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ABSTRACT

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[NOTE TO EDITORS/REFEREEES: In accordance with the directions for L^AT_EX users on the *American Naturalist* website, this document was prepared following AAS_TeX guidelines.]

We synthesize previous theory on ideal free habitat selection to develop a model of predator movement mechanisms, when both predators and prey are mobile. We consider a continuous environment with an arbitrary distribution of resources, randomly diffusing prey that consume the resources, and predators that consume the prey. Our model introduces a very general class of movement rules in which the direction of predators' movement is determined (i) randomly, (ii) by prey density, and/or (iii) by the density of the prey's resource. With this model, we apply an adaptive dynamics approach to two main questions. First, can it be adaptive for predators to base their movement solely on the density of the prey's resource (which the predators do not consume)? Second, should predator movements be exclusively biased toward higher densities of prey/resources, or is there an optimal balance between random and biased movements? We find that, for some resource distributions, predators that track the gradient of the prey's resource have an advantage compared to predators that track the gradient of prey directly. Additionally, we show that matching, overmatching, and undermatching distributions can all be explained by the same general mechanism. Our results provide important groundwork for future investigations of predator-prey dynamics.

Subject headings: predator-prey interactions; resource tracking; reaction-diffusion-advection models; ideal free distribution; habitat selection

16

1. Introduction

18 Predator-prey interactions profoundly influence the distributions and abundances of
organisms at a variety of spatial and temporal scales, and as such, are a central focus
20 of ecology. While most branches of ecology have traditionally ignored the details of the
dynamic, adaptive behavioral interactions between individual predators and prey, there
22 is increasing recognition of the importance of behavioral responses of predators and prey
to one another, for two main reasons. First, individual behaviors and trait-mediated
24 interactions are increasingly being recognized as important determinants of population
dynamics and food web properties (Bolker et al. 2003; Abrams 2007; Abrams et al. 2007).
26 Second, 35 years after May (1972, 1973) ignited the complexity-stability debate, adaptive
responses of predators and prey to one another have become widely acknowledged as
28 potentially stabilizing forces in large, complex food webs (Kondoh 2006; Garcia-Domingo
and Saldana 2007; Kondoh 2007; Uchida and Drossel 2007). The importance of behavioral
30 responses of predators and prey to one another highlights the need for theory that can
predict the fitness consequences and ecological ramifications of these behaviors.

32 The consequences of predator-prey interactions—while manifested at a variety of
spatial and temporal scales—are the combined result of behaviors (and dynamic responses)
34 of individual organisms, often at a small spatial scale and short time scale. Ideal free
distribution theory (Fretwell and Lucas 1969), including its many extensions over nearly
36 four decades, provides a framework focusing on consumer-resource relationships at small
scales. This framework thus provides a rich body of theory for predicting (i) adaptive
38 behaviors by predators and prey and (ii) both the ecological and evolutionary stability of
such behaviors (Cressman et al. 2004; Cressman and Křivan 2006).

40 In general, ideal free distribution (IFD) models ask how consumers should distribute
themselves in space given that each consumer is trying to maximize resource intake (or the

42 ratio of resource intake rate to death rate). In basic models, there is only a single species
of consumer and its resource. Consumers are assumed to be “ideal” in their knowledge of
44 all aspects of the environment (i.e., they know the qualities of patches and the numbers of
competitors and predators therein) and “free” from any constraints on or costs of travel
46 (see Tregenza (1995) for a review of assumptions and models relaxing them). A general
prediction of interest from IFD models is the extent to which consumers are predicted to
48 “match” resources (Tregenza 1995; Flaxman and deRoos 2007). A consumer “matches” a
resource when the proportion of consumers in each patch is the same as the proportion of
50 resources in each patch. “Undermatching” occurs when a species is under-represented in
the best patches compared to perfect matching, and “overmatching” refers to the reverse of
52 the latter. (For general discussions about matching, see Kennedy and Gray (1993), Milinski
(1994), Tregenza (1995), Flaxman and Reeve (2006), and Flaxman and deRoos (2007)).

54 Most IFD models focus on only one species of consumer (reviewed by Tregenza
(1995) and Sih (2005); see also Lima (2002) and Kacelnik et al. (1992)), but a number
56 of models have been developed that focus on simultaneous habitat selection by predators
and prey. These models can be broadly categorized as belonging to one of three types
58 (sensu Kacelnik et al. (1992)). In the first category are models that make predictions
about the nature of evolutionarily stable distributions that predators and prey could
60 simultaneously adopt (Iwasa 1982; Hugie and Dill 1994; Sih 1998; Bouskila 2001; Heithaus
2001; Alonzo 2002; Rosenheim 2004; Sih 2005). Henceforth, we refer to models in this first
62 category as “equilibrium models”, since they assume that an equilibrium is reached without
specifying any behavioral mechanisms that could bring a population to the equilibrium. A
64 second category assumes fixed populations of predators and prey and asks whether certain
movement rules will lead the populations to an ESS (Schwinning and Rosenzweig 1990;
66 Jackson et al. 2004*b*). In the third category are models that add population dynamics
and ask whether certain migration rules lead populations to spatial distributions that are

68 both ecologically and evolutionarily stable (van Baalen and Sabelis 1993; Křivan 1997; van
Baalen and Sabelis 1999; Cressman et al. 2004; Kimbrell and Holt 2004, 2005; Abrams 2007;
70 Abrams et al. 2007). We refer to models in the second and third categories as “mechanistic”
models, since they deal with specific patch-switching or habitat-choice mechanisms. All
72 these models treat the environment as being composed of a finite number of patches, and
with the exception of Jackson et al.’s (2004*b*) model, that number is two.

74 With the exception of Iwasa’s (1982) model, the equilibrium models share a common
prediction, and one that distinguishes them from most singles-species IFD models: for at
76 least some assumptions and particular parameter values, the predators’ distribution will
match the distribution of the prey’s resource (not the distribution of prey), and the prey
78 will be uniformly distributed between patches (for detailed discussions of this prediction,
see Rosenheim (2004), Sih (2005), and Hammond et al. (2007)). Furthermore, for a
80 broad range of parameter values, a number of equilibrium models predict that (i) prey
will undermatch their resource to some extent (instead they will match the resource/risk
82 ratio) and (ii) predators will overmatch the prey and match or slightly undermatch the
prey’s resource. In other words, it is frequently predicted that neither predator nor prey
84 will match their own food source; instead, the dynamic interplay of behaviors will lead to
predators being more common in patches with high levels of the prey’s resource and prey
86 subsequently undermatching their own resource to decrease risk. Sih (2005) termed this
prediction “leap-frogging”, since, superficially, the predators—rather than matching the
88 prey they consume—appear to ignore the prey and pay attention only to the resource, two
trophic levels below, with which they have no direct interaction.

90 Leap-frogging may seem counterintuitive, so the underlying logic of this prediction
merits a brief explanation. The following explanation glosses over the details of individual
92 models, but will hopefully provide the reader with a useful heuristic for understanding why

so many models predict leap-frogging. First, consider the perspective of predators. The
94 predator distribution can only be stable if the prey are distributed such that the per capita
predator payoff is equal in the two patches. In many of the equilibrium models, predators
96 are assumed to (i) compete weakly (if at all) and (ii) have a linear functional response.
With such assumptions, the predator payoff only be equalized between patches when the
98 prey are (nearly) uniformly distributed between patches. However—now considering the
perspective of prey—the prey will only remain at such a distribution if the patches are equal
100 in their food/risk ratios. The latter condition will only be satisfied if predators match the
resource. In sum, predators drive prey to undermatch resources, and prey drive predators
102 to match resources. Extremely few empirical studies have both (i) examined simultaneous
patch choice by predators and prey while (ii) measuring patch qualities (Lima 2002; Sih
104 2005). Of those that have, there is some support for the leap-frogging prediction (Bouskila
2001; Sih 2005; Hammond et al. 2007).

106 The fact that many equilibrium models predict leap-frogging (at least as one possible
distribution) suggests that a very simple behavioral mechanism could be used by predators
108 to reach an evolutionarily stable distribution. Instead of tracking the prey directly, the
predators could use a “resource tracking” strategy, that is, they could make habitat-selection
110 and patch-switching decisions based—exclusively or in part—on the distribution of the
prey’s resource (hereafter, “resource”). While such a patch-choice mechanism has been
112 mentioned casually in a number of previous publications (such as the equilibrium models,
above), surprisingly, mechanistic models have not formally investigated the effectiveness or
114 consequences resource tracking by predators. Instead, these models have all assumed that
predators base their patch switching decisions directly on their own fitness gradient or on
116 the prey gradient (i.e., a “prey tracking” mechanism).

Investigating the effectiveness and the consequences of predators using a “resource

118 tracking” habitat selection mechanism is important for at least two main reasons. First,
there are good reasons to expect that resource tracking could be an adaptive mechanism for
120 predators to employ. When prey are mobile but resources are sessile (e.g., herbivorous prey
and the plants they eat), resource tracking may require much less time and energy than
122 prey tracking. Similarly, if the locations of resources are obvious and predictable, but the
locations of prey are not, resource tracking may be the only feasible option. At the very
124 least, resource tracking could provide predators with a way to narrow down search options.

Second, recent theoretical work has revealed that the details of patch choice mechanisms
126 can have profound consequences for both spatial distributions and population dynamics
(Kimbrell and Holt 2004; Abrams et al. 2007). We might thus expect that resource
128 tracking by predators could alter the ecological and evolutionary dynamics of predator-prey
systems (as compared with prey tracking). For example, spatial and temporal cycles in
130 predator-prey dynamics are a common result in a variety of predator-prey models (e.g.,
Schwinning and Rosenzweig (1990)), and much effort has been devoted to understanding
132 factors that could dampen such cycles. An intuitively appealing hypothesis is that resource
tracking by predators could eliminate such cycles altogether, since predators would not
134 chase prey from patch to patch. As another example, empirical work suggests the hypothesis
that—in addition to potentially stabilizing an equilibrium—resource tracking predators
136 can speed the approach of a predator-prey system to an equilibrium (S. M. Flaxman,
unpublished). Currently, however, there is no theory that can be used to bolster or refute
138 hypotheses such as these, nor is there any theory that has answered a basic question: under
what circumstances is resource tracking a viable habitat selection mechanism for predators?

140 To address these issues, we use reaction-diffusion-advection models to describe
a predator-prey system and to develop a very general class of predator movement
142 mechanisms. In recent years reaction-diffusion-advection models have been used to model

biased movement of species along environmental or fitness gradients for both single species
144 (Belgacem and Cosner 1995; Cosner and Lou 2003; Cosner 2005; Rowell 2007) and two
competing species (Grindrod 1988; Cantrell et al. 2006, 2007; Chen and Lou 2007; Chen
146 et al. 2007) (see also Farnsworth and Beecham (1997) and Cantrell and Cosner (1999)).
Both our model and analytical approach for three species (i.e., two predators and one prey)
148 are along this line of research and make important steps forward.

We consider a three-trophic-level scenario: mobile predators, mobile prey, and a static
150 distribution of resources. Unlike most previous models that consider an environment of
only two discrete patches, we consider a continuous environment (e.g., Kshatriya and
152 Cosner (2002)) with an arbitrary distribution of resources. To make things simple enough
to be analytically tractable, we assume that, while prey are mobile, the prey do not move
154 in response to the distribution of predators; instead, prey move by simple diffusion (we
will relax this assumption in future work). However, because predators kill prey, the
156 equilibrium prey distribution is not fixed and will depend upon both predator behavior and
prey movement. Predator movement is the combined result of (1) random movement, (2)
158 movement in the direction of higher prey density (“prey tracking”), and (3) movement in
the direction of higher densities of the prey’s resource (“resource tracking”). We study two
160 main questions. First, considering the special cases of predators that use either resource
tracking or prey tracking (but not both simultaneously), might resource tracking in some
162 cases be more advantageous than prey tracking? Second, what are the optimal relative
magnitudes of random and biased movement? To answer these questions, we investigate the
164 adaptive dynamics of predator habitat selection mechanisms, where a particular mechanism
can be defined by parameters that determine the relative contributions of each of the three
166 types of movement mentioned above.

2. General model

168 Our goal is to better understand biased movement of predators—that is, movement
in the direction of some feature of the environment—and in particular, we wish to know if
170 there are advantages for predators that track the resources of the prey. For convenience, we
refer to the resources of the prey simply as “resources”. Predators that track the gradient
172 of the resource—moving toward a location of higher habitat quality—are termed resource
trackers. Similarly, predators that track prey directly are referred to as prey trackers. If
174 a species adopts purely random diffusion, we refer to it as a random tracker or random
diffuser.

To compare different predator movement mechanisms, our basic model formulation is
a predator-prey system with two species of predator and one species of prey. We assume
that the prey diffuse randomly, but the dispersal of both species of predators consists of
two components: random diffusion and directed movement along the gradient of some
mixture of the resources of the prey and the density of prey. In other words, both predator
species can sense and evaluate the local environment and local prey density. More precisely,
let $P_i(x, t)$ and $V(x, t)$ denote the densities of the i th predator species ($i = 1, 2$; i always
denotes a species of predator) and the prey species, respectively, at location x and time t ,
and let $R(x)$ denote the intrinsic growth rate of the prey species which measures the habitat
quality (e.g., resource density) at location x . Under our assumptions, the dispersal of the
predators and prey can be described, respectively, in terms of their fluxes

$$J_i = -d_i \nabla P_i + \alpha_i P_i \nabla f_i(R, V), \quad J_v = -d_v \nabla V,$$

where $d_i \nabla P_i$ and $d_v \nabla V$ account, respectively, for random diffusion of the i th species of
predator and the prey, $\alpha_i P_i \nabla f_i(R, V)$ represents biased movement of the i th predator
species along the environmental resource gradient and/or prey density gradient, and f_i are
some functions to be specified later. The positive constants d_i , d_v are random dispersal rates

of the i th predator species and prey, respectively; the non-negative constant α_i measures the tendency of the i th predator species to move along the gradient of the resources and/or the prey density gradient. If we further assume that there is no flux across the boundary of the habitat and also incorporate the simplest population dynamics for predator-prey interactions, we are led to the following reaction-diffusion-advection system:

$$\left\{ \begin{array}{l} P_{i,t} = \nabla \cdot [d_i \nabla P_i - \alpha_i P_i \nabla f_i(R, V)] + P_i(-k_i + a_i V) \quad \text{in } \Omega \times (0, \infty), \\ V_t = d_v \Delta V + V[R(x) - V - b_1 P_1 - b_2 P_2] \quad \text{in } \Omega \times (0, \infty), \\ [d_i \nabla P_i - \alpha_i P_i \nabla f_i(R, V)] \cdot n = \nabla V \cdot n = 0 \quad \text{on } \partial\Omega \times (0, \infty), \end{array} \right. \quad (2.1)$$

176 for $i = 1, 2$.

Our model not only can be derived as the above by the common approach based upon
 178 fluxes (see, e.g., Murray (2002, 2003) for many such examples), but also can be derived as
 limits of discrete models based on random walks (see, e.g., Okubo and Levin (2001)). Here
 180 k_i , a_i , b_i are all positive constants, where k_i is the mortality rate of the i th predator; a_i is
 the consumption rate of prey, and b_i is the predation rate. $\Delta := \sum_{j=1}^N \partial^2 / \partial x_j^2$ is the Laplace
 182 operator in \mathbb{R}^N which describes the random motion of prey, the habitat Ω is assumed to be
 a bounded domain in \mathbb{R}^N with smooth boundary, denoted by $\partial\Omega$. n denotes the outward
 184 unit normal vector on $\partial\Omega$, and the boundary conditions in (2.1) mean that no individuals
 cross the boundary of the habitat.

In order to make fair comparisons between dispersal mechanisms, throughout this
 paper we assume that

$$d_1 = d_2, \quad a_1 = a_2, \quad k_1 = k_2, \quad b_1 = b_2.$$

186 For the sake of simplicity we drop the subscripts and write these parameters as d , a , k , b ,
 respectively.

To address the questions outlined above, we study cases where

$$f_i(R, V) = \tau_i R + (1 - \tau_i)V \quad (2.2)$$

188 for some $\tau_i \in [0, 1]$ and $i = 1, 2$. $\tau_i = 1$ corresponds a situation in which the biased
 movement of the predator is purely affected by the gradient of habitat quality (i.e., the
 190 gradient of resources). Similarly, $\tau_i = 0$ corresponds to biased movement affected only by
 the gradient of prey density.

192 We will focus on two particular situations.

(i) First, to compare resource tracking with prey tracking, we study the case in which
 194 $0 \leq \tau_2 < \tau_1 \leq 1$. In other words, predator 1 is more of a resource tracker than predator 2,
 and predator 2 is more of a prey tracker than predator 1. In order to make fair comparisons,
 196 we assume in this case that $\alpha_1 = \alpha_2$.

(ii) Second, we let $\alpha_1 > \alpha_2 \geq 0$ (assuming $\tau_1 = \tau_2 \in [0, 1]$). For this case, the two predators
 198 give the same relative weight to prey tracking versus resource tracking (they have the same
 biased movement mechanism), but they differ in their relative magnitudes of random versus
 200 biased movement.

Hence from now on, we will study the following system

$$\left\{ \begin{array}{l} P_{i,t} = \nabla \cdot [d\nabla P_i - \alpha_i P_i \nabla [\tau_i R + (1 - \tau_i)V]] + P_i(-k + aV) \quad \text{in } \Omega \times (0, \infty), \\ V_t = d_v \Delta V + V[R(x) - V - bP_1 - bP_2] \quad \text{in } \Omega \times (0, \infty), \\ [d\nabla P_i - \alpha_i P_i \nabla [\tau_i R + (1 - \tau_i)V]] \cdot n = \nabla V \cdot n = 0 \quad \text{on } \partial\Omega \times (0, \infty) \end{array} \right. \quad (2.3)$$

for $i = 1, 2$.

202 The main results of our analysis of this model and particular cases are given in Section
 3. For details of the analysis and proofs of claims, the reader is referred to the Online

204 Appendix. Verbally, some of the important results can be summarized as follows. First,
 both resource trackers and prey trackers seem to do better than random trackers. Second,
 206 if the two species of predators are identical in all ways except in their biased movements,
 we show that, in some cases, (i) the resource trackers can invade before the prey trackers
 208 when they are both rare and (ii) when one predator has invaded and the other is rare, the
 resource trackers can invade the prey trackers but not vice versa. The underlying reason
 210 for the success of the resource tracker is the following. Since the prey track the resources
 quite well, the dispersal strategy of being a resource tracker can be fairly efficient since the
 212 resource gradient can be more sharp than prey density gradient. If the resource gradient
 is sharper than the prey gradient (but both are in the same direction), then predators
 214 following the resource gradient will move to the “right” locations faster than predators
 following the prey gradient per se (assuming $\alpha_1 = \alpha_2$).

216

3. Results

For each of the two situations outlined above (that is, variable τ and variable α),
 218 we shall focus on the adaptive dynamics of rare predator movement mechanisms in two
 scenarios: (i) when both predators are rare, we determine which one can invade first; (ii)
 220 if one predator has invaded in the absence of the other, we determine whether the other
 predator can subsequently invade.

When none of the predators are present, the prey can survive under a variety of
 assumptions about $R(x)$. Consider the scalar equation

$$d\Delta\theta + \theta[R(x) - \theta] = 0 \quad \text{in } \Omega, \quad \nabla\theta \cdot n = 0 \quad \text{on } \partial\Omega, \quad (3.1)$$

222 where $d > 0$ is the dispersal rate of the prey species and $\theta(x)$ is the density of the species at
 location x . We shall always assume that the function $R(x)$ is Hölder continuous in $\bar{\Omega}$, and

224 $\int_{\Omega} R(x) > 0$. Here $\bar{\Omega}$ is the union of Ω and $\partial\Omega$. Under this assumption, it is well known that (3.1) has a unique positive classical solution, denoted by $\theta = \theta(x; d)$ for every $d > 0$.

Clearly, $(0, 0, \theta)$ is always a non-negative non-trivial steady state solution of (2.3). To study its stability, we define $k^* := k^*(\alpha, \tau)$ such that the linear problem

$$d\Delta\psi + \alpha\nabla[\tau R + (1 - \tau)\theta] \cdot \nabla\psi + \psi(a\theta) = k^*\psi \quad \text{in } \Omega, \quad \nabla\psi \cdot n|_{\partial\Omega} = 0 \quad (3.2)$$

226 has a positive solution. See the Online Appendix for more discussions about k^* .

We first consider the case $\alpha_1 = \alpha_2$ (for simplicity we write α_i as α), and $0 \leq \tau_2 < \tau_1 \leq 1$.

228 **Theorem 1** *Suppose that $\alpha_1 = \alpha_2$ (denoted as α), $0 \leq \tau_2 < \tau_1 \leq 1$, $R_x(0) > 0$, $R_{xx} \geq 0$ and $R_{xxx} \leq 0$ in $(0, 1)$. Then for small positive α , $k^*(\alpha, \tau_1) > k^*(\alpha, \tau_2)$. Moreover,*

230 (i) $(0, 0, \theta)$ is stable for $k > k^*(\alpha, \tau_1)$ and unstable for $k < k^*(\alpha, \tau_1)$. When both predators are rare and the prey is present, the first predator can invade if $k < k^*(\alpha, \tau_1)$, and the second
232 predator can not invade for $k \in (k^*(\alpha, \tau_2), k^*(\alpha, \tau_1))$ and can invade when $k < k^*(\alpha, \tau_2)$.

(ii) There exists some $\delta_1 > 0$ independent of α such that for every small positive α , a
234 branch of steady state solutions of (2.3) with the form $(P_1^*, 0, V_1^*)$ bifurcates from $(0, 0, \theta)$ at $k = k^*(\alpha, \tau_1)$, and it can be parameterized by k for the range $k \in (k^*(\alpha, \tau_1) - \delta_1, k^*(\alpha, \tau_1))$;
236 Another branch of steady state solutions with the form $(0, P_2^*, V_2^*)$ bifurcates from $(0, 0, \theta)$ at $k = k^*(\alpha, \tau_2)$, and it can be parameterized by k for the range $k \in (k^*(\alpha, \tau_2) - \delta_1, k^*(\alpha, \tau_2))$.
238 Both P_i^* and V_i^* , $i = 1, 2$, are positive functions in Ω .

(iii) Given any $\delta_2 := \delta_2(\alpha) > 0$ with $\delta_2 \rightarrow 0$ as $\alpha \rightarrow 0$. Then for every small positive α ,
240 $(P_1^*, 0, V_1^*)$ is locally stable for $k \in (k^*(\alpha, \tau_1) - \delta_2, k^*(\alpha, \tau_1))$, and $(0, P_2^*, V_2^*)$ is unstable for $k \in (k^*(\alpha, \tau_2) - \delta_2, k^*(\alpha, \tau_2))$.

242 The proofs of all parts of Theorem 1 are given in the Online Appendix.

If we let k , the predator mortality rate, vary and be a bifurcation parameter, then, at
 244 least for some habitats, the steady state $(0, 0, \theta)$ is stable for $k > k^*(\alpha, \tau_1)$, and becomes
 unstable as k decreases and crosses $k_1^*(\alpha, \tau_1)$: a branch of steady state solutions in the
 246 form of $(P_1^*, 0, V_1^*)$, with both P_1^* and V_1^* positive, bifurcates from $(0, 0, \theta)$, and the first
 predator (the resource tracker) invades when both predators are rare if $k < k^*(\alpha, \tau_1)$. Such
 248 $(P_1^*, 0, V_1^*)$ is locally stable, and we conjecture that $(P_1^*, 0, V_1^*)$ is globally stable when it
 exists. As k decreases further and crosses $k^*(\alpha, \tau_2)$, another bifurcation occurs: a steady
 250 state branch of the form $(0, P_2^*, V_2^{**})$, with both P_2^* and V_2^{**} positive, bifurcates from $(0, 0, \theta)$.
 However, $(0, P_2^*, V_2^{**})$ is unstable.

252 In verbal terms, Theorem 1 and the paragraph following it can be interpreted as
 follows. The predator mortality rate, k , determines whether or not a given level of predation
 254 success is sufficient for survival of a predator species. If k is too high, predators can not
 offset mortality losses, and they go extinct, but if k is below some threshold, a predator
 256 population can be stable. This threshold is dependent upon the movement mechanism:
 the better the mechanism is at getting the predators to the right spot, the more predation
 258 success they will have and the higher their threshold value of k will be. For the conditions
 given in Theorem 1, the resource tracker can stably exist at higher values of k than the
 260 prey tracker. Furthermore, the resource tracker not only will invade before the prey tracker
 when both predators are rare, but also can invade when the prey tracker is present. In
 262 contrast, the prey tracker can invade when the resource tracker is absent, but may not be
 able to invade if the resource tracker is present.

264 The reason for the success of the resource tracker is as follows. For at least some
 resource distributions (conditions given above in Theorem 1), the resource gradient and the
 266 prey gradient will both have the same direction for all x , but, due to the random diffusion

of the prey, the resource gradient will be sharper than the prey gradient. Thus, resource
 268 trackers will move in the directions of higher prey densities (since that is the same as the
 direction of higher resource densities), and they will do so at a faster rate than the prey
 270 trackers (since the magnitude of the resource gradient is larger than the magnitude of the
 prey gradient).

272 Next we consider the case when $\alpha_1 > \alpha_2$ and $\tau_1 = \tau_2$ (for simplicity we write τ_i as τ).

Theorem 2 *Suppose that $\alpha_1 > \alpha_2$, $\tau_1 = \tau_2$ (denoted as τ), and $R_x > 0$ in $[0, 1]$. Then
 274 there exists some small positive constant δ such that if either $\alpha_2 < \alpha_1 \leq \delta$ or $\alpha_2 < \delta$ and
 $\alpha_1 > 1/\delta$, $k^*(\alpha_1, \tau) > k^*(\alpha_2, \tau)$. Moreover, whenever $k^*(\alpha_1, \tau) > k^*(\alpha_2, \tau)$,*

276 (i) $(0, 0, \theta)$ is stable for $k > k^*(\alpha_1, \tau)$ and unstable for $k < k^*(\alpha_1, \tau)$; i.e., none of the two
 predators can invade for $k > k^*(\alpha_1, \tau)$.

278 (ii) the first predator can invade if $k < k^*(\alpha_1, \tau)$; the second predator can not invade for
 $k \in (k^*(\alpha_2, \tau), k^*(\alpha_1, \tau))$ and can invade only when $k < k^*(\alpha_2, \tau)$.

280 The proof of Theorem 2 is given in the Online Appendix.

We do not know whether $\alpha_1 > \alpha_2$ always implies that $k^*(\alpha_1, \tau) > k^*(\alpha_2, \tau)$. If this
 282 were the case, from an evolutionary point of view this would mean that natural selection
 would favor ever-increasing α . That is, selection would favor rapid biased movement and
 284 would disfavor any movement mechanisms that caused movements down the resource/prey
 gradients. We suspect that there is some intermediate optimal α for the following
 286 reason. For very large α , all the predators—whether resource- or prey-tracking—would
 aggregate tightly in a single location (i.e., extreme overmatching). None of the equilibrium
 288 predator-prey IFD models predict such a distribution. Furthermore, prey trackers with
 large α would respond dramatically to even small changes in prey density. This would

290 likely lead to cyclic, non-equilibrium distributions of predators and prey, as predators would
continually chase prey from location to location.

292

4. Discussion

Predator-prey habitat selection models fall into two broad categories (Kacelnik et al.
294 1992): (i) equilibrium models which make predictions about the nature of evolutionarily
stable locations (i.e., simultaneous ideal free distributions) of predators and prey and (ii)
296 mechanistic models which examine the distributions resulting from particular movement
rules. Since the inception of ideal free distribution (IFD) theory, many models of both
298 types have been developed. As discussed above, a common prediction from the equilibrium
models is that the distribution of top predators will match the distribution of their prey's
300 resource (i) more closely than the predators' distribution will match that of their own prey
and (ii) more closely than the prey will match the resources (Rosenheim 2004; Sih 2005).
302 This prediction has received some empirical support (Bouskila 2001; Hammond et al. 2007),
and it suggests that many predators in nature could achieve optimal distributions simply by
304 using a habitat selection mechanism involving tracking the locations of the prey's resource,
a mechanism we have called "resource tracking". While previous work has suggested that
306 predators may indeed be resource trackers, mechanistic models have not formally considered
the effectiveness or consequences of resource tracking.

308 Investigating resource tracking is important for at least three reasons. First, tracking
a sessile resource may be much less costly than trying to track mobile prey, especially if
310 prey are fast moving and/or unpredictable. In such cases, resource tracking might be a
highly adaptive mechanism providing predators with an easy way to achieve, or at least
312 approximate, an evolutionarily stable distribution. Second, a great deal of theoretical work

on habitat selection has focused on trying to elucidate general mechanisms that would
314 lead populations to (or prevent them from achieving) equilibrium (e.g., Abrahams (1986);
Bernstein et al. (1988); Schwinning and Rosenzweig (1990); Bernstein et al. (1991); Hugie
316 and Grand (1998); Ruxton and Humphries (1999); Hugie and Grand (2003); Cressman
et al. (2004); Jackson et al. (2004*a*); Kimbrell and Holt (2004); Safran (2004); Cressman
318 and Křivan (2006)). Predator habitat selection mechanisms based on knowledge of prey or
knowledge of fitness directly are more complicated than resource tracking and frequently do
320 not lead to stable dynamics and/or the IFD. Resource tracking is simple and—since it does
not involve predators chasing prey directly—is potentially more likely to produce stable
322 habitat use dynamics (although we need to investigate this hypothesis with future work).
Third, the details of behavioral mechanisms matter, not just for individual fitness, but also
324 for population level patterns and the stability of predator-prey systems (Kimbrell and Holt
2004; Abrams et al. 2007; Safran et al. 2007). The details of habitat selection behaviors
326 determine whether habitat selectors can converge on a predicted equilibrium distribution
and whether predator-prey abundances can stabilize. As such, understanding habitat
328 selection mechanisms can inform questions at a variety of spatial and temporal scales.

We have developed a very general model of predator-prey spatial distributions in
330 which predators can move (i) randomly, (ii) by tracking the gradient of the prey’s resource
 (“resource tracking”), and/or (iii) by tracking the gradient of the prey (“prey tracking”).
332 Our model is not restricted to a finite number of patches or a particular resource distribution
(as many previous IFD models are). By studying the adaptive dynamics of different
334 strategies, we have shown that, in at least some cases, a resource tracking predator may
perform slightly better than prey tracking predator. This result is not necessarily expected,
336 since, apart from their movement mechanisms, prey trackers and resource trackers were
assumed to be identical (i.e., they had the same intrinsic mortality rates, birth rates, etc.).
338 For example, if prey are mobile but resources are sessile, we might expect that a prey

tracker would often pay higher search costs than a resource tracker. We did not include
340 such costs in our basic model, but doing so would enhance any relative advantage the
resource tracker has.

342 In addition to demonstrating the effectiveness of resource tracking, our model provides a
very general treatment of animal movement mechanisms. In our model, predator movement
344 is the combined result of random movements and biased movements toward particular
environmental features. It could be further generalized to incorporate any number of sources
346 of biased movement (e.g., movement in the direction of potential mates, movement due to
physical features of the environment such as wind or water currents). While both predators
348 and prey are mobile in its current formulation, an important extension of the model will
be to allow the prey biased movement as well so that they can respond to predators in an
350 adaptive fashion. We were unable to produce analytic results for the latter case, but will
explore it in future work.

352 As an example of the generality of our model, consider the following. Several previous
models (Hugie and Grand 1998; Ruxton and Humphries 1999; Hugie and Grand 2003)
354 have considered random movements as “non-ideal” explanations that can account for
undermatching (i.e., too few consumers found in good patches relative to the predicted
356 IFD). Our model provides a different perspective on matching and random movements.
Suppose that—as most researchers believe to be true in nature—predators have only
358 limited, mostly local information about prey and competitors. Such predators must use
simple rules of thumb if they are to achieve (nearly) optimal distributions. These rules of
360 thumb are most likely to be based on good predictors of fitness (i.e., the prey gradient or
the gradient of the prey’s resource). As our model shows, if predators always responded
362 rapidly and strongly to local gradients (i.e., large α), predators would likely aggregate more
strongly than optimal in “good” areas (i.e., overmatching). Conversely, if they responded

364 only weakly to local gradients, they would be more uniformly distributed than is optimal
(i.e., undermatching). It is thus a balance between random and biased movements that can
366 lead a population to an evolutionarily stable distribution. Thus, while previous models have
seen random movements as causing “mistakes” which lead to undermatching deviations
368 from the IFD, our model highlights how a single parameter (α) can tune the relative
influences of random and biased movement, and thus how a single movement rule could
370 evolve to produce matching, undermatching, or overmatching, depending on what is favored
by selection.

372 Finally, an important conclusion is that very simple rules can lead predators to optimal
(or nearly optimal) distributions. Without knowing the locations of prey or conspecifics,
374 but simply by responding to local environmental gradients, predator distributions can
move in the direction of evolutionary stability. Simply by tuning the strength of biased
376 movements, selection can fashion behavioral mechanisms to suit a wide variety of habitat
selection challenges.

378 5. Conclusions

Our model is a step toward building a more general and predictive theory of predator
380 movement mechanisms and predator-prey interactions than currently exists. We have
synthesized previous equilibrium and mechanistic models to investigate the effectiveness
382 of simple movement mechanisms that could allow predators to achieve or approximate
evolutionarily stable distributions. These results lay essential groundwork for future
384 investigations of both ecological and evolutionary consequences of optimal predator
movement. Several intriguing questions await answers. For example, does resource tracking
386 by predators impact the dynamics and equilibrium of prey habitat selection? Does resource

tracking eliminate cycles in behavioral and/or population dynamics? Does resource tracking
388 by predators create the opportunity for prey to use similarly simple rules to optimally
balance resource gathering with predation risk? These questions will be foci of future
390 studies.

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7. Online Enhancement: Online Appendix

398

Online Appendix: Proofs of Theorems and Other Details of Analyses

7.1. Properties of $\theta(x)$

400

In this subsection of the Online Appendix we discuss several properties of $\theta(x)$ which are used in our analyses.

Lemma 7.1 *Suppose that R is a non-constant function. Then*

$$\min_{\bar{\Omega}} R < \theta(x) < \max_{\bar{\Omega}} R$$

402

for every $x \in \bar{\Omega}$.

Proof. If $\min_{\bar{\Omega}} R \leq 0$, the first inequality automatically holds. Hence we may assume that $R > 0$ in $\bar{\Omega}$. Choose some $x_0 \in \bar{\Omega}$ such that $\theta(x_0) = \min_{\bar{\Omega}} \theta$. By Proposition 2.2 (Lou and Ni 1996), we have $\theta(x_0) \geq R(x_0) \geq \min_{\bar{\Omega}} R$, i.e., $\min_{\bar{\Omega}} \theta \geq \min_{\bar{\Omega}} R$. Set $w = \theta - \min_{\bar{\Omega}} R$, which is non-negative in Ω . It remains to show that $w > 0$ in $\bar{\Omega}$. Direct calculation shows that

$$d\Delta w + w(R - 2\min_{\bar{\Omega}} R - w) = -\min_{\bar{\Omega}} R[R - \min_{\bar{\Omega}} R] \leq 0.$$

404

Since $w \geq 0$ and it satisfies the zero Neumann boundary condition, by the strong maximum principle (Protter and Weinberger 1984) we see that either $w \equiv 0$ or $w > 0$ in $\bar{\Omega}$. Since R is a non-constant function, we see that $w \not\equiv 0$, hence $w > 0$ in $\bar{\Omega}$. The second inequality can

406

be proved similarly, so we omit it. \square

Lemma 7.2 *Suppose that $\Omega = (0, 1)$, $R_x \geq 0$ and $R_x \not\equiv 0$. Then $\theta_x > 0$ in $(0, 1)$.*

Proof. Differentiate the equation of θ and set $w = \theta_x$. Then

$$dw_{xx} + (R - 2\theta)w = -\theta R_x \quad \text{in } (0, 1), \quad w(0) = w(1) = 0.$$

408 By the equation of θ we see that the smallest eigenvalue of the operator $d(d^2/dx^2) + (R - 2\theta)$ with zero Neumann boundary condition is positive. Hence, the operator $d(d^2/dx^2) + (R - 2\theta)$ 410 with zero Dirichlet boundary condition is positive. Since θR_x is non-negative and not identically equal to zero, by maximum principle we see that $\theta_x > 0$ in $(0, 1)$. \square

412 **Lemma 7.3** *Suppose that $R_x(0) > 0$, $R_{xx} \geq 0$ and $R_{xxx} \leq 0$ in $(0, 1)$. Then $R_x \geq \theta_x$ in $[0, 1]$.*

Proof. We argue by the contradiction. If not, suppose that $\min_{[0,1]}(R_x - \theta_x) < 0$. By assumption, $R_x > 0$ in $[0, 1]$. Since $\theta_x(0) = \theta_x(1) = 0$, $R_x(0) > 0$ and $R_x(1) > 0$, we see that there exists some $x_0 \in (0, 1)$ such that $R_x(x_0) - \theta_x(x_0) = \min_{[0,1]}(R_x - \theta_x) < 0$. In particular,

$$R_{xx}(x_0) = \theta_{xx}(x_0), \quad R_{xxx}(x_0) \geq \theta_{xxx}(x_0).$$

By the equation of θ , we have

$$\theta(x_0)[\theta(x_0) - R(x_0)] = d\theta_{xx}(x_0) = dR_{xx}(x_0) \geq 0,$$

i.e., $R(x_0) \leq \theta(x_0)$. Differentiate the equation of θ and evaluate at $x = x_0$, we find

$$d\theta_{xxx}(x_0) + \theta_x(x_0)(R(x_0) - \theta(x_0)) + \theta(x_0)(R_x(x_0) - \theta_x(x_0)) = 0.$$

414 Since $\theta(x_0) > 0$, $\theta_x(x_0) > 0$ (Lemma 7.2), $R(x_0) \leq \theta(x_0)$ and $R_x(x_0) < \theta_x(x_0)$, we see that $\theta_{xxx}(x_0) > 0$. This together with $R_{xxx}(x_0) \geq \theta_{xxx}(x_0)$ ensures that $R_{xxx}(x_0) > 0$, which 416 contradicts our assumption $R_{xxx} \leq 0$ in $(0, 1)$. \square

7.2. Stability of $(0, 0, \theta)$

The stability of $(0, 0, \theta)$ is closely connected with the principal eigenvalue of the linear problem

$$\nabla \cdot [d\nabla\varphi - \alpha\varphi\nabla m] + c(x)\varphi = -\lambda\varphi \quad \text{in } \Omega, \quad [d\nabla\varphi - \alpha\varphi\nabla m] \cdot n = 0 \quad \text{on } \partial\Omega \quad (7.1)$$

for proper functions $m(x)$ and $c(x)$. By the transform $\psi = e^{-(\alpha/d)m}\varphi$, we see that ψ satisfies

$$d\Delta\psi + \alpha\nabla m \cdot \nabla\psi - c(x)\psi = -\lambda\psi \quad \text{in } \Omega, \quad \nabla\psi \cdot n|_{\partial\Omega} = 0. \quad (7.2)$$

418 It is known that equation (7.2) (and thus the same for equation (7.1)) has a principal
eigenvalue, denoted by $\lambda = \lambda(\alpha)$, which is real, simple, and the corresponding eigenfunctions
420 can be chosen positive in Ω , and all other eigenvalues have real parts larger than $\lambda(\alpha)$.

The stability of $(0, 0, \theta)$ is determined by the linear eigenvalue problem

$$\left\{ \begin{array}{l} \nabla \cdot [d\nabla\varphi_i - \alpha_i\varphi_i\nabla[\tau_i R + (1 - \tau_i)\theta]] + \varphi_i(-k + a\theta) = -\lambda\varphi_i \quad \text{in } \Omega, \\ [d\nabla\varphi_i - \alpha_i\varphi_i\nabla[\tau_i R + (1 - \tau_i)\theta]] \cdot n = 0 \quad \text{on } \partial\Omega, \end{array} \right. \quad (7.3)$$

where $i = 1, 2$.

Let $\lambda(\alpha, \tau)$ denote the principal eigenvalue of

$$\left\{ \begin{array}{l} \nabla \cdot [d\nabla\varphi - \alpha\varphi\nabla[\tau R + (1 - \tau)\theta]] + \varphi(-k + a\theta) = -\lambda\varphi \quad \text{in } \Omega, \\ [d\nabla\varphi - \alpha\varphi\nabla[\tau R + (1 - \tau)\theta]] \cdot n = 0 \quad \text{on } \partial\Omega. \end{array} \right. \quad (7.4)$$

Set $\psi = e^{(\alpha/d)[\tau R + (1-\tau)\theta]}\varphi$, the linear problem (7.4) can be transformed into

$$d\Delta\psi + \alpha\nabla[\tau R + (1 - \tau)\theta] \cdot \nabla\psi + \psi(-k + a\theta) = -\lambda\psi \quad \text{in } \Omega, \quad \nabla\psi \cdot n|_{\partial\Omega} = 0. \quad (7.5)$$

422 Recall that $k^*(\alpha, \tau)$ is defined as in equation (3.2), i.e., $\lambda(\alpha, \tau) = 0$ if and only if
 $k = k^*(\alpha, \tau)$.

424 **Lemma 7.4** $(0, 0, \theta)$ is stable if $k > \max\{k^*(\alpha_1, \tau_1), k^*(\alpha_2, \tau_2)\}$, and unstable if
 $k < \max\{k^*(\alpha_1, \tau_1), k^*(\alpha_2, \tau_2)\}$.

426 *Proof.* Define $\lambda_i = \lambda(\alpha_i, \tau_i)$, $k_i^* = k^*(\alpha_i, \tau_i)$, $i = 1, 2$. By the definitions of λ_i and k_i^* , we have
 $k - \lambda_i = k_i^*$. Hence, we have $\lambda_i > 0$ if and only if $k > k_i^*$, and $\lambda_i < 0$ if and only if $k < k_i^*$.
 428 Since the eigenvalue of equation (7.3) with the smallest real part is given by $\min\{\lambda_1, \lambda_2\}$,
 we see that Lemma 7.4 holds. Moreover, from previous argument we see that when both
 430 predators are rare, the i -th predator can invade $(0, 0, \theta)$ if $k < k^*(\alpha_i, \tau_i)$ and can not invade
 if $k < k^*(\alpha_i, \tau_i)$. \square

432 **7.3. Asymptotic behavior of $k^*(\alpha, \tau)$ for small α**

For small α small, we can write

$$k^*(\alpha, \tau) = k_0 + \alpha k_1(\tau) + O(\alpha^2), \quad \psi(\alpha, \tau) = \psi_0 + \alpha \psi_1 + O(\alpha^2),$$

where the positive function ψ_0 and the positive constant k_0 ($= k^*(0, \tau)$ for all τ) are uniquely determined by $\|\psi\|_\infty = 1$ and the linear problem

$$d\Delta\psi_0 + (a\theta - k_0)\psi_0 = 0 \quad \text{in } \Omega, \quad \nabla\psi_0 \cdot n = 0 \quad \text{on } \partial\Omega.$$

By direct calculations we have

$$k_1(\tau) = \int_{\Omega} \psi_0 [\tau \nabla R + (1 - \tau) \nabla \theta] \cdot \nabla \psi_0,$$

and thus

$$\frac{dk_1}{d\tau} = \int_{\Omega} \psi_0 \nabla(R - \theta) \cdot \nabla \psi_0.$$

It is rather difficult to determine the sign of $k_1(\tau)$ and its derivative in general. From
 434 now on we restrict to the case when Ω is an interval and R is monotone.

Lemma 7.5 *Suppose that $\Omega = (0, 1)$, $R_x \geq 0$ and $R_x \not\equiv 0$. Then $\psi_{0,x} > 0$ in $(0, 1)$.*

Proof. Note that ψ_0 satisfies

$$d\psi_{0,xx} = (k_0 - a\theta)\psi \quad \text{in } (0, 1), \quad \psi_x(0) = \psi_x(1) = 0.$$

436 As $k_0 - a\theta$ changes sign in $(0, 1)$ and θ is strictly increasing (Lemma 7.2), $k_0 - a\theta$ is strictly
decreasing and changes sign exactly once, say, at some $x^* \in (0, 1)$. Therefore, $\psi_{0,xx} > 0$ in
438 $(0, x^*)$ and $\psi_{0,xx} < 0$ in $(x^*, 1)$. Since $\psi_x(0) = \psi_x(1) = 0$, we see that $\psi_{0,x} > 0$ in $(0, 1)$. \square

By Lemma 7.3, $R_x - \theta_x \geq 0$ and is not identically equal to zero. Since $\psi_{0,x} > 0$ and
440 $\psi_0 > 0$ in $(0, 1)$, we see that the following holds:

Corollary 7.6 *Suppose that $R_x(0) > 0$, $R_{xx} \geq 0$ and $R_{xxx} \leq 0$ in $(0, 1)$. Then $dk_1/d\tau > 0$
442 for every $\tau \in [0, 1]$.*

Proof of part (i) of Theorem 1. By Corollary 7.6, $\partial k^*/\partial\tau(0, \tau) = dk_1/d\tau > 0$ for every
444 $\tau \in [0, 1]$. This implies that $k^*(\alpha, \tau_1) > k^*(\alpha, \tau_2)$ for small positive α . The rest of part (i)
follows from Lemma 7.4 and its proof. \square

446 The following result is an immediate consequence of Lemma 7.5:

Lemma 7.7 *Suppose that $\Omega = (0, 1)$, $R_x \geq 0$ and $R_x \not\equiv 0$. Then $k_1(1) > 0$.*

448 For $k_1(0)$, we have a more general result which holds for all convex domains.

Lemma 7.8 *Suppose that Ω is convex. Then $k_1(0) > 0$.*

Proof. Differentiate the equation of ψ_0 with respect to x and then take the inner product with $\nabla\psi_0$ we have

$$d\nabla(\Delta\psi_0) \cdot \nabla\psi_0 = (k_0 - a\theta)|\nabla\psi_0|^2 - a(\nabla\theta \cdot \nabla\psi_0)\psi_0.$$

Substituting the identity

$$\nabla(\Delta\psi_0) \cdot \nabla\psi_0 = -|Hess\psi_0|^2 + \frac{1}{2}\Delta(|\nabla\psi_0|^2)$$

into the previous equation and integrating in Ω , we have

$$a \int_{\Omega} (\nabla\theta \cdot \nabla\psi_0)\psi_0 = \int_{\Omega} [d|Hess\psi_0|^2 + (k_0 - a\theta)|\nabla\psi_0|^2] - \frac{d}{2} \int_{\Omega} \Delta(|\nabla\psi_0|^2).$$

By the definition of ψ_0 , we see that the smallest eigenvalue of the operator $-d\Delta + (k_0 - a\theta)$ with zero Neumann boundary condition is zero, which implies that

$$\int_{\Omega} |\nabla\psi|^2 \geq \int_{\Omega} (a\theta - k_0)\psi^2$$

for any $\psi \in H^1(\Omega)$, with equality holds if and only if ψ is a scalar multiplier of ψ_0 . Setting $\psi = \psi_{0,x_i}$ for every $1 \leq i \leq N$ and summing up in i , we have

$$\int_{\Omega} |Hess\psi_0|^2 > \int_{\Omega} (a\theta - k_2(0))|\nabla\psi_0|^2,$$

where the strict inequality follows from the fact that ψ_{0,x_i} is not a scalar multiplier of ψ_0 for at least some i . Since $\partial\psi_0/\partial n = 0$ on $\partial\Omega$ and Ω is convex, by a result of Casten and Holland (1978) and Matano (1979), we have $\partial(|\nabla\psi_0|^2)/\partial n \leq 0$ on $\partial\Omega$. In particular, this implies that

$$\int_{\Omega} \Delta(|\nabla\psi_0|^2) = \int_{\partial\Omega} \partial(|\nabla\psi_0|^2)/\partial n \leq 0.$$

Hence, we have

$$\int_{\Omega} (\nabla\theta \cdot \nabla\psi_0)\psi_0 > 0,$$

i.e., $k_1(0) > 0$. \square

Since $k_1(\tau)$ is a linear function of τ , Lemmas 7.7 and 7.8 imply that the following holds
452 for $k_1(\tau)$:

Lemma 7.9 *Suppose that $\Omega = (0, 1)$, $R_x \geq 0$ and $R_x \not\equiv 0$. Then $k_1(\tau) > 0$ for every
454 $\tau \in [0, 1]$.*

7.4. Asymptotic behavior of $k^*(\alpha, \tau)$ for large α

456 Let $\lambda(\alpha)$ denote the principal eigenvalue of the problem (7.2). We will need the following asymptotic result for $\lambda(\alpha)$ as established by Chen and Lou (2007):

Lemma 7.10 *Assume that $m \in C^2(\bar{\Omega})$ and $c \in C(\bar{\Omega})$ and all critical points of m are non-degenerate. Let \mathcal{M} be the set of points of local maximum of m . Then*

$$\lim_{\alpha \rightarrow \infty} \lambda(\alpha) = \min_{x \in \mathcal{M}} c(x).$$

458 **Lemma 7.11** *Suppose that $\Omega = (0, 1)$, $R_x > 0$ in $[0, 1]$. Then for every $\tau \in [0, 1]$, all critical points of $\tau R + (1 - \tau)\theta$ are non-degenerate and its set of local maxima consists of
460 only $x = 1$.*

Proof. By the assumption we have $\theta_x > 0$ in $(0, 1)$. Hence the only possible critical points
462 of $\tau R + (1 - \tau)\theta$ are $x = 0, 1$ and $x = 1$ is the only local maximum. For non-degeneracy of critical points, it suffices to show that $\theta_{xx}(1) < 0$ and $\theta_{xx}(0) > 0$. Since R is not a
464 constant function, Lemma 7.2 implies that $\max_{\bar{\Omega}} \theta < \max_{\bar{\Omega}} R$, which together with the monotonicity of R and θ imply that $\theta(1) < R(1)$. This along with the equation of θ implies
466 that $\theta_{xx}(1) < 0$. Similarly, one can show that $\theta_{xx}(0) > 0$. \square

By Lemmas 7.10 and 7.11, we have the following asymptotic behavior of $k^*(\alpha, \tau)$:

Lemma 7.12 *Suppose that $\Omega = (0, 1)$, $R_x > 0$ in $[0, 1]$. Then*

$$\lim_{\alpha \rightarrow \infty} k^*(\alpha, \tau) = a\theta(1).$$

468 *Proof of Theorem 2.* By Lemma 7.9 we see that $\partial k^*/\partial \alpha(0, \tau) > 0$ for every $\tau \in [0, 1]$.

Hence there exists $\delta_1 > 0$ such that if $0 \leq \alpha_2 < \alpha_1 < \delta_1$ and $0 \leq \tau \leq 1$ we have

470 $k^*(\alpha_1, \tau) > k^*(\alpha_2, \tau)$. For large α , by Lemma 7.12 we see that $k^*(\alpha, \tau) \rightarrow a\theta(1)$ as $\alpha \rightarrow \infty$.

Since $a\theta - k_0$ must change sign, we see that $k^*(0, \tau) \equiv k_0 < a \max_{\bar{\Omega}} \theta = a\theta(1)$. Hence

472 there exists some $\delta_2 > 0$ such that if $\alpha_2 \in [0, \delta_2)$ and $\alpha_1 > 1/\delta_2$, $k^*(\alpha_1, \tau) > k^*(\alpha_2, \tau)$. Set

$\delta = \min\{\delta_1, \delta_2\}$, this finishes the proof of the first part of Theorem 2. The rest follows from

474 Lemma 7.4 and its proof. \square

7.5. Local bifurcation of steady states

We are interested in a complete classification of all steady state solutions of (2.3) for k close to $k^*(\alpha, \tau_i)$ ($i = 1, 2$) and (P_1, P_2, V) close to $(0, 0, \theta)$. There are two types of such solutions, one with the form $(P_1^*, 0, V_1^*)$ and the other of the form $(0, P_2^*, V_2^*)$, which are close to $(0, 0, \theta)$ at $k = k^*(\alpha, \tau_1)$ and $k = k^*(\alpha, \tau_2)$, respectively. Hence, it suffices to classify all steady state solutions of the following reduced system (i.e., one dimension less than original system (2.3))

$$\left\{ \begin{array}{l} \nabla \cdot [d\nabla P - \alpha P \nabla [\tau R + (1 - \tau)V]] + P(-k + aV) = 0 \quad \text{in } \Omega, \\ d_v \Delta V + V[R(x) - V - bP] = 0 \quad \text{in } \Omega, \\ [d\nabla P - \alpha P \nabla [\tau R + (1 - \tau)V]] \cdot n = \nabla V \cdot n = 0 \quad \text{on } \partial\Omega \end{array} \right. \quad (7.6)$$

for (k, P, V) close to $(k^*(\alpha, \tau), 0, \theta)$. To find such classifications, we will apply the local bifurcation theorem of Crandall and Rabinowitz (1971). In order to use their abstract result, we need to introduce some functional spaces and operators. Define

$$X = \{(P, V) \in C^2(\bar{\Omega}) \times C^2(\bar{\Omega}) : (d\nabla P - \alpha\tau\nabla R) \cdot \nabla n = \nabla V \cdot n = 0 \text{ on } \partial\Omega\}$$

and $Y = C(\bar{\Omega})$. Define the operator $F(k, P, V) : (0, \infty) \times X \rightarrow Y$ by

$$F(k, P, V) = (\nabla \cdot [d\nabla P - \alpha P \nabla [\tau R + (1 - \tau)V]] + P(-k + aV), d_v \Delta V + V[R(x) - V - bP]).$$

Note that $F(k, 0, \theta) \equiv 0$ for all k . Clearly, the derivatives $D_k F$, $D_{(P,V)} F$, and $D_k D_{(P,V)} F$ exist and are continuous. We first check that the operator $D_{(P,V)} F|_{(k^*, 0, \theta)}$ has one-dimensional kernel and its range in Y is of codimension one. As

$$D_{(P,V)} F|_{(k^*, 0, \theta)}(\varphi, \varphi_v) \tag{7.7}$$

$$= (\nabla \cdot [d\nabla \varphi - \alpha \varphi \nabla [\tau R + (1 - \tau)\theta]] + \varphi(-k^* + a\theta), d_v \Delta \varphi_v + \varphi_v(R - 2\theta) - b\theta \varphi),$$

we see that the kernel of $D_{(P,V)} F|_{(k^*, 0, \theta)}$ is spanned by (φ^*, φ_v^*) , where $\varphi^* > 0$ is the unique positive solution of

$$\nabla \cdot [d\nabla \varphi - \alpha \varphi \nabla [\tau R + (1 - \tau)\theta]] + \varphi(-k^* + a\theta) = 0 \quad \text{in } \Omega, \quad [d\nabla \varphi - \alpha \varphi \nabla [\tau R + (1 - \tau)\theta]] \cdot n|_{\partial\Omega} = 0$$

with $\|\varphi^*\|_\infty = 1$, and φ_v^* is uniquely determined by

$$d_v \Delta \varphi_v^* + \varphi_v^*(R - 2\theta) = b\theta \varphi^* \quad \text{in } \Omega, \quad \nabla \varphi_v^* \cdot n|_{\partial\Omega} = 0;$$

and its range in Y is complement to $(\varphi^*, 0)$ and thus is of codimension one. Finally, since $D_k D_{(P,V)}|_{(k^*, 0, \theta)}(\varphi^*, \varphi_v^*) = (-\varphi^*, 0)$, we have $D_k D_{(P,V)}|_{(k^*, 0, \theta)}(\varphi^*, \varphi_v^*) \notin R(D_{(P,V)} F|_{(k^*, 0, \theta)})$. Hence, by the local bifurcation theorem of Crandall and Rabinowitz (1971) we see that there exists some $\delta > 0$, some function $\tilde{k}(s) \in C^2(-\delta, \delta)$ with $\tilde{k}(0) = k^*$ such that all steady state solutions of system (7.6) close to $(k^*, 0, \theta)$ can be parameterized as

$$(k, P, V) = (\tilde{k}(s), s\varphi^* + O(s^2), \theta + s\varphi_v^* + O(s^2)), \quad 0 < s < \delta.$$

476 Note that we choose $s > 0$ such the corresponding P, V are both positive. Also note that
 we can choose δ independent of both $\tau \in [0, 1]$ and all small positive α . This fact will be
 478 useful later.

It is important to determine the bifurcation direction of the solution branch. To this
 end, by direct calculations we have

$$\begin{aligned} & \frac{d\tilde{k}}{ds}(0) \int_{\Omega} e^{-\frac{\alpha}{d}[\tau R+(1-\tau)\theta]}(\varphi^*)^2 \\ &= a \int_{\Omega} e^{-\frac{\alpha}{d}[\tau R+(1-\tau)\theta]} \varphi_v^*(\varphi^*)^2 + \alpha(1-\tau) \int_{\Omega} e^{\frac{\alpha}{d}[\tau R+(1-\tau)\theta]} \varphi^* \nabla(e^{-\frac{\alpha}{d}[\tau R+(1-\tau)\theta]} \varphi^*) \cdot \nabla \varphi_v^*. \end{aligned} \quad (7.8)$$

For general value of α , it is difficult to determine the sign of $d\tilde{k}/ds$ at $s = 0$. For small
 positive values of α , we have

$$\lim_{\alpha \rightarrow 0^+} \frac{d\tilde{k}}{ds}(0) = \frac{a \int_{\Omega} \psi_0^2 \psi_v}{\int_{\Omega} \psi_0^2}, \quad (7.9)$$

where ψ_0 is given in the beginning of part 7.3 of this Online Appendix, and ψ_v is the unique
 positive solution of

$$d_v \Delta \psi_v + \psi_v(R - 2\theta) = b\theta \psi_0 \quad \text{in } \Omega, \quad \nabla \psi_v \cdot n|_{\partial\Omega} = 0. \quad (7.10)$$

By the equation of θ we see that the operator $-d_v \Delta + (-R + 2\theta)$ with zero Neumann
 480 boundary condition is a positive operator. Since $\psi_0 > 0$ in Ω , by the maximum principle we
 see that $\psi_v < 0$ in Ω . This implies that the right hand side of (7.9) is negative. Hence, for
 482 $\tau \in [0, 1]$ and positive small α , we have $d\tilde{k}/ds < 0$ at $s = 0$.

The above discussions lead to the following result:

484 **Lemma 7.13** *There exists some $\delta > 0$ such that for sufficiently small positive α , all
 solutions of (2.3) close to $(0, 0, \theta)$ for the parameter range $k \in (\delta, \max\{k^*(\alpha, \tau_1), k^*(\alpha, \tau_2)\})$
 486 consists exactly of three smooth branches in the space $C^2(\bar{\Omega}) \times C^2(\bar{\Omega}) \times C^2(\bar{\Omega})$:*

$(0, 0, \theta)$, $(P_1^*, 0, V_1^*)$ with $k \in (\delta, k^*(\alpha, \tau_1))$ and $(0, P_2^*, V_2^*)$ with $k \in (\delta, k^*(\alpha, \tau_2))$, where
 488 $P_i^*, V_i^*, i = 1, 2)$ are positive functions which are smooth in k .

7.6. Stability of steady states

We first study the stability of $(P_1^*, 0, V_1^*)$ for $k \in (k^*(\alpha, \tau_1) - \delta_2(\alpha), k^*(\alpha, \tau_1))$ for any given $\delta_2(\alpha)$ with $\delta_2 \rightarrow 0$ as $\alpha \rightarrow 0+$. To this end, consider the linear eigenvalue problem

$$\left\{ \begin{array}{l} \nabla \cdot [d\nabla\varphi_1 - \alpha\varphi_1\nabla f_1(R, V_1^*) - \alpha(1 - \tau_1)P_1^*\nabla\varphi_v] + \varphi_1(-k + aV_1^*) + aP_1^*\varphi_v = -\lambda\varphi_1, \\ \nabla \cdot [d\nabla\varphi_2 - \alpha\varphi_2\nabla f_2(R, V_1^*)] + \varphi_2(-k + aV_1^*) = -\lambda\varphi_2, \\ d_v\Delta\varphi_v + \varphi_v[R(x) - 2\theta - bP_1^*] - bV_1^*\varphi_1 - bV_1^*\varphi_2 = -\lambda\varphi_v \end{array} \right. \quad (7.11)$$

in Ω and corresponding boundary conditions

$$[d\nabla\varphi_1 - \alpha\varphi_1\nabla f_1(R, V_1^*) - \alpha(1 - \tau_1)P_1^*\nabla\varphi_v] \cdot n = 0 \quad \text{on } \partial\Omega, \quad (7.12)$$

$$[d\nabla\varphi_2 - \alpha\varphi_2\nabla f_2(R, V_1^*)] \cdot n = \nabla\varphi_v \cdot n = 0 \quad \text{on } \partial\Omega.$$

We first consider the principal eigenvalue, denoted by $\lambda(\alpha)$, of the linear problem

$$\nabla \cdot [d\psi - \alpha\psi\nabla f_2(R, V_1^*)] + \psi(-k + aV_1^*) = -\lambda\psi \quad \text{in } \Omega, \quad [d\nabla\psi - \alpha\psi\nabla f_2(R, V_1^*)] \cdot n|_{\partial\Omega} = 0$$

490 with corresponding eigenfunction uniquely determined by $\psi > 0$ in Ω and $\|\psi\|_\infty = 1$.

Lemma 7.14 *The following holds:*

$$\lim_{\alpha \rightarrow 0+} \frac{\lambda(\alpha)}{\alpha} = \frac{\tau_1 - \tau_2}{\int_\Omega \psi_0^2} \int_\Omega \psi_0 \nabla(R - \theta) \cdot \nabla\psi_0. \quad (7.13)$$

Proof. Rewriting the equation of ψ as

$$d\nabla \cdot [e^{\frac{\alpha}{d}f_2(R,V_1^*)}\nabla(e^{-\frac{\alpha}{d}f_2(R,V_1^*)}\psi)] + \psi(-k + aV_1^*) = -\lambda(\alpha)\psi,$$

multiplying it by $e^{-\frac{\alpha}{d}f_1(R,V_1^*)}P_1^*$ and integrating in Ω , we have

$$\begin{aligned} & -d \int_{\Omega} e^{\frac{\alpha}{d}f_2(R,V_1^*)}\nabla[e^{-\frac{\alpha}{d}f_1(R,V_1^*)}P_1^*] \cdot \nabla[e^{-\frac{\alpha}{d}f_2(R,V_1^*)}\psi] + \int_{\Omega} e^{-\frac{\alpha}{d}f_1(R,V_1^*)}P_1^*\psi(-k + aV_1^*) \\ & = -\lambda(\alpha) \int_{\Omega} e^{-\frac{\alpha}{d}f_1(R,V_1^*)}P_1^*\psi. \end{aligned} \tag{7.14}$$

Similarly, rewrite the equation of P_1^* as

$$d\nabla \cdot [e^{\frac{\alpha}{d}f_1(R,V_1^*)}\nabla(e^{-\frac{\alpha}{d}f_1(R,V_1^*)}P_1^*)] + P_1^*(-k + aV_1^*) = 0,$$

multiplying it by $e^{-\frac{\alpha}{d}f_2(R,V_1^*)}\psi$ and integrating in Ω , we have

$$-d \int_{\Omega} e^{\frac{\alpha}{d}f_1(R,V_1^*)}\nabla[e^{-\frac{\alpha}{d}f_1(R,V_1^*)}P_1^*] \cdot \nabla[e^{-\frac{\alpha}{d}f_2(R,V_1^*)}\psi] + \int_{\Omega} e^{-\frac{\alpha}{d}f_2(R,V_1^*)}P_1^*\psi(-k + aV_1^*) = 0. \tag{7.15}$$

We subtract equation (7.14) from equation (7.15) and divide it by $\|P_1^*\|_{\infty}$ to find

$$\begin{aligned} & \lambda(\alpha) \int_{\Omega} e^{-\frac{\alpha}{d}f_1(R,V_1^*)} \frac{P_1^*}{\|P_1^*\|_{\infty}} \psi \\ & = d \int_{\Omega} [e^{\frac{\alpha}{d}f_2(R,V_1^*)} - e^{\frac{\alpha}{d}f_1(R,V_1^*)}] \nabla[e^{-\frac{\alpha}{d}f_1(R,V_1^*)} \frac{P_1^*}{\|P_1^*\|_{\infty}}] \cdot \nabla[e^{-\frac{\alpha}{d}f_2(R,V_1^*)}\psi] \\ & + \int_{\Omega} [e^{-\frac{\alpha}{d}f_2(R,V_1^*)} - e^{-\frac{\alpha}{d}f_1(R,V_1^*)}] \frac{P_1^*}{\|P_1^*\|_{\infty}} \psi(-k + aV_1^*). \end{aligned} \tag{7.16}$$

Note that

$$e^{\frac{\alpha}{d}f_2(R,V_1^*)} - e^{\frac{\alpha}{d}f_1(R,V_1^*)} = \frac{\alpha}{d}(\tau_1 - \tau_2)(V_1^* - R) + O(\alpha^2)$$

and

$$e^{-\frac{\alpha}{d}f_2(R,V_1^*)} - e^{-\frac{\alpha}{d}f_1(R,V_1^*)} = \frac{\alpha}{d}(\tau_1 - \tau_2)(R - V_1^*) + O(\alpha^2).$$

As $\alpha \rightarrow 0+$, $k \rightarrow k^*(0, \tau_1)$, $V_1^* \rightarrow \theta$, $P_1^* \rightarrow 0$, $P_1^*/\|P_1^*\|_\infty \rightarrow \psi_0$, $\psi \rightarrow \psi_0$, so we have

$$\lim_{\alpha \rightarrow 0+} \frac{\lambda(\alpha)}{\alpha} = \frac{\tau_1 - \tau_2}{d \int_\Omega \psi_0^2} [d \int_\Omega (\theta - R) |\nabla \psi_0|^2 + \int_\Omega (R - \theta) [-k^*(0, \tau_1) + a\theta] \psi_0^2].$$

Multiplying the equation of ψ_0 by $(R - \theta)\psi_0$ and integrating in Ω , we have

$$\int_\Omega (R - \theta) [a\theta - k^*(0, \tau_1)] \psi_0^2 = d \int_\Omega (R - \theta) |\nabla \psi_0|^2 + d \int_\Omega \psi_0 \nabla(R - \theta) \cdot \nabla \psi_0.$$

Hence,

$$\lim_{\alpha \rightarrow 0+} \frac{\lambda(\alpha)}{\alpha} = \frac{\tau_1 - \tau_2}{\int_\Omega \psi_0^2} \int_\Omega \psi_0 \nabla(R - \theta) \cdot \nabla \psi_0.$$

This completes the proof of Lemma. \square

Proof of part (iii), Theorem 1. We first show that for small $\alpha > 0$, if system (7.11)-(7.12) has an eigenvalue λ with non-positive real part, then $\varphi_2 \equiv 0$. If not, Corollary 7.6 and Lemma 7.13 imply that for small positive α , $\lambda(\alpha) > 0$, which is a contradiction. Hence, φ_1 and φ_v satisfies

$$\begin{cases} \nabla \cdot [d\nabla\varphi_1 - \alpha\varphi_1\nabla f_1(R, V_1^*) - \alpha(1 - \tau_1)P_1^*\nabla\varphi_v] + \varphi_1(-k + aV_1^*) + aP_1^*\varphi_v = -\lambda\varphi_1 & \text{in } \Omega, \\ d_v\Delta\varphi_v + \varphi_v[R(x) - 2\theta - bP_1^*] - bV_1^*\varphi_1 = -\lambda\varphi_v & \text{in } \Omega \end{cases} \quad (7.17)$$

492 with no-flux boundary conditions.

Next we show that $\varphi_1 \equiv 0$. If not, after scaling we may assume that $\|\varphi_1\|_\infty = 1$ and φ_1 is positive somewhere in Ω (this ensures that $\varphi_1 \rightarrow \psi_0$ as $\alpha \rightarrow 0+$). Multiplying the equation of φ_1 by $e^{-(\alpha/d)f_1(R, V_1^*)}P_1^*$ and the equation of P_1^* by $e^{-(\alpha/d)f_1(R, V_1^*)}\varphi_1$, subtracting and integrating in Ω , similar as in the proof of Lemma 7.13, after integration by parts and rearrangement we have

$$-\lambda \int_\Omega e^{-\frac{\alpha}{d}f_1(R, V_1^*)}P_1^*\varphi_1 = a \int_\Omega (P_1^*)^2\varphi_v e^{-\frac{\alpha}{d}f_1(R, V_1^*)} + \alpha(1 - \tau_1) \int_\Omega P_1^*\nabla(e^{-\frac{\alpha}{d}f_1(R, V_1^*)}P_1^*) \cdot \nabla\varphi_v.$$

Dividing the above equation by $\|P_1^*\|_\infty^2$, since $P_1^* \rightarrow 0$, $P_1^*/\|P_1^*\|_\infty \rightarrow \psi_0$, $V_1^* \rightarrow \theta$, $\varphi_1 \rightarrow \psi_0$, we find that

$$\lim_{\alpha \rightarrow 0} \frac{\lambda(\alpha)}{\|P_1^*\|_\infty} = -\frac{a \int_\Omega \psi_0^2 \psi_v}{\int_\Omega \psi_0^2},$$

where ψ_v is the unique solution of (7.10). Similarly as in part 7.5 of this Online Appendix, we see that $\psi_v < 0$ in Ω , which implies that $\lambda(\alpha) > 0$ for small positive α . This contradicts our assumption $Re(\lambda) \leq 0$. Hence, $\varphi_1 \equiv 0$ and thus φ_v satisfies

$$d_v \Delta \varphi_v + \varphi_v [R(x) - 2V_1^* - bP_1^*] = -\lambda \varphi_v \quad \text{in } \Omega, \quad \nabla \varphi_v \cdot n|_{\partial\Omega} = 0.$$

Since $P_1^* \rightarrow 0$ and $V_1^* \rightarrow \theta$ as $\alpha \rightarrow 0$, we see that if λ has non-positive real part, then for small positive α , $\varphi_v \equiv 0$. This is a contradiction since $(\varphi_1, \varphi_2, \varphi_v) \not\equiv (0, 0, 0)$. Hence, all eigenvalues of (7.11)-(7.12) must have positive real part, i.e., $(P_1^*, 0, V_1^*)$ is stable.

For the instability of $(0, P_2^*, V_2^*)$, the corresponding linear eigenvalue problem is

$$\left\{ \begin{array}{l} \nabla \cdot [d \nabla \varphi_1 - \alpha \varphi_1 \nabla f_1(R, V_2^*)] + \varphi_1(-k + aV_2^*) = -\lambda \varphi_1, \\ \nabla \cdot [d \nabla \varphi_2 - \alpha \varphi_2 \nabla f_2(R, V_2^*) - \alpha(1 - \tau_2)P_2^* \nabla \varphi_v] + \varphi_2(-k + aV_2^*) + aP_2^* \varphi_v = -\lambda \varphi_2, \\ d_v \Delta \varphi_v + \varphi_v [R(x) - 2\theta - bP_2^*] - bV_2^* \varphi_1 - bV_2^* \varphi_2 = -\lambda \varphi_v \end{array} \right. \quad (7.18)$$

in Ω and corresponding no-flux boundary conditions. Let $\lambda(\alpha)$ denote the principal eigenvalue of the linear problem

$$\nabla \cdot [d\psi - \alpha\psi \nabla f_1(R, V_2^*)] + \psi(-k + aV_2^*) = -\lambda\psi \quad \text{in } \Omega, \quad [d \nabla \psi - \alpha \psi \nabla f_1(R, V_2^*)] \cdot n|_{\partial\Omega} = 0$$

with $\|\psi\|_\infty = 1$. Then the following holds (its proof is identical to that of Lemma 7.14 by switching f_1 with f_2 , and switch V_1^* with V_2^*):

$$\lim_{\alpha \rightarrow 0^+} \frac{\lambda(\alpha)}{\alpha} = \frac{\tau_2 - \tau_1}{\int_\Omega \psi_0^2} \int_\Omega \psi_0 \nabla(R - \theta) \cdot \nabla \psi_0. \quad (7.19)$$

496 Since $\tau_2 < \tau_1$, we see that $\lambda(\alpha) < 0$ for all small positive α . One can further show that λ
is also an eigenvalue for (7.18) (e.g., first solve (φ_2, φ_v) for $\alpha = 0$ and then perturb in α),
498 which implies the instability of $(0, P_2^*, V_2^*)$ for small α and $k \in (k^*(\alpha, \tau_2) - \delta_2, k^*(\alpha, \tau_2))$.

□

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