy either one at a same time or simultaneously (see dynamical solution concepts in Section 4). Using behavior dynamics has three theoretical consequences: First, from a game theoretical point of view, the game solution concept of Nash is slightly generalized.

Secondly, 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 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 is Abrams 2010; Abrams and Matsuda 2004; Abrams et al. 2007; Cressman and Krivan 2013; Cressman et al. 2004; Fryxell and Lundberg 1994, 1998). The novelty of the present paper is the introduction of a new game between the optimal forager and its dispersing prey in a short enough time scale that changes in prey density can be ignored (as is assumed in optimal foraging theory). The behavioral cycles 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.

Lastly, the dynamical 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 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 only use 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 in Section 5). 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 Section 2, we introduce a mechanistic prey dispersal and predator enter-and-leave game, called the *Dispersal-Foraging Game* (DFG). In Sections 3 and 4, we study two solution concepts for DFG. We then compare these solution concepts (Section 5) before the final Discussion section.

2 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 (respectively, y_2) the number of patches of type A_1 (respectively, 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 $d_1 = \frac{y_1}{y_1+y_2}$and $d_2 = \frac{y_2}{y_1+y_2}$ 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 only visit 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 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 the local prey density x_1 in each type A_1 patch is the same (i.e. $x_1 = \frac{sx}{y_1}$) and the prey density in each type A_2 patch is exactly $x_2 = \frac{(1-s)x}{y_2}$. 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 will make simplifying assumptions on its possible behaviors in the following.

Forager behavior: The foraging process involves several steps. In the first step, the forager spends time τ_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 the patch encounter probabilities will 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), on finding a patch, assume the forager immediately recognizes the patch type. The forager then makes two conditional decisions: whether to enter the recognized patch or not and how long to stay in the chosen patch. a) "*Enter strategy*": Let $p_i \in [0,1]$, $i = 1,2$ denote the probability to enter an encountered A_i patch (cf. Charnov 1976*a*,*b*) "*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 (cf. 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, τ) 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 includes the information necessary to calculate fitness (see also Cressman et al. (2014) who develop a general method based on such decision trees).

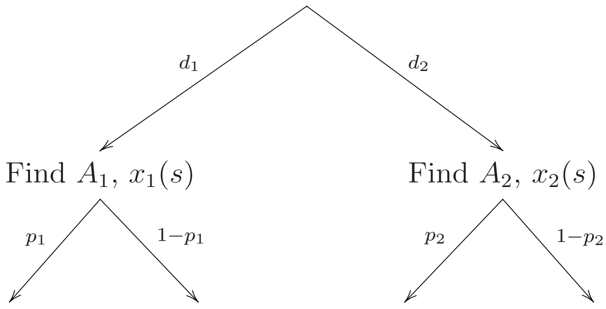
Payoff function for forager: Since optimal foraging theory postulates that the forager maximizes its average net energy intake per unit time (Turelli et al. 1982), forager payoff is taken as this intake rate. When the forager enters an A_i patch, the net energy gain from the prey, $g_i(x_i, \tau_i)$, depends on the local prey density x_i there and the amount of time τ_i that the forager spends in this patch. Biologically reasonable properties of this function are that it is increasing in both x_i and τ_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 $d_1 p_1$; etc. Since we assume that the players' strategies, $s \in [0, 1]$, $p_i \in [0, 1]$, $\tau_i \geq 0$, the parameters d_i, 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

$$E(\tau) = \tau_0 + d_1 p_1 \tau_1 + d_2 p_2 \tau_2. \tag{1}$$

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

$$E(G) = d_1 p_1 g_1(s, x, \tau_1) + d_2 p_2 g_2(s, x, \tau_2) - c, \tag{2}$$



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	$\tau_0+\tau_1$	τ_0	$\tau_0+\tau_2$	τ_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 τ_i) and energy intake of each activity. Based on this information, we can calculate the strategy dependent functional response and so, the net energy intake rate of forager.

where c is the fixed energy cost of finding a patch. Based on our Basic Condition that encounter (and thus activity) probabilities do not change during T, Garay and Móri (2010), using Wald's equality (Wald 1944), show that the forager's expected payoff function is (see Appendix A)

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

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 proportion of patch types among visited and among non-visited patches is the same and 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 Ψ 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 (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 prey are only killed 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 fitness 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 (cf. Garay and Varga 2011). To this end, let α 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 $\frac{g_i(s,x,\tau_i)}{\alpha}$ 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 in A_i patches killed per unit time is $\frac{d_i p_i}{\tau_0+d_1p_1\tau_1+d_2p_2\tau_2}\frac{g_i(s,x,\tau_2)}{\alpha}$ and so the individual survival rate of prey in an A_i patch (i.e. their payoff) is then

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

It is important to point out here that there is an essential difference between prey and forager payoff functions, χ_i and Ψ 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, i.e. for the prey, we have a population game (cf. Broom and Rychtar 2013).

The above prey and predator behaviors together with their payoff functions define the DFG as a union of IFD and Charnov's two models of optimal foraging theory. The assumptions underlying DFG and these components are identical. More precisely, if we fix the predator behavior, then we get back the IFD from DFG, and if we fix the prey behavior we get back the optimal foraging model from DFG. Now the theoretical problem arises: What is the solution concept for DFG? We investigate two possibilities in Sections 3 and 4, respectively, when prey and their predator cannot change their strategies at the same time, and when these strategies change simultaneously.

3 Static solution concepts based on 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 forager can change its strategy at a particular time. Then, the strategy pair s^* and (p^*, τ^*) is *a static solution*, if the following two conditions, (5) and (6), hold.

a) *Solution for prey*: With forager strategy fixed at (p^*, τ^*), the prey are engaged in a single-species habitat selection game (Cressman et al. 2004). (Cressman et al. 2004). As stated in the Introduction, s^* is an IFD (as introduced by Fretwell and Lucas (1969) Fretwell & Lucas(1969) before its connection with evolutionary game theory was recognized) if (i) prey payoffs in all occupied patches are the same and (ii) 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^*, τ^*), condition (5) is equivalent to s^* being a NE of the prey habitat selection game as shown by Cressman and Krivan (2006). That is, an IFD s^* is a NE.

Applying the IFD definition 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 forager's gain from different patches are also equal. For instance, the prey patch preference does not take account varying searching costs of the forager in different patches.

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

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

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

Appendix C 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), 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.

3.1 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 $\sigma_2 \in S_2$ strategy choices of two players. In our case, player one (the forager) has a multi-dimensional strategy set S_1 and player two 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 (σ_1, σ_2). The payoff function of the forager is then $\Gamma_1(\sigma_1, \sigma_2) := \frac{G(\sigma_1,\sigma_2)}{T(\sigma_1,\sigma_2)}$. Since we concentrate here on the NE behavior of the forager, the payoff function Γ_2 for the second player can be arbitrary and its strategy fixed at σ_2^*. If the optimal foraging behavior σ_1^* is unique (for example, the inequality in (6) is strict), 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, (σ_1^*, σ_2^*) is a strict NE with respect to the behavior of player one.

If the forager changes its strategy, there are two consequences: intake changes by $DG(\sigma_1) := G(\sigma_1, \sigma_2^*) - G(\sigma_1^*, \sigma_2^*)$; and time duration changes by $DT(\sigma_1) := T(\sigma_1, \sigma_2^*) - T(\sigma_1^*, \sigma_2^*)$, simultaneously. In Appendix B, an elementary proof shows that (σ_1^*, σ_2^*) is a strict NE (with respect to forager behavior) if and only if

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

for any other forager strategy σ_1. In particular, if there is no difference in the time duration of strategies σ_1 and σ_1^* (i.e. $DT(\sigma_1) = 0$), then the energy intake must be higher at the strict NE. We note that (7) is a version McNamara's potential function (1982) : "*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 (7), we have the following two rules:

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

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

for all σ_1 with $DT(\sigma_1) > 0$.

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

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

for all σ_1 with $DT(\sigma_1) < 0$.

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^*, τ^*) of the dispersal-foraging game. These results follow from considering NE behavior with respect to p^* and τ^* respectively, assuming prey behavior is fixed at their 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 not this patch? That is, it must decide on p_i^*. If it does use the patch, it spends time τ_i^* there. A straightforward calculation shows that changing its strategy to p_i results in $\frac{DG(p_i,\tau_i^*)}{DT(p_i,\tau_i^*)} = \frac{g_i(s^*,x,\tau_i^*)}{\tau_i^*}$. Since this is independent of the choice of p_i, the rule of time average (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 (10) is reversed. This is the well-known zero-one rule (Charnov 1976*a*) that either a given patch type is always entered when encountered or never entered.

Remark 2 (Marginal value theorem). Consider a forager who has spend τ_i in an A_i patch (thus $p_i^* = 1$) and has collected energy $g_i(s^*, x, \tau_i)$ from there. Now the question of the forager is: leave or not from this patch? If the forager spends extra time in this used patch, an easy calculation shows that $DT = d_i \Delta\tau_i$ and $DG = d_i \left[g_i(s^*, x, \tau_i + \Delta\tau_i) - g_i(s^*, x, , \tau_i)\right]$. Using (8) we find that the forager does not leave if $\frac{g_i(s^*,x,\tau_i+\Delta\tau_i)-g_i(s^*,x,\tau_i)}{\Delta\tau_i} > \Psi(s^*; p^*, \tau^*)$ which implies the well-known Charnov's marginal value theorem (Charnov 1976*b*):

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

That is, the forager leaves the patch at that time where its energy intake rate once in the patch matches its energy intake rate from all patches.

4 Dynamic solution concept based on game dynamics

The above static solution concept (and its dynamic characterization in Appendix C) 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 there is a separation of time scales between behavioral changes by prey compared to that of the predator. In biology, there is no general reason for ruling out that these counter interested agents change their strategies on the same time scale. Secondly, random perturbation cannot be excluded in biology and so no "player" keeps his strategy unchanged. Thirdly, forager and prey can adjust their behaviors to the opponent's current strategy immediately (see e.g. Juliana et al. 2011; Katz et al. 2010, 2013). Hence, solutions given by the Nash paradigm need to be examined to see if they correspond to the expected outcome of the real biological system. This situation can be treated by game dynamics that describe the behavior changes of prey and forager, leading to the following concept.

Game dynamic 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 DFG game is a mixture of evolutionary and classical games, we must combine two different type 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.

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

From Appendix C, an IFD s^* will be stable with respect to (12) at fixed (p,τ) if and only if it is an ESS of the prey habitat selection game.

Secondly, 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 either based on 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.

$$\begin{aligned}
\dot{p}_1 &= p_1(1-p_1)\frac{\partial\Psi(s,p_1,p_2,\tau_1,\tau_2)}{\partial p_1} && (13)\\
\dot{p}_2 &= p_2\,(1-p_2)\,\frac{\partial\Psi(s,p_1,p_2,\tau_1,\tau_2)}{\partial p_2} && (14)\\
\dot{\tau}_1 &= \tau_1\frac{\partial\Psi(s,p_1,p_{2,}\tau_1,\tau_2)}{\partial\tau_1} && (15)\\
\dot{\tau}_2 &= \tau_2\frac{\partial\Psi(s,p_1,p_2,\tau_1,\tau_2)}{\partial\tau_2} && (16)
\end{aligned}$$

In Appendix C, we show that optimal foraging behavior (p^*,τ^*) 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 counter-interested “players” (prey population and forager) simultaneously change their strategies according to the opponents’ current strategies. The game dynamic solution is then a locally asymptotically stable rest point (s^*,p^*,τ^*) of (12), (13), (14), (15) and (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.

5 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^*,τ_1^*,τ_2^*) of (12), (15) and (16) with $0 < s^* < 1$, and τ_1^*,τ_2^* both positive. The combined dynamics is then

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

It is clear that, if $(s^*, \tau_1^*, \tau_2^*)$ is a dynamic solution of DFG, then s^* a static solution for the prey (i.e. it satisfies inequality (5) since $\chi_1 = \chi_2$ at $(s^*, \tau_1^*, \tau_2^*)$). However, as we will see in the following two sections that use Holling type III and II functional responses respectively 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 τ_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 τ_1 and τ_2 at (τ_1^*, τ_2^*), then s^* is stable (i.e. an ESS) for the prey dynamics (12) and (τ_1^*, τ_2^*) is stable for the predator adaptive dynamics (15) and (16). Global concavity in τ_1 and τ_2 implies (τ_1^*, τ_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 an unstable for the prey dynamics (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 following two subsection.

5.1 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.

$\frac{g_i(x_i(s),\tau_i)}{x_i(s)}$ 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 Krivan (2006) prove 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 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 (12) for fixed patch leaving times τ_1 and τ_2 of the predator. For large prey density in both patch types, this is no longer the case as we will see in the following subsection on Holling II gain functions.

For the predator dynamics, we have an optimization problem in the patch leaving times τ_1 and τ_2 (see Appendix C). Since both leaving times τ_1^* and τ_2^* are positive, local asymptotic stability with respect to perturbations in the predator population (i.e. stability under the predator dynamics (15) and (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^*,τ_1^*,τ_2^*) (i.e. $g_i(x_i(s),\tau_i)$ is locally concave in τ_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 $g_i(x_i,\tau_i)=a_ix_i^2\tau_i/(x_i^2+a_ix_i\tau_i+a_i)$ 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 and become concave for larger x_i) that increase to the saturated consumption level of $a_i\tau_i$ at large prey density. They are also globally concave in leaving time τ_i with all prey consumed if the predator stays in this patch type sufficiently long. Thus, if (s^*,τ_1^*,τ_2^*) is a rest point of the (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 (τ_1^*,τ_2^*) as shown in Figure 2a. 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 DFG since the equilibrium forager strategy corresponding to these values of s is not (τ_1^*, τ_2^*).

There is consistency with these NE results and the stability of $(s^*, \tau_1^*, \tau_2^*)$ under (17) in that the game dynamic solution is a stable equilibrium for small values of x and a stable limit cycle for large x (Figure 2b). 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 Figure 2a) is different than the transition value of $x = 1.66$ from stability to instability of $(s^*, \tau_1^*, \tau_2^*)$ in Figure 2b. Specifically, for intermediate total population size x, we find $(s^*, \tau_1^*, \tau_2^*)$ is stable under (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 dynamic solution.

Observe that, in cases where stable behavior cycles emerge as the game dynamic solution, neither prey nor forager keep a fixed behavior but 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 than 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.

5.2 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 Appendix C). There may also be a second

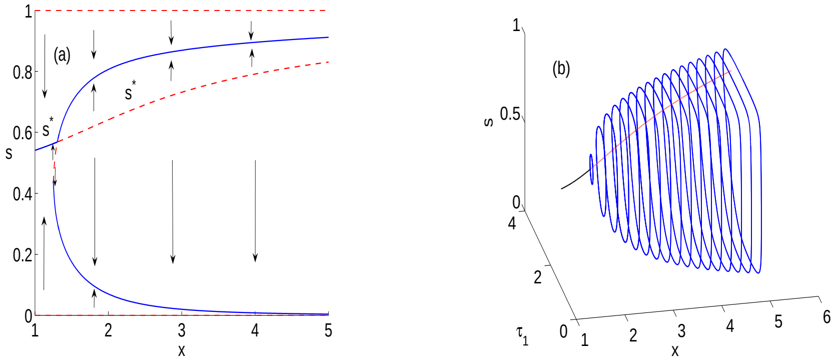


Figure 2: Trajectories of the game dynamics for typical Holling III gain functions of the form $g_i(x_i, \tau_i) = a_i x_i^2 \tau_i/(x_i^2 + a_i x_i \tau_i + a_i)$ where $a_1 = 0.3$ and $a_2 = 0.5$. (a) The prey replicator dynamics with predator strategy fixed at (τ_1^*, τ_2^*) as a function of x. The interior equilibrium s^* is globally stable until $x = 1.3$ (blue solid curve) and then becomes unstable for $x > 1.3$ (dashed red curve), in which case the prey evolve to different mixed equilibria of (12) (i.e. the solid blue curves) that are locally asymptotically stable but do not correspond to rest points of (17). (b) For $x < 1.66$, trajectories of (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 dotted 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 $y_1 = y_2 = 1, \alpha = 0.5, \tau_0 = 0.4, d_1 = d_2 = \frac{1}{2}, c = 0$.

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 $(s^*, \tau_1^*, \tau_2^*)$) 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 a NE, it is not stable with respect to perturbations in the prey population (i.e. it is not stable under the prey dynamics (12)). This phenomenon is discussed by Fretwell and Lucas (1969) and raises the question whether such an s^* should be considered an IFD (see Appendix C).

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 large prey density. Thus, if $(s^*, \tau_1^*, \tau_2^*)$ is a rest point of the (17), then the prey NE s^* is not an ESS when the forager strategy is fixed at (τ_1^*, τ_2^*) (see Figure 3a). 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 Section 5.1, these gain functions are globally concave in leaving time τ_i with all prey consumed if the predator stays in this patch type sufficiently long. That is, (τ_1^*, τ_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 (17). However, as seen in Figure 3b, $(s^*, \tau_1^*, \tau_2^*)$ is in fact stable under (17) (i.e. it is a game dynamic solution) for large total population size x. This example shows more clearly than Figure 2 that a game dynamic equilibrium solution may not be a stable static solution for the prey population (i.e. s^* may not be stable for (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.

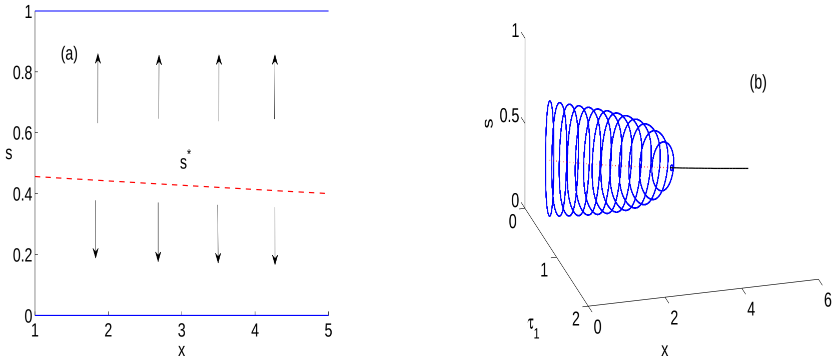


Figure 3: Trajectories of the game dynamics for typical Holling II gain functions of the form $g_i(x_i, \tau_i) = a_i x_i \tau_i/(x_i + a_i \tau_i + 1)$ where $a_1 = 0.9$ and $a_2 = 0.8$. (a) The prey dynamics with predator strategy fixed at (τ_1^*, τ_2^*) as a function of x. The interior equilibrium 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 (17). For small values of x, trajectories of (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 panel a). On the other hand, for larger values of x, trajectories of (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 $y_1 = y_2 = 1, \alpha = 0.8, \tau_0 = 0.4, d_1 = d_2 = \frac{1}{2}, c = 0$.

6 Discussion

The Dispersal-Foraging Game 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 DFG. The static NE concept (Section 3) 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 (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.

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: i.e.. 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), then the static solution predicts that prey use only one patch type, whereas the game dynamic solution predicts mixed habitat use (see Figure 3b where either the combined dynamics leads to a stable equilibrium or to 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" prey based on 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 Figure 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 that, not only should we expect cycling in predator-prey population sizes over long periods of time, game-theoretic reasoning predicts 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 (Figure 3), or vice versa (Figure 2). This phenomenon is parallel with 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.

Below we recall some biological considerations and examples which serve to justify our dynamical solution concept.

Firstly, we agree with Lima (2002) 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 IFD fit with observations. These issues also arise in applied ecology. Specifically, it is generally acknowledged that optimal foraging theory and

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 the reproductive success varies between habitats (Julliar 2000). At the same time, predatory mites of *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 USA, 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 *P. persimilis*, released onto groundcover, may eliminate spider mites before they migrate onto fruit trees (Takahashi et al. 1998; Takafuji and Amano 2001). In similar situations, it can be tested by field trials whether game theory leads to a deeper understanding of predation, especially whether stable behavior cycles should occur when optimal foraging theory and/or IFD do not predict observed behavior.

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 classic IFD/ESS, whereas the forager can stabilize the prey's mixed habitat use at the game dynamic solution. The existence of such examples is a strong argument to justify the dynamic solution concept.

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7 Appendix

In the Appendix, we only consider non-degenerate gain functions. In particular, we assume that $\frac{\partial^2}{\partial s^2} g_i(s, x, \tau_i) \neq 0$ and $\frac{\partial^2}{\partial \tau_i^2} g_i(s, x, \tau_i) \neq 0$.

8 Appendix A: Derivation of functional response with fixed prey's and forager's strategies

Following Holling (1959), we calculate the average amount of food consumed by the predator during a time period T. The functional response is defined by a time average during a foraging time duration T. Garay and Móri (2010) show that the average number of j-th activity Z_j during T is

$$E(Z_j) = \frac{T}{E(\tau)} P_j \tag{18}$$

where P_j denotes the probability of the j-th activity. The intuitive background of (18) is the following. If, during time period T, the encounter probabilities do not change, then the average time of one activity is the expected time, $E(\tau)$, of an activity chosen at random. Thus, the average expected number of activities during T is $\frac{T}{E(\tau)}$, and according to the assumption of independent repetitions, P_j is the part of the expected activity that belongs the j-th one. It is straightforward to obtain the payoff function (3) from this.

Another mathematical derivation of functional response and/or intake rate is based on renewal theory (e.g. Johns and Miller 1963) that uses the limit as the time duration tends to infinity. Although this does not match with our assumptions on T, other authors consider renewal cycles with short renewal time period (e.g. McNamara 1985; McNamara and Houston 1999). An issue then arises: if used patches are quickly renewed (e.g. renewal time is shorter than the searching time), the forager will optimize energy intake by staying in the richest patch type once one is encountered and so obtain an expected payoff greater than (3) by also decreasing the total searching time during T.

9 Appendix B: Rule of time average for forager

Consider a two-person formal game $(S_1, S_2; \Gamma_1; \Gamma_2)$, where the payoff function of the first player is defined as a time average of income, formally $\Gamma_1(\sigma_1, \sigma_2) := \frac{G(\sigma_1,\sigma_2)}{T(\sigma_1,\sigma_2)}$, where time duration function $T : (\sigma_1, \sigma_2) \to R$ gives the time duration corresponding to the players' decisions; and income function $G : (\sigma_1, \sigma_2) \to R$ gives income determined by these decisions as well. The well known strict Nash equilibrium condition (Hofbauer and Sigmund 1998) is the following: for all $(\sigma_1, \sigma_2) \neq (\sigma_1^*, \sigma_2^*)$

$$\begin{aligned}\Gamma_1(\sigma_1^*, \sigma_2^*) &> \Gamma_1(\sigma_1, \sigma_2^*)\\ \Gamma_2(\sigma_1^*, \sigma_2^*) &> \Gamma_2(\sigma_1^*, \sigma_2).\end{aligned}$$

From now on, we will concentrate exclusively on the time average payoff function Γ_1 of the first player and introduce the following notation $DG(\sigma_1) := G(\sigma_1, \sigma_2^*) - G(\sigma_1^*, \sigma_2^*)$ and $DT(\sigma_1) := T(\sigma_1, \sigma_2^*) - T(\sigma_1^*, \sigma_2^*)$.

Equation (7) in the main text is equivalent to each of the following inequalities

$$\begin{aligned}\left(G(\sigma_1, \sigma_2^*) - G(\sigma_1^*, \sigma_2^*)\right) T(\sigma_1^*, \sigma_2^*) &< \left(T(\sigma_1, \sigma_2^*) - T(\sigma_1^*, \sigma_2^*)\right) G(\sigma_1^*, \sigma_2^*)\\ G(\sigma_1, \sigma_2^*) T(\sigma_1^*, \sigma_2^*) &< T(\sigma_1, \sigma_2^*) G(\sigma_1^*, \sigma_2^*)\\ \frac{G(\sigma_1, \sigma_2^*)}{T(\sigma_1, \sigma_2^*)} &< \frac{G(\sigma_1^*, \sigma_2^*)}{T(\sigma_1^*, \sigma_2^*)}\\ \Gamma_1(\sigma_1, \sigma_2^*) &< \Gamma_1(\sigma_1^*, \sigma_2^*).\end{aligned}$$

That is, (σ_1^*, σ_2^*) is a strict NE if and only if $DG(\sigma_1) T(\sigma_1^*, \sigma_2^*) < DT(\sigma_1) G(\sigma_1^*, \sigma_2^*)$ holds for all $\sigma_1 \neq \sigma_1^*$. Furthermore, if $DT(\sigma_1) > 0$ (i.e. $T(\sigma_1, \sigma_2^*) > T(\sigma_1^*, \sigma_2^*) > 0$), then $\frac{G(\sigma_1^*,\sigma_2^*)}{T(\sigma_1^*,\sigma_2^*)} > \frac{DG(\sigma_1)}{DT(\sigma_1)}$ and, similarly, if $DT(\sigma_1) < 0$ (i.e. $T(\sigma_1^*, \sigma_2^*) > T(\sigma_1, \sigma_2^*) > 0$), then $\frac{G(\sigma_1^*,\sigma_2^*)}{T(\sigma_1^*,\sigma_2^*)} < \frac{DG(\sigma_1)}{DT(\sigma_1)}$. That is, we have

Case 1. If $T\left(\sigma_1, \sigma_2^*\right) > T\left(\sigma_1^*, \sigma_2^*\right) > 0$ then $\frac{G\left(\sigma_1^*,\sigma_2^*\right)}{T\left(\sigma_1^*,\sigma_2^*\right)} > \frac{DG(\sigma_1)}{DT(\sigma_1)}$

Case 2. If $T\left(\sigma_1^*, \sigma_2^*\right) > T\left(\sigma_1, \sigma_2^*\right) > 0$ then $\frac{G\left(\sigma_1^*,\sigma_2^*\right)}{T\left(\sigma_1^*,\sigma_2^*\right)} < \frac{DG(\sigma_1)}{DT(\sigma_1)}$

and these correspond to the +Rule of time average and −Rule of time average respectively as stated in the main text.

10 Appendix C: Dynamical characterization of static solution of DFG

Now the question arises: What kind of stability property does the static solution concept possess, under the basic Nash assumption that one player can change its strategy while the other keeps its strategy at equilibrium)? The following two subsections consider this question for the prey and the predator respectively.

10.1 Prey solution

In Section 4, we claim that an IFD s^* for the prey population at fixed predator strategy (p^*, τ^*) will be stable with respect to the replicator equation,

$$\dot{s} = s(1-s)\left[\chi_1(s,x;p^*,\tau^*) - \chi_2(s,x;p^*,\tau^*)\right], \tag{19}$$

if and only if it is an ESS of the prey habitat selection game.

When there are two patch types, this game (Cressman et al. 2004) has two pure strategies; namely, choose patch A_i (which we label strategy A_i) for $i = 1, 2$. The payoff to strategy A_i is the survival probability $\chi_i(s, x, p, \tau)$ when the prey population has strategy s. Then, the expected payoff of an individual prey who uses strategy s' (i.e. a prey that spends s' and $1 - s'$ of its time in A_1 and A_2 patches respectively) is

$$\Phi_{s'}(s) \equiv s'\chi_1(s,x,p^*,\tau^*) + (1-s')\,\chi_2(s,x,p^*,\tau^*). \tag{20}$$

s^* is an ESS (Maynard Smith 1982) if a resident prey population using strategy s^* cannot be invaded by a small mutant subpopulation using strategy s'. If ε is the proportion of the mutant subpopulation, then the resident-mutant system has proportion $(1-\varepsilon)s^* + \varepsilon s'$ of the prey in patch A_1. The mutant cannot invade if its payoff is less than that of s^* whenever ε is sufficiently small (i.e. if $\Phi_{s'}((1-\varepsilon)s^* + \varepsilon s') < \Phi_{s^*}((1-\varepsilon)s^* + \varepsilon s')$). From (20), this is equivalent to

$$(s' - s^*)\left(\chi_1((1-\varepsilon)s^* + \varepsilon s', x, p^*, \tau^*) - \chi_2((1-\varepsilon)s^* + \varepsilon s', x, p^*, \tau^*)\right) < 0 \tag{21}$$

for all ε sufficiently small.

We first consider the case when $0 < s^* < 1$. From (21), $\chi_1(s^*, x, p^*, \tau^*) = \chi_2(s^*, x, p^*, \tau^*)$ (i.e. s^* is an IFD/NE since prey have the same survival probability in both occupied patches). Furthermore, this NE will be an ESS if and only if

$$\frac{\partial}{\partial s}\left(\chi_1(s, x, p^*, \tau^*) - \chi_2(s, x, p^*, \tau^*)\right) < 0. \tag{22}$$

(Note that the degenerate condition where this derivative is 0 is assumed not to occur.) Since (22) is equivalent to the linearization of (19) at s^* having negative eigenvalue (i.e. $s^*(1-s^*)\frac{\partial}{\partial s}\left(\chi_1(s, x, p^*, \tau^*) - \chi_2(s, x, p^*, \tau^*)\right)|_{s=s^*} < 0$), s^* is stable if and only if it is an ESS.

Next, suppose $s^* = 1$. Then $s' < s^*$ and so (21) will be true if and only if $\chi_1(1, x, p^*, \tau^*) > \chi_2(1, x, p^*, \tau^*)$ (where the degenerate condition $\chi_1(1, x, p^*, \tau^*) = \chi_2(1, x, p^*, \tau^*)$ is assumed not to occur). That is, s^* is an ESS if and only if it is a strict NE. It is also clear that $\dot{s} > 0$ for s close to $s^* = 1$ if and only if $\chi_1(1, x, p^*, \tau^*) > \chi_2(1, x, p^*, \tau^*)$. The analogous results hold for $s^* = 0$ and so, for all $0 \le s^* \le 1$, s^* is an ESS if and only if it is stable under the replicator equation.

From (4),

$$\frac{\partial}{\partial s}\chi_1(s, x, p^*, \tau^*) = -\frac{d_1 p_1^*}{\tau_0 + d_1 p_1^* \tau_1^* + d_2 p_2^* \tau_2^*}\frac{y_1}{\alpha x}\left(\frac{\partial g_1(s, x, \tau_1^*)}{\partial s} - \frac{g_1(s, x, \tau_1^*)}{s}\right)$$

for $0 < s \le 1$. Since $g_1(0, x, \tau_1^*) = 0$, $\frac{g_1(s,x,\tau_1^*)}{s}$ is the slope of the line from the origin to $(s, g_1(s, x, \tau_1^*))$ and so $\frac{\partial}{\partial s}\chi_1(s, x, p^*, \tau^*) < 0$ if $\frac{g_1(s,x,\tau_1^*)}{s}$ is an increasing function of s (i.e. if $g_1(s, x, \tau_1^*)$ is a convex function of s). Similarly, if $g_2(s, x, \tau_2^*)$ is a convex function of s, $\frac{\partial}{\partial s}\chi_2(s, x, p^*, \tau^*) > 0$ since this is equivalent to $\frac{\partial g_2(s,x,\tau_2^*)}{\partial s} + \frac{g_2(s,x,\tau_2^*)}{1-s} < 0$. Thus, if both gain functions are convex in s, there is a unique IFD and it is an ESS.

On the other hand, if both gain functions are concave in s, then $\frac{\partial}{\partial s}\chi_1(s, x, p^*, \tau^*) > 0$ and $\frac{\partial}{\partial s}\chi_2(s, x, p^*, \tau^*) < 0$ for all $0 < s < 1$. If $\chi_1(1, x, p^*, \tau^*) > \chi_2(1, x, p^*, \tau^*)$, then $s^* = 1$ is an ESS. Otherwise $\chi_1(0, x, p^*, \tau^*) < \chi_1(1, x, p^*, \tau^*) \le \chi_2(1, x, p^*, \tau^*) < \chi_2(0, x, p^*, \tau^*)$ and so $s^* = 0$ is an ESS. If both $\chi_1(1, x, p^*, \tau^*) > \chi_2(1, x, p^*, \tau^*)$ and

$\chi_1(0,x,p^*,\tau^*) < \chi_2(0,x,p^*,\tau^*)$, both pure strategies are ESSs and there is a unique $0 < s^* < 1$ for which $\chi_1(s^*,x,p^*,\tau^*) = \chi_2(s^*,x,p^*,\tau^*)$. This s^* is an IFD but not an ESS since $\frac{\partial}{\partial s}\left(\chi_1(s,x,p^*,\tau^*) - \chi_2(s,x,p^*,\tau^*)\right) > 0$ at s^*. It should be noted here that some authors (Krivan et al. 2008) question whether this latter unstable s^* should be called an IFD. Consequences for the expected prey behavior in such circumstances have been considered by Morris (2002) and more recently by Krivan (2014) and Tran and Cressman (2015).

10.2 Predator solution

At fixed prey strategy s^*, the predator faces an optimization problem. From the predator dynamics (13-16), $\frac{d\Psi(s^*;p,\tau)}{dt}$ is given by

$$\begin{aligned}
& \frac{\partial\Psi(s^*;p,\tau)}{\partial p_1}\frac{dp_1}{dt} + \frac{\partial\Psi(s^*;p,\tau)}{\partial p_2}\frac{dp_2}{dt} + \frac{\partial\Psi(s^*;p,\tau)}{\partial \tau_1}\frac{d\tau_1}{dt} + \frac{\partial\Psi(s^*;p,\tau)}{\partial \tau_2}\frac{d\tau_2}{dt} \\
= \;& p_1(1-p_1)\left(\frac{\partial\Psi(s^*;p,\tau)}{\partial p_1}\right)^2 + p_2(1-p_2)\left(\frac{\partial\Psi(s^*;p,\tau)}{\partial p_2}\right)^2 \\
& +\tau_1\left(\frac{\partial\Psi(s^*;p,\tau)}{\partial \tau_1}\right)^2 + \tau_2\left(\frac{\partial\Psi(s^*;p,\tau)}{\partial \tau_2}\right)^2 \\
\geq \;& 0.
\end{aligned}$$

That is, $\Psi(s^*;p,\tau)$ is a Lyapunov function for this dynamics and so every trajectory converges to $E \equiv \{(p,\tau) \mid \frac{d\Psi(s^*;p,\tau)}{dt} = 0\}$ (Hofbauer and Sigmund 1998). Moreover, any strict local maximum of $\Psi(s^*;p,\tau)$ is a locally asymptotically stable rest point and any (connected) set of local maxima is locally asymptotically stable. In particular, the set of strategies corresponding to optimal foraging behavior (i.e. $\{(p^*,\tau^*) \mid \Psi(s^*;(p^*,\tau^*)) \geq \Psi(s^*;p,\tau)$ for all $(p,\tau)\}$) is locally asymptotically stable.

To provide more details for the stability of the predator dynamics, notice that E consists of the set of rest points of the predator dynamics at fixed prey strategy s^*.

Consider the following partial derivatives of $\Psi(s^*;p,\tau) = \frac{d_1p_1g_1(s^*,x,\tau_1)+d_2p_2g_2(s^*,x,\tau_2)-c}{\tau_0+d_1p_1\tau_1+d_2p_2\tau_2}$,

$$\frac{\partial\Psi(s^*;p,\tau)}{\partial p_1} = \frac{d_1g_1(s^*,x,\tau_1)\left(\tau_0+d_2p_2\tau_2\right)-\left(d_2p_2g_2(s^*,x,\tau_2)-c\right)d_1\tau_1}{\left(\tau_0+d_1p_1\tau_1+d_2p_2\tau_2\right)^2} \tag{23}$$

$$\begin{aligned}\frac{\partial\Psi(s^*;p,\tau)}{\partial \tau_1} &= \frac{\begin{pmatrix} d_1p_1\frac{\partial g_1(s^*,x,\tau_1)}{\partial\tau_1}\left(\tau_0+d_1p_1\tau_1+d_2p_2\tau_2\right) \\ -\left(d_1p_1g_1(s^*,x,\tau_1)+d_2p_2g_2(s^*,x,\tau_2)-c\right)d_1p_1 \end{pmatrix}}{\left(\tau_0+d_1p_1\tau_1+d_2p_2\tau_2\right)^2} \\ &= \frac{d_1p_1}{\tau_0+d_1p_1\tau_1+d_2p_2\tau_2}\left[\frac{\partial g_1(s^*,x,\tau_1)}{\partial\tau_1}-\Psi(s^*;p,\tau)\right]. \end{aligned} \tag{24}$$

All points with $p^* = (p_1^*, p_2^*) = (0,0)$ are rest points in E. However, these all correspond to the minimum value $-\frac{c}{\tau_0}$ of $\Psi(s^*;p,\tau)$ (i.e. $\Psi(s^*;(p^*,\tau)) \le \Psi(s^*;p,\tau)$ if for all (p,τ)). Thus, no trajectory converges to this subset of E unless the initial value of $\Psi(s^*;p,\tau)$ is also at this minimum.

Now suppose that, at some point in E, $p^* = (p_1^*, p_2^*) = (p_1^*, 0)$ with $p_1^* \neq 0$. Since the sign of $\frac{\partial\Psi(s^*;p,\tau)}{\partial p_1}$ in (23) does not depend on p_1, the zero-one rule applies and so $p_1^* = 1$ (since $p_1^* \neq 0$). Then (p^*,τ) for some τ is in E if and only if $\tau_1\frac{\partial\Psi(s^*;p,\tau)}{\partial\tau_1} = 0$. Since $\tau_1 = 0$ again corresponds to the minimum value of $\Psi(s^*;p,\tau)$, stability of (p^*,τ^*) implies that $\tau_1^* > 0$. Then, from (24), $\frac{\partial g_1(s^*,x,\tau_1)}{\partial\tau_1} = \Psi(s^*;p^*,\tau)$ (i.e. Charnov's marginal value theorem (11) holds in patch 1). Moreover, stability on this boundary implies that $\frac{\partial^2\Psi(s^*;p,\tau)}{\partial\tau_1^2} < 0$ at (p^*,τ^*). Furthermore, from (24), $\tau_1^*\frac{\partial^2\Psi(s^*;p,\tau)}{\partial\tau_1^2} = \frac{d_1p_1^*}{\tau_0+d_1p_1^*\tau_1^*+d_2p_2^*\tau_2^*}\frac{\partial^2 g_1(s^*,x,\tau_1)}{\partial\tau_1^2}$ at (p^*,τ^*) since $\frac{\partial\Psi(s^*;p,\tau)}{\partial\tau_1} = 0$ and $\frac{\partial g_1(s^*,x,\tau_1)}{\partial\tau_1} - \Psi(s^*;p,\tau) = 0$ there. Thus, if this (p^*,τ^*) is stable, the gain function $g_1(s^*,x,\tau_i)$ is concave in τ_1. A similar argument applies when $p^* = (p_1^*, p_2^*) = (0, p_2^*)$ with $p_2^* \neq 0$.

Finally, consider a point (p^*,τ^*) in E where the zero-one rule implies that $p^* = (p_1^*, p_2^*) = (1,1)$. If $\tau_i^* = 0$ for some $i = 1,2$, then (p^*,τ^*) is equivalent to a point in E with $p_i^* = 0$ and so the analysis of the preceding paragraph applies. Thus, we assume that the patch leaving times τ_i^* are both positive from now on.

The linearization of (13-16) is

$$\begin{bmatrix} -\frac{\partial\Psi(s^*;p,\tau)}{\partial p_1} & 0 & 0 & 0 \\ 0 & -\frac{\partial\Psi(s^*;p,\tau)}{\partial p_2} & 0 & 0 \\ * & * & \tau_1^*\frac{\partial^2\Psi(s^*;p,\tau)}{\partial\tau_1^2} & 0 \\ * & * & 0 & \tau_2^*\frac{\partial^2\Psi(s^*;p,\tau)}{\partial\tau_2^2} \end{bmatrix}$$

where all partial derivatives are evaluated at (p^*, τ^*). (Here, we use the facts that $\frac{\partial^2\Psi(s^*;p,\tau)}{\partial\tau_1\partial\tau_2} = -\frac{d_1}{\tau_0+d_1\tau_1^*+d_2\tau_2^*}\frac{\partial\Psi(s^*;p,\tau)}{\partial\tau_2} = 0$ at (p^*, τ^*) and that the entries indicated by an asterisk (*) are not needed for the analysis). From the zero-one rule, $\frac{\partial\Psi(s^*;p,\tau)}{\partial p_1} > 0$ and $\frac{\partial\Psi(s^*;p,\tau)}{\partial p_2} > 0$. Thus, all eigenvalues are negative at (p^*, τ^*) if and only if $\tau_i^*\frac{\partial^2\Psi(s^*;p,\tau)}{\partial\tau_i^2} < 0$ for $i = 1, 2$. That is, (p^*, τ^*) is locally asymptotically stable if and only if both gain functions $g_i(s^*, x, \tau_i)$ are concave in τ_i. In particular, this will be true if (p^*, τ^*) is the absolute maximum value of $\Psi(s^*; p, \tau)$ (i.e. the optimal foraging behavior when prey strategy is fixed at s^*). (Note that we are assuming that the degenerate condition $\frac{\partial^2\Psi(s^*;p,\tau)}{\partial\tau_i^2} = 0$ does not occur.)

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