

Evolutionary ecology of movement by predators and prey

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Received: 27 August 2010 / Accepted: 26 January 2011
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Abstract An essential key to explaining the mechanistic basis of ecological patterns lies in understanding the consequences of adaptive behavior for distributions and abundances of organisms. We developed a model that simultaneously incorporates (a) ecological dynamics across three trophic levels and (b) evolution of behaviors via the processes of mutation, selection, and drift in populations of variable, unique individuals. Using this model to study adaptive movements of predators and prey in a spatially explicit environment produced a number of unexpected results. First, even though predators and prey had limited information and sometimes moved in the “wrong” direction, evolved movement mechanisms allowed them to achieve average spatial distributions approximating optimal, ideal free distributions. Second, predators’ demographic parameters had marked, nonlinear effects on the evolution of movement mechanisms in the prey: As the predator mortality rate was increased past a critical point, prey abruptly shifted from making very frequent movements away from predators to making infrequent movements mainly in response to resources.

Third, time series analyses revealed that adaptive, conditional movements coupled ecological dynamics across species and space. Our results provide general predictions, heretofore lacking, about how predators and prey should respond to one another on both ecological and evolutionary time scales.

Keywords Predator–prey interactions · Individual-based model · Movements · Ideal free distribution · Conditional dispersal · Migration

Introduction

Adaptive behaviors are key building blocks of ecological and evolutionary patterns (Abrams 2009; Amarasekare 2010; Lazzaro et al. 2009; Levin 1992, 1998, 2005; Nathan 2008; Nathan et al. 2008). Organismal movements—such as those involved in migration, dispersal, and habitat selection—are behaviors of particular importance for such patterns because of the crucial role that movement plays in determining distributions and abundances at a wide variety of biological scales (Gouhier et al. 2010; Nathan 2008; Nathan et al. 2008; Torney et al. 2010). Movement determines where an organism is at a given time, which determines the potential interactions it can have with factors that influence its fitness. Simply put, two organisms (or one organism and a feature of its abiotic environment) cannot directly interact unless they are spatially coincident. Movement is thus a crucial determinant of ecological dynamics (e.g., range limits) and evolutionary fitness and, hence, of populations’ responses to environmental change (Bowler and Benton 2005; Nathan 2008; Nathan et al. 2008).

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Like other traits, movement arises from evolved mechanisms operating within an organism (McNamara and Houston 2009; Nathan et al. 2008). In general, we expect that these “movement mechanisms” will have been shaped by evolution to respond in dynamic, adaptive ways to relevant features—such as habitat quality, predators or prey, parasites or hosts—of the organism’s environment (Nathan et al. 2008). However, until recently, most (though certainly not all) models of movement made the simplistic assumption that organisms move independently of their conditions (Amarasekare 2010; Bowler and Benton 2005; Ruxton and Rohani 1998). Additionally, the majority of studies of movement (and other behaviors as well) have been focused on just one species at a time and have thereby ignored the dynamic details of interactions and coevolution (Hammond et al. 2007; Koella and Restif 2001; Lambrechts et al. 2006; Lima 2002; Restif and Koella 2003; Sih 2005). As a result, biologists have a general “...lack of knowledge concerning the space and time dimensions of coevolutionary interactions and their influence on population distribution...” (Ricklefs 2010, p. 1265).

These gaps between theory and real organisms have become widely recognized, and biologists now benefit from a large body of theory that has explored patterns resulting from more realistic movement mechanisms, including the spatial patterns arising from interacting predators and prey (e.g., Abrams and Matsuda 2003; Abrams 2007, 2009; Alonzo 2002; Amarasekare 2008, 2010; Bouskila 2001; Cressman and Garay 2009; Cressman et al. 2004; Filotas et al. 2008; Heithaus 2001; Hugie and Dill 1994; Iwasa 1982; Jackson et al. 2004; Kimbrell and Holt 2005; Křivan 1997; Křivan and Cressman 2009; Rosenheim 2004; Schwinning and Rosenzweig 1990; Sih 1984; van Baalen and Sabelis 1999; Wang and Takeuchi 2009) and hosts and parasites (e.g., Comins and Hassell 1979; Comins et al. 1992; Godfray 1994; Green 2009; Hassell and May 1974; Hassell and Pacala 1990; Hassell et al. 1991, 1994; Jones et al. 1993; Pacala et al. 1990).

Many of the previous predator–prey models have explicitly built upon ideal free distribution theory (Fretwell and Lucas 1969; see also reviews by Tregenza 1995 and Křivan et al. 2008), asking if predator–prey systems are predicted to reach stable distributions that are also ideal free distributions. An ideal free distribution (IFD) is a spatial distribution characterized by no individual being able to improve its fitness by moving to a different location in its habitat (Fretwell and Lucas 1969). When applied to just a single species, the IFD has been shown to be a very robust prediction about both behavior and distributions: (a) A population can reach

an IFD even when individual organisms (occasionally) move suboptimally, (b) strategies that produce IFDs are evolutionarily stable (sensu Maynard Smith and Price 1973; Maynard Smith 1982), and (c) population dynamics equilibria are also IFDs (Cressman and Křivan 2006; Křivan et al. 2008; McPeck and Holt 1992; but see Cressman and Křivan 2010). However, models incorporating multiple species (such as those cited in the previous paragraph) have produced a wide variety of results, which contrast with the simpler view provided by single-species models. In particular, when predators and prey are both on the move, many models predict departures from IFDs and, in some cases, the absence of any equilibrium at all, though the specific predictions are highly sensitive to the particular movement mechanisms or parameter values that are chosen. The latter results beg questions about the applicability of the IFD concept to realistic communities (where many species interact) and also about the kinds of movement mechanisms we expect real organisms to use.

Hence, our investigations build upon the foundation previous models provide by utilizing a model with several features that allow us to simultaneously explore the evolution of movement mechanisms and the patterns and dynamics resulting from movement. First, the model we use takes an individual-level approach that incorporates variability (populations are not monomorphic), interactions, and stochasticity within populations, which are key determinants of dynamics at larger scales (Pascual and Levin 1999). Second, conditional movement in our model is based upon local information individuals have about densities (e.g., Křivan 2008), which is more realistic than the assumption—made by a number of previous models—that organisms move based upon direct knowledge of fitness (Amarasekare 2010; Flaxman and Lou 2009). Third, movement mechanisms evolve within our model via mutation, selection, and drift, rather than being fixed by the modeler; what constitutes an adaptive movement mechanism emerges as a result of the model, rather than being an assumption. While a number of models have studied the evolution of dispersal rates in a single species, consideration of *how strategies for conditional movement evolve simultaneously in interacting species* has been largely unexplored. Finally, the evolution of movement mechanisms in our model allows the relative time scaling of movement and population dynamics to evolve, rather than being fixed by the modeler. The model thus incorporates all three time scales relevant to evolutionary ecology—individual behavior, population dynamics, and evolutionary changes (Calcagno et al. 2010; Cressman and Křivan 2010)—but does not force

a particular separation of scales. The realism in our model, however, has not come at the expense of generality, as the movement mechanisms we model can be adapted to represent passive, random, or conditional movement in nearly any taxon (Flaxman and Lou 2009).

Here we use this model to explore two general questions about the evolutionary ecology of predator–prey interactions and movement. First, how does evolution shape algorithms for conditional movement when predators and prey interact in a spatially and temporally variable environment? Second, what are the ecological consequences of evolved behaviors? That is, how do evolved behaviors of individuals shape the patterns and dynamics seen in distributions and abundances? The model yields answers to these questions in the form of a number of unexpected, empirically testable predictions.

Methods

An evolutionary individual-based model of movements by predators and prey

The model considers a tritrophic system of predators, prey, and resources (consumed by the prey only). Population dynamics occur at all three levels. Predators and prey are capable of movement, but resources are not. What we call “movement” in this model is alternatively called “dispersal,” “migration,” or “habitat selection” by various investigators. We use “movement” to keep the presentation general and to avoid the connotations that some but not all investigators associate with the other terms. We do distinguish here between “random movement” and “conditional movement,” defined as follows: The probability and direction of a conditional movement depend upon environmental features (e.g., densities of resources or heterospecifics), whereas the probability and direction of a random movement do not. Each run of the model begins by initializing populations of predators and prey with randomly chosen values of the parameters that comprise each individual’s movement mechanism (described below). The simulation then proceeds with T iterations of a three-part cycle: movement \rightarrow reproduction \rightarrow death. Simulations are programmed in C (source code available upon request). Table 1 defines all the parameters and variables used in the model, as well as the “default” values used in preparing results shown here, and Fig. 1 gives a schematic representation of how these parameters and variables produce the model’s dynamics. To date, nearly 2,200 runs of the model have been completed,

exploring a wide range of values for these parameters. Results with alternative parameter values are available upon request.

The “full” model with adaptive, conditional movements

N discrete patches of habitat are arranged in a circle and are indexed $1, 2, \dots, N$. During a single time step, movements of predators and prey can only occur between adjacent patches (i.e., movement from patch n is possible only to patch $n - 1$ or patch $n + 1$; if $n = N$, movement is possible to patch $N - 1$ or patch 1 ; similarly, if $n = 1$, movement is possible to patch N or patch 2). Suppose that the i th predator is located in patch n at time t . The probability that this predator will move to adjacent patch m ($= n - 1$ or $n + 1$) is

$$\mu_{i,m} = \Delta t (d_P + \alpha_{P,i} [\tau_{P,i} g(R_{m,t}, R_{n,t}) + (1 - \tau_{P,i}) g(V_{m,t}, V_{n,t})]), \quad (1)$$

where Δt is the size of each discrete time step (chosen to be small to prevent artificial changes due to the discretization of time), d_P is a constant of random movement, $R_{n,t}$ is the abundance of resources (consumed by prey only) in patch n at time t , and $V_{n,t}$ is the number of prey in patch n at time t . $\alpha_{P,i}$ (≥ 0) and $\tau_{P,i}$ ($\in [0, 1]$) are individual-specific variables that comprise the i th predator’s movement mechanism. $\alpha_{P,i}$ influences the probability of conditional movement, with large values magnifying that probability and small values ($\alpha_{P,i} < 1$) diminishing it. $\tau_{P,i}$ determines whether the i th predator’s conditional movements are mainly in response to resources ($\tau_{P,i} \approx 1$), prey ($\tau_{P,i} \approx 0$), or a mix of the two ($0 < \tau_{P,i} < 1$). We allow predators the capability of movement in response to resources that they do not consume because many ideal free distribution models predict that optimal predator distributions match the distribution of the resource rather than that of the prey (reviewed by Sih 2005). Additionally, previous work shows that movement by predators in response to resources can in some cases be more adaptive than movement in response to prey (Flaxman and Lou 2009). The function $g(X_{m,t}, X_{n,t}) := \max(0, \frac{X_{m,t} - X_{n,t}}{X_{m,t} + X_{n,t}})$ provides a unit-less measure of relative differences between adjacent patches in the predators, prey, or resources that they contain. If $\mu_{i,n-1} + \mu_{i,n+1} > 1$, then the probability of moving to patch $n + 1$ is scaled as $\frac{\mu_{i,n+1}}{\mu_{i,n+1} + \mu_{i,n-1}}$ and similarly for the probability of moving to patch $n - 1$.

For prey, movement probabilities are calculated similarly. If the j th individual prey is located in patch n at time t , then its probability of moving to adjacent

Table 1 Definitions and values of parameters and variables used in the individual-based model

Parameter	Definition	Units	Default value
Δt	Size of discrete time step	Time	0.01
T	Number of time steps in one simulation run	Unitless	2.5×10^8
N	Number of patches	Unitless	8
d_P	Predator's random movement constant ("full" model only)	Unitless	0.025
d_V	Prey's random movement constant ("full" model only)	Unitless	0.025
S	Patch size	Area	50
K	Resource carrying capacity per patch	Density	100
r_n	Resource intrinsic growth rate in patch n	Time ⁻¹	See text
b_P	Predator's search rate	Area per time	0.1
b_V	Prey's search rate	Area per time	0.1
t_P	Predator's handling time	Time	0.05
t_V	Prey's handling time	Time	0.05
e_P	Predator's conversion efficiency	Births per prey consumed	0.1
e_V	Prey's conversion efficiency	Births per unit of resource consumed	0.1
k_V	Prey's intrinsic mortality parameter	Time ⁻¹	0.05
k_P	Predator's intrinsic mortality parameter	Time ⁻¹	Varied
ϵ	Probability of mutation per locus per offspring	Unitless	0.05
σ	Standard deviation parameter for mutations	Unitless	0.025
$\alpha_{P,i}, \alpha_{V,j}$	i th predator's or j th prey's sensitivity to inter-patch differences in making movements ("full" model only)	Unitless	Evolves
$\tau_{P,i}, \tau_{V,j}$	Determines what i th predator or j th prey is sensitive to in making movements ("full" model only)	Unitless	Evolves
$d_{P,i}, d_{V,j}$	i th predator's or j th prey's movement probability ("null" model only)	Unitless	Evolves

Where noted, certain parameters or variables appear in only the "full" version (see "The "full" model with adaptive, conditional movements" section) or "null" version (see "A "null" version of the model lacking conditional movements" section) of the model

patch m is $\mu_{j,m} = \Delta t(d_V + \alpha_{V,j}[\tau_{V,j}g(R_{m,t}, R_{n,t}) + (1 - \tau_{V,j})g(P_{n,t}, P_{m,t})])$, where $P_{n,t}$ is the number of predators in patch n at time step t . Values of $\mu_{j,n+1}$ and $\mu_{j,n-1}$ were scaled (if necessary) as above for predators. Note that the order of the arguments in the function g means that conditional movements cause prey to move to patches with *more* resources and/or *fewer* predators (depending upon the value of $\tau_{V,j}$).

Abundances of prey, predators, and resources change due to births, consumption, and deaths. Resource abundance in patch n changes according to:

$$R_{n,t+1} = R_{n,t} + \Delta t \left(r_n R_{n,t} \left(1 - \frac{R_{n,t}/S}{K} \right) \right) - c_{R_{n,t}}, \quad (2)$$

where $c_{R_{n,t}} := \min(R_{n,t}, \Delta t V_{n,t} (\frac{1}{b_V R_{n,t} + t_V}))$ is the total consumption of resources in patch n during time step t by prey with a type II (saturating) functional response (Holling 1959). The second term on the right-hand side of Eq. 2 represents logistic growth of the resource, where S is the size of each patch and thus scales density, K is the resource carrying capacity (expressed as a density) of a patch, and r_n is the intrinsic growth rate of resources in patch n (constant over time but variable across patches). In the results we show below, we used $N = 8$ patches of habitat with $[r_1, r_2, \dots, r_8] =$

[1, 1.25, 1.5, 1.75, 2, 1.75, 1.5, 1.25]. Thus, patch #1 is the lowest quality patch, and patch #5 is the highest quality patch. b_V is a search-area-per-time constant for prey, and t_V is the number of units of time it takes an individual prey to handle one unit of resource.

An individual prey in patch n at time t consumes an amount of resources equal to $c_{R_{n,t}}/V_{n,t}$, and its expected number of offspring is simply $e_V c_{R_{n,t}}/V_{n,t}$, where e_V is a coefficient that represents how efficiently prey convert consumed resources into offspring. This expected number is converted stochastically to an integer as follows: If the expected number is $X.YZ$, then an individual prey produces $X + 1$ offspring with probability $0.YZ$ and X offspring with probability $1 - 0.YZ$. Offspring are neither reproductively mature nor vulnerable to predation until the next time step.

Rather than inventing an algorithm for pairing individual predators with individual prey, we model predation and deaths from it, using a mean field approach (Chandler 1987). Predators are assumed to have a type II functional response, and the expected total consumption of prey in patch n during time step t is given by $c_{V_{n,t}} := \min(V_{n,t}, \Delta t [P_{n,t} (\frac{1}{S/(b_P V_{n,t}) + t_P})])$, where b_P is a search-area-per-time constant for predators and t_P is the number of units of time it takes a predator to handle one prey. Individual prey can thus die stochastically

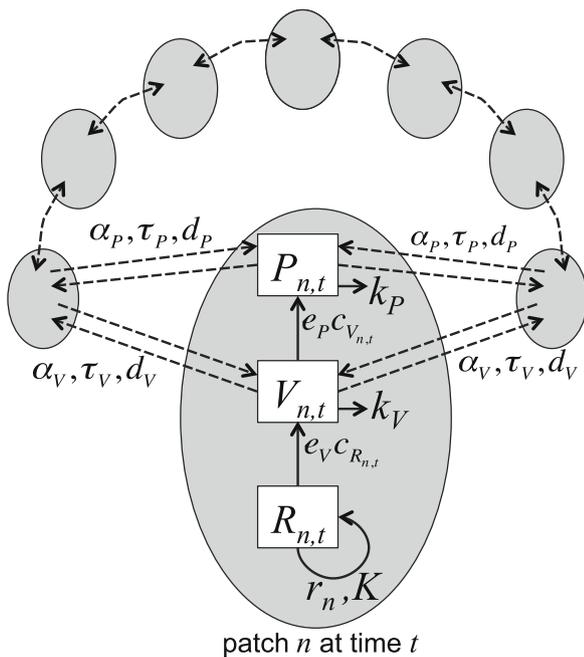


Fig. 1 Dynamics in the individual-based model, as shown for one focal patch. *Filled ovals* represent discrete habitat patches; *rectangles* represent the abundance of a given population in the patch; *solid lines* represent birth, death, and consumption processes; and *dashed lines* represent movement between patches. Items are labeled with important parameter(s) or variable(s) that influence them (defined in the text and Table 1). Each process shown is probabilistic at the level of the individual

due to predation (with probability $c_{V_{n,t}}/V_{n,t}$) or due to intrinsic mortality with probability $\Delta t k_V$. If an individual prey dies, it is removed from the population; if it survives, it goes on to the next time step of the model.

The integer number of offspring for a predator in patch n at time t is calculated in an analogous manner as for prey, with the expected number of offspring by an individual predator given by $e_P c_{V_{n,t}}/P_{n,t}$. After reproduction, the probability of death for a predator is a constant, $\Delta t k_P$. Values of $\alpha_{P,i}$ and $\tau_{P,i}$ in any predator's offspring (or $\alpha_{V,j}$ and $\tau_{V,j}$ in any prey's offspring) are the same as its parent's values unless mutation occurs. Mutations occur independently in the two traits with probability ϵ . If a mutation occurs, the value of the mutated trait in the offspring is chosen from a normal distribution with mean equal to the parental value and standard deviation σ scaled by the mean.

We remark that the way we discretize time (discrete steps with rates scaled by Δt) is an implementation of the Euler method, which is used widely in simulations within and outside of biology (for a different example with explanation, see p. 94 of Drossel et al. 2001). Two concerns may arise with the use of this method to discretize time. The first is a general concern that if func-

tions are being approximated cumulatively (over time in our model), then the Euler method can be subject to rounding errors (Nelson 1995). The second, a concern specifically for models like ours, is that discretization can cause artificial demographic stochasticity: If time steps are not sufficiently small, a large number of birth or death events may happen in each time step causing the system to fluctuate artificially. Both concerns can be minimized by choosing Δt to be sufficiently small. Additionally, regarding the first concern, the only quantities we are actually calculating cumulatively over time with this method are resource abundances, $R_{n,t}$ (Eq. 2). Like predator and prey abundances (Fig. 2), resource abundances fluctuate around central values; that is, we are not approximating some increasing (or decreasing) function, in which case approximation errors could potentially be systematically compounded over time to cause ever-increasing divergence from a continuous-time process. To explore the second concern, we have varied Δt over several orders of magnitude compared to our default, $\Delta t = 0.01$. In runs with an order of magnitude “slower” time scaling, $\Delta t = 0.001$ (and an order of magnitude increase in T), Δt is small enough to scale probabilities such that very few birth and death events (usually 0, 1, or 2 across the entire population of predators or prey) are actually happening in a given time step of the model. In essence, with small Δt , our model converges toward what would be seen in continuous time (in which just one event would happen at a time). Importantly, results with $\Delta t = 0.001$ produce results that are qualitatively and largely quantitatively, the same as those we show here. Hence, we use $\Delta t = 0.01$ because it shortens time required for simulations (compared to $\Delta t = 0.001$) without making time steps too large.

A “null” version of the model lacking conditional movements

To examine the consequences of adaptive, conditional movement behavior per se, we have also constructed a “null” version of the model. The null model differs in only two ways from the “full” model. First, the parameters that govern the rate of random movement, d_P and d_V , are replaced with individual-specific variables: $d_{P,i}$ (for the i th predator) and $d_{V,j}$ (for the j th prey). These variables are allowed to evolve just as $\alpha_{P,i}$, $\tau_{P,i}$, $\alpha_{V,j}$, and $\tau_{V,j}$ do in the full model. We allow the random movement rates to evolve in order to give the null model the greatest possible chance of producing adaptive behavior. Second, we eliminate conditional movement by setting $\alpha_{P,i} = \alpha_{V,j} = 0$ for all i, j . Thus, in the null model, in any one time step, the probability of

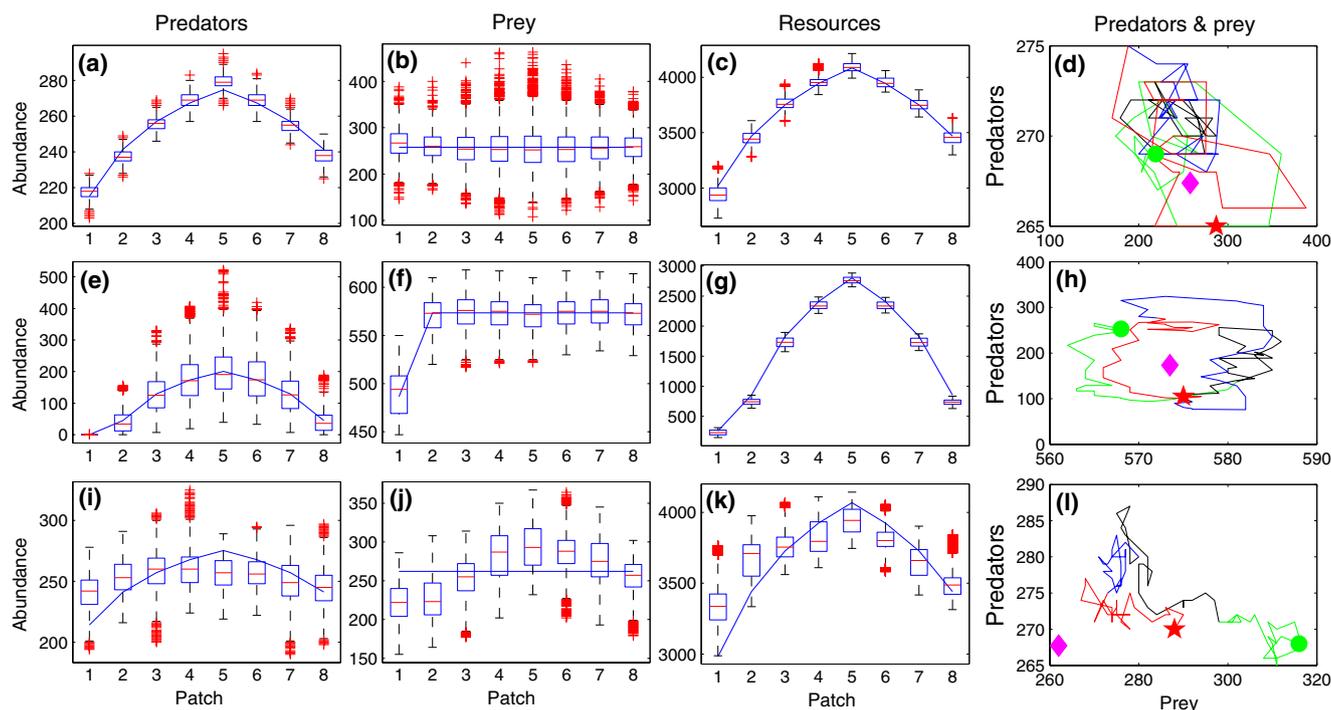


Fig. 2 Distributions and abundances of predators, prey, and resources in three example simulation runs. **a–d** Full model, $k_P = 0.05$, fast-prey regime; **e–h** full model, $k_P = 0.11$, slow-prey regime; **i–l** null model, $k_P = 0.05$. *Box plots* display the complete ranges of numbers of predators (**a**, **e**, and **i**), numbers of prey (**b**, **f**, and **j**), and resource abundance (**c**, **g**, and **k**) within the $N = 8$ patches over the last 5,000 time steps of a simulation (*red line* = median; *bottom and top of box* = 25th and 75th percentiles;

whiskers = $1.5 \times$ interquartile range; plus signs = data points beyond whiskers). The *solid blue line* is the ideal free distribution (IFD). Resource abundance units are arbitrary. **d**, **h**, **l** Parametric plots of predator and prey numbers within one patch over 100 steps of time: *green circle* = initial numbers, *red star* = ending numbers, *magenta diamond* = IFD. For clarity, these 100 time steps are broken into different-colored segments of 25 steps each, with the temporal progression *green* \rightarrow *black* \rightarrow *blue* \rightarrow *red*

movement to an adjacent patch by the i th predator or j th prey is, respectively, $\Delta t d_{P,i}$ or $\Delta t d_{V,j}$.

Statistical methods

Spatial distributions and ideal free distributions

In the results on spatial distributions (Fig. 2), we display the last 5,000 time steps of distribution and abundance data for example runs of the model. We define an ideal free distribution in the same way as Fretwell and Lucas (1969), with their original definition extended to multiple species: An ideal free distribution is a combined spatial distribution of predators and prey at which no individual of either species can improve its expected payoff by switching to a different patch. Ideal free distributions shown in Fig. 2 were calculated numerically using the average numbers of prey and predators and average resource abundance present across all patches combined over the last 5,000 time steps of a run. The expected payoff for a predator or prey in a patch was defined as the expected per capita birth rate minus the

expected per capita death rate for that patch. We also confirmed numerically that the ideal free distribution found using those payoffs was the same as the population dynamics equilibrium that would be predicted in the absence of movement (Cressman and Křivan 2006; Křivan et al. 2008; Křivan and Cressman 2009) for a given set of parameters.

Evolution of movement mechanisms

For results on the evolution of movement mechanisms, we present average values of movement traits that are present within a population at the end of a single simulation run, denoted $\bar{\alpha}_P$, $\bar{\tau}_P$, $\bar{\alpha}_V$, and $\bar{\tau}_V$. For example, $\bar{\alpha}_P$ is calculated as $\bar{\alpha}_P = \frac{1}{P_T} \sum_i \alpha_{P,i}$ (where P_T is the total number of predators present in the system across all patches at ending time T). We analyzed how these means varied with model parameters using MATLAB's general linear model fitting function (`glmfit`). To model non-linear shifts in evolved values with `glmfit`, we used an indicator variable that was set equal to zero for parameter values below a hypothesized threshold

and set equal to one for parameter values above the threshold.

Abundance fluctuations: time series analyses

Each simulation run generates long time series of data on distributions and abundances of predators, prey, and resources. To statistically explore the fluctuations in abundances over time and the potential coupling between fluctuations across species and across different patches, we used spectral and coherence analyses (Brillinger 2001). Spectral analysis provides a statistical characterization of an individual time series (e.g., whether or not abundance fluctuations over time are significantly different from white noise). Coherence analysis can be used to detect whether two time series (e.g., abundances of predators and prey) are significantly coupled. For spectral and coherence analyses, we examined the last 2^{15} ($= 32,768$) time steps of abundance data within patches of habitat. These time series were divided into 64 overlapping epochs of 1,024 time samples (with an overlap of 512 samples). So that statistical patterns could be examined and presented from many different simulation runs (rather than examining runs in isolation), we pooled spectra and coherence values across runs. Methods for pooling and for determining statistical significance of coherence values were derived from Amjad et al. (1997) and Brillinger (2001).

Results

In spite of incomplete knowledge, simple movement rules, and multiple sources of stochasticity constantly perturbing the system, the abundances of predators, prey, and resources within patches fluctuated around the optimal values predicted by IFD theory, and the median abundances in each patch were very close to the IFD (Fig. 2a–c, e–g). This was not true in the null model, in which predators were more uniformly distributed than the predicted IFD (Fig. 2i), prey were more aggregated than the IFD (Fig. 2j), and resource abundance was more uniform than the IFD (Fig. 2k). Additionally, in the full model, within patches there was an intuitive four-part cycle (with stochastic regularities) generated by the movements of individuals: prey increased \rightarrow predators increased \rightarrow prey decreased \rightarrow predators decreased and so on, and this cycle tended to oscillate around the ideal free distribution (Fig. 2d, h). By contrast, in the null model, such cycles were not observed (Fig. 2l).

The movement mechanisms that gave rise to these distributions evolved in unexpected ways: As model parameters were manipulated, there was an abrupt change akin to a phase shift observed in the evolved movement mechanisms. Two movement “regimes” are easily seen by looking at how movement mechanisms evolved for different values of the predator mortality rate, k_P (Fig. 3). For smaller values of k_P , we observed a “fast-prey” regime in which prey evolved very frequent movement ($\bar{\alpha}_V > 10^1$; Fig. 3a), and predators tended to evolve less frequent movement ($10^{-1} < \bar{\alpha}_P < 10^1$; Fig. 3a). However, as k_P was increased, there was a threshold, k_P^* , above which predators and prey qualitatively switched in their evolved movement frequencies ($k_P^* \approx 0.1$ in Fig. 3) resulting in a “slow-prey” regime: Predators evolved frequent movement (large $\bar{\alpha}_P$), and the prey evolved very infrequent movement ($\bar{\alpha}_V \approx 10^{-1}$). For the combination of parameter values shown in Fig. 3, the transition from the fast-prey regime to the slow-prey regime was characterized by a drop in $\bar{\alpha}_V$ of 1.9 orders of magnitude (general linear model (GLM): $t = -8.28$, $p < 10^{-12}$, $SE = 0.23$, $df = 94$,

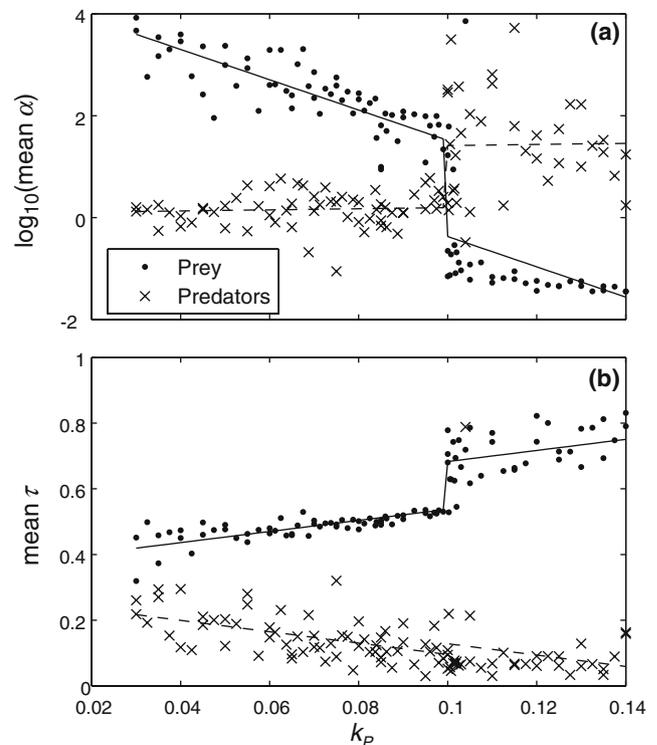


Fig. 3 Linear trends and phase shifts in the evolution of movement traits in the full model. Each point is a value of **a** $\bar{\alpha}_P$ or $\bar{\alpha}_V$, or **b** $\bar{\tau}_P$ or $\bar{\tau}_V$ within a population of predators or prey present at the end of one simulation run. Data are from 97 simulation runs with identical parameter values (except k_P). Lines (solid for prey, dashed for predators) are fits from general linear models (see text)

$N = 97$ simulation runs) and an increase in $\bar{\alpha}_P$ of 1.2 orders of magnitude (GLM: $t = 5.49$, $p < 10^{-6}$, $SE = 0.22$, $df = 94$, $N = 97$). $\bar{\tau}_V$ also shifted significantly at k_P^* : In the transition from the fast-prey to the slow-prey regime, $\bar{\tau}_V$ increased by 0.15 (GLM: $t = 9.58$, $p < 10^{-14}$, $SE = 0.015$, $df = 94$, $N = 97$; Fig. 3b). While $\bar{\tau}_P$ did not show a significant shift at k_P^* , it did show a significant linear decline over the entire range of k_P (GLM: $t = -3.44$, $p < 0.0009$, $SE = 0.50$, $df = 94$, $N = 97$; Fig. 3b).

The prediction of the two regimes in the full model was robust to variation in parameter values. Changing parameters could shift the location of k_P^* , but did not change the existence of fast-prey and slow-prey regimes. For example, making conditions harsher for predators by increasing handling time, t_P , or decreasing conversion efficiency, e_P , reduced the value of k_P^* (data not shown). By contrast, only a single regime (i.e., only linear trends) was observed in the null model in the evolved values of \bar{d}_P and \bar{d}_V (Fig. 4).

The two regimes displayed in the evolution of movement parameters provided the opportunity to examine the effects of different adaptive behaviors on population dynamics at all three trophic levels. Hence, to characterize these effects, we pooled power spectra and coherence values from runs of the full model into two different categories: (a) runs with $k_P \leq 0.095$ (34 runs) and (b) runs with $k_P \geq 0.105$ (13 runs). We compared these sets of runs to each other and to pooled results from sets of runs from the null model (i.e., the version lacking conditional movement) with corresponding ranges of k_P .

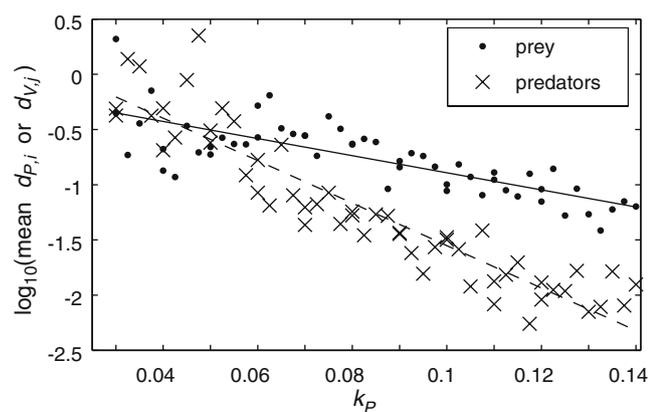


Fig. 4 Mean evolved values of $d_{P,i}$ and $d_{V,j}$ in the null model as a function of k_P . Each point is a value of \bar{d}_P or \bar{d}_V measured at the end of one simulation run (total of 55 independent runs with varying values of k_P). Lines are fits from general linear models (predators: dashed line, $\log_{10} \bar{d}_P = 0.37 - 19.22k_P$, $t = -17.88$, $p < 10^{-23}$, $SE = 1.08$, $df = 53$; prey: solid line, $\log_{10} \bar{d}_V = 0.62 - 4.66k_P$, $t = -9.03$, $p < 10^{-11}$, $SE = 0.86$, $df = 53$)

Examination of within-patch abundance time series revealed two findings of general interest. First, in the null model, all time series displayed $1/f$ (power-law) decay in their power spectra (Fig. 5, dotted lines). This is a widespread property of systems with complex dynamics, and its significance is discussed elsewhere (Bak et al. 1987; Halley 1996; Rikvold 2009). However, adaptive behavior produced marked departures from this statistical pattern. In the fast-prey regime (solid

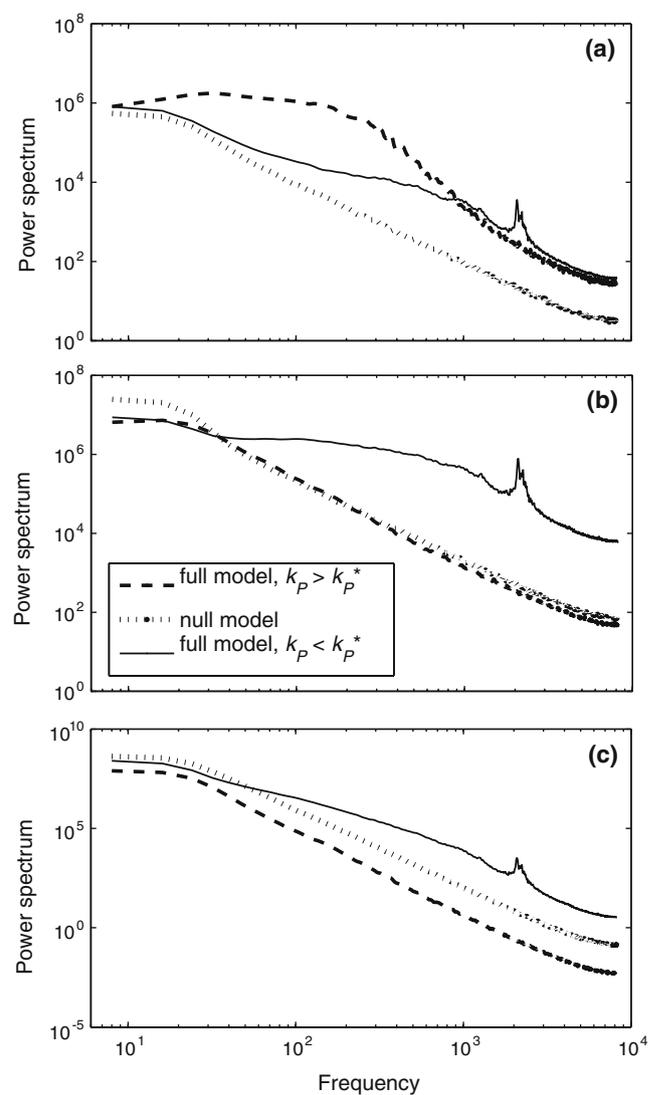


Fig. 5 Pooled power spectra for within-patch abundance time series for **a** predators, **b** prey, and **c** resources. Spectra shown are averages for three sets of simulation runs (all with parameter values as in Table 1): dashed lines = full model with adaptive behavior in the slow-prey regime, pooled over 13 independent simulation runs; solid lines = full model with adaptive behavior in the fast-prey regime, pooled over 34 runs; dotted lines = null model, pooled over 26 runs. Time series were from patch #7 (arbitrarily chosen; patterns from other patches are qualitatively similar)

lines in Fig. 5), there was a local peak in the power spectra at relatively high frequencies, corresponding to the very frequent movements made by prey (i.e., very large $\bar{\alpha}_V$). This peak was seen not only in the spectra of prey abundance but also in the abundance spectra of both predators and resources (Fig. 5). By contrast, in the slow-prey regime (dashed lines in Fig. 5), power law decay—like that in the null model—was seen in both prey and resource spectra (Fig. 5b, c), but the predator

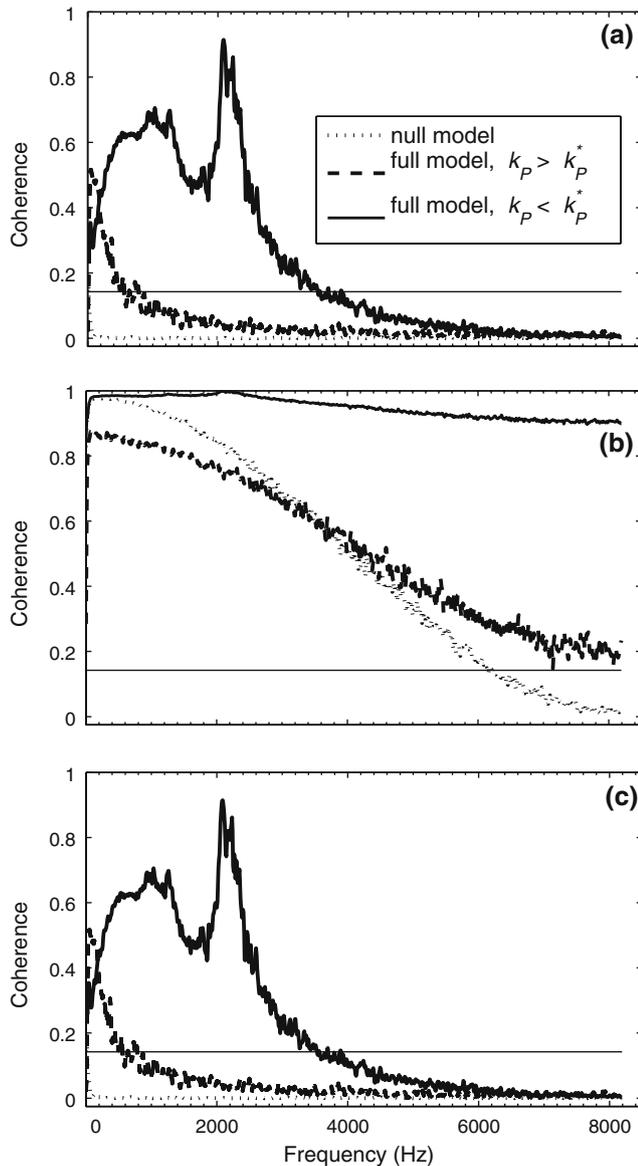


Fig. 6 Pooled coherence analyses of within-patch abundance time series demonstrate correlations in the fluctuations of **a** predators and prey, **b** prey and resources, and **c** predators and resources. Values of coherence above the *solid horizontal line* are significant at the 99% confidence level. Data used, pooling, and lines are as in Fig. 5

spectra showed a broad peak in power over a wide range of lower frequencies (Fig. 5a). The latter was attributable to the increased frequency of movement by predators in the slow-prey regime (as compared to the fast-prey regime; see Fig. 3a).

Second, conditional movement behavior was a causal mechanism that coupled spatial and temporal dynamics of interacting species, both within a patch and across patches. The only significant coupling of abundance dynamics in the null model was for prey and resources within a patch (Fig. 6b, dotted line). By contrast, in both regimes of the full model, conditional movements coupled within-patch abundance dynamics in all pairwise comparisons among the three trophic levels. Prey and resource fluctuations were significantly correlated over the entire frequency range in both regimes (Fig. 6b). Predator–prey and predator–resource couplings were the strongest in the fast-prey regime (solid lines, Fig. 6a, c), but are also significant at low frequencies in the slow-prey regime (dashed lines, Fig. 6a, c). In the fast-prey regime, all pairwise comparisons among the three trophic levels also showed significant coupling between adjacent patches (e.g., predators in patch n with prey in patch $n - 1$; Fig. 7). Significant between-patch couplings in the slow-prey regime were only present at the lowest frequencies or not at all; no significant between-patch couplings were found for the null model (data not shown).

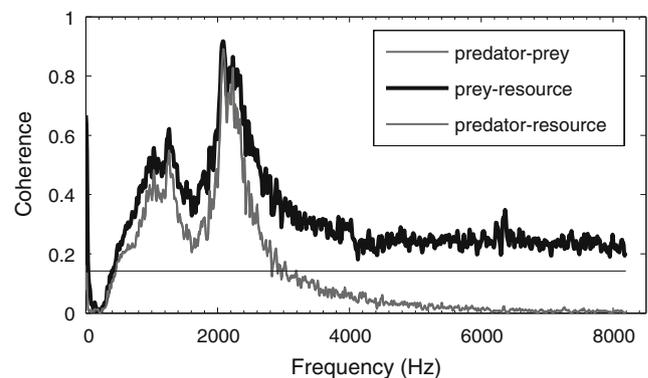


Fig. 7 Coherence analyses of between-patch abundance time series in the fast-prey regime of the full model. The plot displays the pooled values (34 simulation runs) of coherence between predators in patch 7 and prey in patch 6, predators in patch 7 with resources in patch 6 (both shown by the *thin, gray line*), and prey in patch 7 with resources in patch 6 (*thick black line*). Values of coherence above the *solid horizontal line* are significant at the 99% confidence level at a given frequency. What appears as a single, *thin gray line* represents both the predator–prey and predator–resource coherence values because the values were nearly identical

Discussion

Recent reviews of predator–prey interactions, habitat selection, and IFDs (Křivan et al. 2008; Lima 2002; Sih 2005) have highlighted a lack of investigations that (1) elucidate connections between adaptive behaviors and ecological dynamics, (2) connect time scales from individual behavior to evolutionary change, and (3) add sufficient biological realism in the form of trophic levels, underlying mechanisms, and the nature of (limited) information use. We have formulated a model that addresses these gaps in order to study how generalized movement mechanisms should evolve and how these movement mechanisms shape and respond to ecological dynamics.

Previous theory on a single species considered in isolation has shown that even consumers with occasional suboptimal movement (i.e., movement in the direction of lower fitness) can achieve IFDs if they also have conditional movements that balance out the suboptimal movements (Křivan et al. 2008; McPeck and Holt 1992). Our results generalize these findings to a tritrophic system: Simple mechanisms, when allowed to evolve, overcame the limitations of incomplete information, conflicting interests, and random (suboptimal) movements. While abundances within patches fluctuated continuously, in the full model with conditional movements, average spatial distributions were very close to the IFD. This was true in both evolutionary regimes of the full model, but not in the null model.

These results were by no means expected or foregone conclusions. By contrast, a number of previous models (discussed above; see also reviews by Křivan et al. 2008 and Lima 2002) have predicted the failure of predator–prey systems to achieve IFDs and have called into question whether evolutionarily stable movement mechanisms may even exist when one considers multiple species simultaneously. Our results are all the more surprising given that a number of previous works have also found that the (realistic) type II functional responses (Holling 1959) we modeled will tend to destabilize dynamics (Křivan et al. 2008). To be sure, distributions in our model fluctuate continuously, but these fluctuations happen in an intuitive way around the IFD (Fig. 2d, h) as one would expect for a system that is near an equilibrium but is constantly perturbed by multiple sources of stochasticity. Furthermore, starting with random initial populations, the movement mechanisms evolved in predictable ways: The results shown in Fig. 3 suggest that either of two evolutionary attractors for predator and prey movement mechanisms may exist, with the observed attractor dependent upon demographic parameters.

What explains the existence of the two evolutionary regimes (Fig. 3), in which prey either move very frequently or very rarely (and predators do the reverse of the prey)? Intuitively, very frequent movements (large $\alpha_{V,j}$) help the prey avoid predators but also produce dense aggregations in patches with relatively low predator-to-resource ratios. Compared to the slow-prey regime (Fig. 2f, h), within-patch abundances of prey in the fast-prey regime (Fig. 2b, d) deviate significantly more from the IFD (ANOVA comparing deviations from IFD in Fig. 2b, f: $F_{79,998}^1 = 9,583.1$, $p < 10^{-15}$). As such, once predation risk is sufficiently reduced (i.e., k_P increased above k_P^*), prey shift to infrequent movements (small $\alpha_{V,j}$), enabling individuals to stay closer to the IFD and minimize costly exploitative competition. Infrequent movements and a lack of response to the distribution of predators are often assumed to be constraints upon prey, yet our results show that, counterintuitively, such behaviors may actually be outcomes of adaptive evolution. Our results also offer testable predictions about why, in nature, some prey species are relatively sedentary and unresponsive to the distribution of predators, while other prey are nearly constantly on the move. Namely, in comparative studies, we should observe that relatively sedentary prey species face lower overall predation risk than prey species which are constantly on the move. We should also observe that predators of relatively sedentary prey should be more sensitive to the distribution of their prey and switch patches more frequently in response to prey than predators of more mobile prey. Our future research will use comparative meta-analyses to test these predictions.

The model also provides predictions about the consequences of adaptive behavior for the dynamics of populations. The $1/f$ noise (power law decay) we observed in abundance time series (Fig. 5) is a common property of power spectra from ecological time series (Halley 1996). $1/f$ noise can be created by very different physical processes: fractal renewal processes, interrupted and perennial aging processes, nonlinear stochastic differential equations, and superposition of many relaxation processes (Eliazar and Klafter 2010). In the context of evolutionary ecology, power laws have been observed with species-based and individual-based models of coevolution (e.g., Caldarelli et al. 1998; Laird et al. 2008; Rikvold and Zia 2003; Rikvold 2009) and have been interpreted as the presence of self-organized criticality (Bak et al. 1987). In our results, there is a direct interpretation in the time domain: The $1/f$ decay indicates that there is a long-time correlation of the abundances of across several decades of generations. This dependence becomes weaker the farther into the

future one goes, due to the stochasticity in the system (Halley 1996; Keshner 1982).

While $1/f$ noise was seen over most of the frequency range in the null model, conditional movements (full model) produced marked departures from it (Fig. 5). The biologically significant conclusion here is that time series of abundances, without observations of movement per se, provide detectable signatures of the occurrence of adaptive, conditional movements. The presence or absence of such signatures in time series could potentially be used as a way to identify the relevant time scale of dispersal or migration events, even without observing those events.

Additionally, evolved, conditional movements coupled population dynamics across species and space: In the null model, fluctuations of prey and resources within a patch were correlated, but no other significant correlations in abundance fluctuations were found (Fig. 6). By contrast, in the full model, all within-patch pairwise comparisons (predator–prey, prey–resource, and predator–resource) show significant correlations of abundance fluctuations (Fig. 6). Adaptive, conditional movements also coupled dynamics across patches in the fast-prey regime (Fig. 7). Consistent with previous work, these results show that movement behaviors play a key role in shaping ecological dynamics across space and time (e.g. Gouhier et al. 2010), specifically by coupling the dynamics of multiple species, even species that do not directly interact (e.g., predators and resources). Furthermore, the model offers testable predictions about the signatures of adaptive behaviors in ecological dynamics.

Our model provides several unanticipated, general predictions about the ecological and evolutionary outcomes of predator–prey interactions. Furthermore, while previous work (reviewed by Sih 2005) has long debated whether predators or prey should “win” the evolutionary race between the two, our results show that (a) movement mechanisms can evolve that allow both species to achieve optimal habitat use and (b) either species may evolve to dominate the movement dynamics of the system (i.e., prey movements dominate the short time scale in the fast-prey regime; predator movements dominate in the slow-prey regime).

Acknowledgements We thank V. Krivan, P. Abrams, R. J. Safran, and an anonymous reviewer for feedback on manuscript drafts and participants of the Fields Institute Workshop on Adaptive Movement of Interacting Species for comments on an earlier version of the model. We thank R. J. Safran for use of computing equipment and W. Franz for logistical support. The research of YL was partially supported by a grant from the National Science

Foundation. We also wish to thank Alan Hastings for organizing this special issue of *Theoretical Ecology* in honor of Simon Levin and in recognition of Simon’s vast and important contributions as a researcher, collaborator, and mentor.

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