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EVOLUTION OF MOBILITY IN PREDATOR-PREY SYSTEMS

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ABSTRACT. We investigate the dynamics of a predator-prey system with the assumption that both prey and predators use game theory-based strategies to maximize their per capita population growth rates. The predators adjust their strategies in order to catch more prey per unit time, while the prey, on the other hand, adjust their reactions to minimize the chances of being caught. We assume each individual is either mobile or sessile and investigate the evolution of mobility for each species in the predator-prey system. When the underlying population dynamics is of the Lotka-Volterra type, we show that strategies evolve to the equilibrium predicted by evolutionary game theory and that population sizes approach their corresponding stable equilibrium (i.e. strategy and population effects can be analyzed separately). This is no longer the case when population dynamics is based on the Holling II functional response, although the strategic analysis still provides a valuable intuition into the long term outcome. Numerical simulation results indicate that, for some parameter values, the system has chaotic behavior. Our investigation reveals the relationship between the game theory-based reactions of prey and predators, and their population changes.

1. Introduction. In this work, we investigate a prey-predator system with the assumption that both prey and predators adjust their foraging modes to maximize their individual fitness. Huey and Pianka [24] stressed the importance of different foraging modes on species' ecological niche. They distinguish two end-points of foraging modes: ambush ("sit-and-wait strategy") and active ("widely foraging"). In their seminal article, they proposed including these foraging modes in models of optimal foraging (e.g. [9, 29, 36, 38]) that predict diet composition of a predator depending on the prey available and their ecological characteristics. Optimal foraging theory assumes that individuals maximize their net food intake rate which is a proxy of their fitness. The net food intake rate is proportional to the resource uptake rate, thus to the functional response. In the simplest case of the Lotka–Volterra resource-consumer models the functional response is a linear function of prey density with the proportionality constant that measures the per prey encounter rate of

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a searching predator. Alternative nonlinear functional responses were developed by Holling [23].

To understand the effect of a foraging mode on food intake rate, one has to describe the relation between the foraging mode and the prev encounter rate. Several authors derived functional dependencies of prey encounter rate on predator and prev velocities [37, 40, 41]. Provided predator and prev movement is non-directional (i.e., random) these dependencies predict that the encounter rate increases both with prey as well as predator movement velocity. In other words, from the predator perspective, it is beneficial to move as fast as possible, but from the prey perspective the best strategy is not to move at all. Thus, from this perspective, predators should be active and widely foraging, while prey should be sit-and-wait foragers. On the other hand, Scharf et al. [33] modeled a situation where animal movement is non-random, but correlated, as often observed in nature. These authors showed that, if predators move slower than prey as originally proposed by Huey and Pianka [24], it is better to be a sit-and-wait predator. They also showed that active predators have a higher prey encounter rate than sit-and-wait predators, but only when predator movement is non-directional. For example, when predator movement is directional and prey movement non-directional, sit-and-wait predators will get a higher encounter rate with prev when compared to active predators. These results show that the encounter rate is not a simple increasing function of prey and predator velocities once their movement is non-random.

Schmitz [34] considered three hunting modes: sit-and-wait in which an ambush predator remains at a given location for long periods; sit-and-pursue where the predator after attacking a prev usually returns to its location (or, if prev are scarce, they move to a new location); and active hunting mode where predators are continuously on the prowl seeking prey. Other predator and prey modes were defined relative to the portion of habitat they share. If the prey and/or predators share the habitat with predators, then they have a "narrow domain"; otherwise (i.e. if they use different habitats) they are classified as having a "broad" domain. Based on this classification, Schmitz et al. [35] hypothesized that when prey have a narrow domain, they should reduce the time during which they are active for any predator hunting mode. On the other hand, when prey have the possibility of escaping predators (i.e., when they have the broad domain), their optimal strategy is to move to another habitat when predators have a narrow domain, while for broad predator domain use they should show no behavioral response when predators are active hunters, while for sit-and-pursue predators, prev should decrease their activity or escape to a different habitat.

To investigate the effects of different foraging modes, we assume that the predators have two foraging strategies called the mobile (active) strategy and the sessile (ambush) strategy. We also assume that prey are either mobile or sessile and then examine how these predator and prey strategies evolve in the predator-prey system and how this evolution affects the population dynamics (i.e. the changes in predator and prey densities).

Since the results in the preceding three paragraphs show that the prey encounter rate is not always a simple increasing function of prey and predator velocities, we cannot *a priori* expect that all predators will be mobile and prey sessile. Section 2 develops our model that combines strategy evolution with population dynamics where the latter is assumed to be a Gause-type predator-prey interaction [18, 22] with predator functional response either linear or the Holling type II. Sections 3 and

4 analyze the model for these respective two types of functional responses, paying particular attention to predictions of the eventual foraging mode. The results are discussed in Section 5 as well as summarized in tabular form there.

2. The model. The underlying predator-prey dynamics is modelled by the Gause model

$$\begin{aligned} \dot{x} &= xr(x) - yF(x) \\ \dot{y} &= -\mu y + cyF(x) \end{aligned}$$
(1)

where x is the prey population density and y is predator density. Here r(x) is the per capita growth rate of the prey population in the absence of predators (i.e. the average fitness of an individual prey) and F(x) is the number of prey killed by one predator per unit time (i.e. the functional response). The death rate of predators is μ and c is the conversion factor that expresses the predator's fitness increase due to one prey killed.

In this article, we assume that the prey population exhibits logistic growth (i.e. $r(x) = rx\left(1 - \frac{x}{K}\right)$ where r is the intrinsic growth rate and K is the carrying capacity) and that functional responses are either linear or Holling type II. That is, either $F(x) = \alpha x$ where α is the predator foraging efficiency (corresponding to a Lotka-Volterra predator-prey model) or $F(x) = \frac{\alpha x}{1 + \alpha hx}$ where h is the handling time of one prey that is captured (corresponding to the Rosenzweig and MacArthur [31] model).

Moreover, we consider two extreme cases of foraging modes: individual predators and prey are either fully mobile or fully sessile. To include interspecific strategic effects of mobility, let θ_x and θ_y respectively denote the proportions of prey and predators that are using their mobile strategy at a particular time. Obviously, the proportions of prey and predators that are sessile are then given by $1 - \theta_x$ and $1 - \theta_y$, respectively. Also, let α_{MM} and α_{MS} denote the foraging efficiencies (also called interaction strengths) of the mobile predator chasing mobile prey and sessile prey, respectively. That is, α_{MM} and α_{MS} describe the effectiveness of the mobile predator strategy in terms of the prey strategy. Similarly, the foraging efficiencies of a sessile predator catching mobile and sessile prey are α_{SM} and α_{SS} , respectively. Table 1 summarizes these strategic effects that are then incorporated into the predator-prey dynamics (1) in the remainder of this section.

			Prey	
		Mobile	Sessile	
Predator	Mobile	α_{MM}	α_{MS}	
	Sessile	α_{SM}	α_{SS}	

TABLE 1. Predator foraging efficiency. For example, the entry α_{MS} is the interaction strength when a mobile (M) predator encounters a sessile (S) prey.

If θ_x and θ_y are the current mobile proportions in the system, then the expected number of prey killed per unit time by a randomly selected predator, $F(x; \theta_x, \theta_y)$, is given by

$$F(x;\theta_x,\theta_y) = \theta_y \left[F_{MM}(\theta_x x) + F_{MS}((1-\theta_x)x)\right] + (1-\theta_y) \left[F_{SM}(\theta_x x) + F_{SS}((1-\theta_x)x)\right]$$
(2)

where F_{AB} is the functional response of a predator using strategy A when prey use strategy B with $A, B \in \{M, S\}$. For example, $F_{MS}((1-\theta_x)x)$ equals $\alpha_{MS}(1-\theta_x)x$ for the Lotka-Volterra (LV) model and $\frac{\alpha_{MS}(1-\theta_x)x}{1+\alpha_{MS}h(1-\theta_x)x}$ for the Rosenzweig-MacArthur (RM) model. The population dynamics is then given by (1) with F(x) replaced by $F(x; \theta_x, \theta_y)$.

Notice that, under this dynamics, mobility does not affect either the logistic growth r(x) of the prey or the death rate μ of the predator. That is, the only difference in fitness of being mobile compared to being sessile is a result of predation. Coevolutionary systems where r(x) and/or μ depend on the level of mobility are also important to study since there are other trade-offs associated with these foraging modes. For example, prey have to trade-off their safety from predation to food acquisition. Similarly, predators trade-off their active hunting strategy to increased predation risk by their own predators. The effects of such trade-offs were studied especially in the context of plasticity of predator and/or prey activity level (e.g. [1, 7, 8, 26, 27]). For example, in the Lotka–Volterra predator-prev model where activity levels of both prey and predators are plastic traits, it is optimal for prey to be maximally active when predators are at low numbers and inactive when predators are abundant. Similarly, predators should be active when prey numbers are high enough and inactive when rare. In other models where functional responses are nonlinear functions of prey/predator activity levels, intermediate activity levels can be optimal (e.g. [1, 27]). Such other trade-offs are beyond the scope of this paper.

Whether these other trade-offs are included or not, the predators (respectively, prey) will also be adjusting their behaviors depending on how successful their strategies are in catching prey (respectively, avoiding capture). To model these effects, we assume that the proportion of mobile individuals in each population is evolving in the direction to maximize its per capita growth rate. A general class of strategy dynamics that satisfy this assumption are the monotone selection dynamics ([10, 32]). When a population has two strategies (as in our case), these dynamics increase the proportion of the population using the strategy that currently has the higher individual fitness. In this paper, we will consider two such dynamics.

The first is the standard replicator equation [21] given by $\dot{\theta}_y = \theta_y (1 - \theta_y) (W_M - W_S)$ where W_M (respectively, W_S) is the fitness of a mobile (respectively, sessile) predator due to predation together with the analogous expression for $\dot{\theta}_x$ in terms of the difference between the fitness of mobile and sessile prey due to predation. For instance, if the individual fitness of a mobile predator due to predation (W_M) is greater than that of a sessile predator (W_S) , then the proportion of mobile predators (θ_y) will increase. From the notation introduced above,

$$W_M \equiv c \left(F_{MM}(\theta_x x) + F_{MS}((1 - \theta_x) x) \right)$$

and

$$W_S \equiv c \left(F_{SM}(\theta_x x) + F_{SS}((1 - \theta_x) x) \right).$$

The probability per unit time that an individual mobile prey is killed by a mobile predator and by a sessile predator are $F_{MM}(\theta_x x) \frac{\theta_y y}{\theta_x x}$ and $F_{SM}(\theta_x x) \frac{(1-\theta_y)y}{\theta_x x}$, respectively. From the analogous expressions for sessile prey, the prey fitness difference between these two strategies due to predation is $-F_{MM}(\theta_x x) \frac{\theta_y y}{\theta_x x} - F_{SM}(\theta_x x) \frac{(1-\theta_y)y}{\theta_x x} +$

 $F_{MS}((1-\theta_x)x)\frac{\theta_y y}{(1-\theta_x)x} + F_{SS}((1-\theta_x)x)\frac{(1-\theta_y)y}{(1-\theta_x)x}$. Thus, the strategy dynamics corresponding to the replicator equation becomes

$$\dot{\theta}_{x} = u\theta_{x}\left(1-\theta_{x}\right)\left[-\frac{F_{MM}(\theta_{x}x)\theta_{y}y}{\theta_{x}x} - \frac{F_{SM}(\theta_{x}x)(1-\theta_{y})y}{\theta_{x}x} + \frac{F_{MS}((1-\theta_{x})x)\theta_{y}y}{(1-\theta_{x})x} + \frac{F_{SS}((1-\theta_{x})x)(1-\theta_{y})y}{(1-\theta_{x})x}\right]
\dot{\theta}_{y} = v\theta_{y}\left(1-\theta_{y}\right)\left[c\left(F_{MM}(\theta_{x}x) + F_{MS}((1-\theta_{x})x)\right) - c\left(F_{SM}(\theta_{x}x) + F_{SS}((1-\theta_{x})x)\right)\right].$$
(3)

Here, u and v are positive parameters that denote the sensitivity of the prey and predator species to their fitness differences, respectively. They also indicate the time scale between the population process (1) and the behavioral process (3). In particular, if u and v are both large, then strategic effects occur on a much faster time scale than changes in population sizes. Conversely, if u and v are close to 0, population sizes evolve faster than the evolutionary time scale describing foraging patterns.

The second strategy dynamics that we consider has the form

$$\dot{\theta}_y = \theta_y \left(1 - \theta_y\right) \frac{e^{nW_M} - e^{nW_S}}{\theta_y e^{nW_M} + (1 - \theta_y) e^{nW_S}} = \frac{\theta_y e^{nW_M}}{\theta_y e^{nW_M} + (1 - \theta_y) e^{nW_S}} - \theta_y.$$
(4)

Here, the parameter n indicates how quickly the predator adjusts its foraging mode in the direction of its current best response. From W_M and W_S above and analogous expressions for prey fitnesses, this strategy dynamics is

$$\dot{\theta}_{x} = \frac{\theta_{x}e^{m\left(-\frac{F_{MM}(\theta_{x}x)\theta_{y}y}{\theta_{x}x} - \frac{F_{SM}(\theta_{x}x)(1-\theta_{y})y}{\theta_{x}x}\right)}}{\theta_{x}A + (1-\theta_{x})B} - \theta_{x}$$

$$\dot{\theta}_{y} = \frac{\theta_{y}e^{nc\left(F_{MM}(\theta_{x}x) + F_{MS}((1-\theta_{x})x)\right)}}{\theta_{y}e^{nc\left(F_{MM}(\theta_{x}x) + F_{MS}((1-\theta_{x})x)\right)} + (1-\theta_{y})e^{nc\left(F_{SM}(\theta_{x}x) + F_{SS}((1-\theta_{x})x)\right)}} - \theta_{y},$$

$$(5)$$

where

$$A \equiv e^{m\left(-\frac{F_{MM}(\theta_x x)\theta_y y}{\theta_x x} - \frac{F_{SM}(\theta_x x)(1-\theta_y)y}{\theta_x x}\right)}$$

and

$$B \equiv e^{m\left(-\frac{F_{MS}((1-\theta_x)x)\theta_y y}{(1-\theta_x)x} - \frac{F_{SS}((1-\theta_x)x)(1-\theta_y)y}{(1-\theta_x)x}\right)}.$$

For $0 < \theta_y < 1$, the predator strategy dynamics approaches $\dot{\theta}_y = 1 - \theta_y$ (respectively, $\dot{\theta}_y = -\theta_y$) as $n \to \infty$ if mobile predators have higher fitness (respectively, lower fitness) than sessile predators and so the proportion of mobile predators is evolving toward $\theta_y = 1$ (respectively, $\theta_y = 0$). This limiting dynamics is known as the best response dynamics and, for this reason, we will call the monotone selection dynamics (5) the smoothed best response dynamics.¹ In (5), *m* and *n* take the role of *u* and *v* in (3) respectively.

Dynamics similar to the smoothed best response were introduced by Abrams [2] to model behavioral evolution in predator-prey systems (see also [3] and [4] where it is also argued these dynamics are more suitable than the replicator equation in these situations). The replicator equation (3) and the smoothed best response

¹Smoothed best response dynamics are also introduced by Fudenberg and Levine [17] when individuals make strategy choices based on observing perturbed fitness. The primary example [20] of such a dynamics, $\dot{\theta}_y = \frac{e^{nW_M}}{e^{nW_M} + e^{nW_S}} - \theta_y$, is quite similar to (4) but not a monotone selection dynamics. We will follow [20] by referring to this dynamics as the perturbed best response.

dynamics (5) have the same equilibria. These are when all individuals in each population have the same strategy (e.g. all predators are mobile and all prey sessile corresponding to the monomorphic equilibrium $(\theta_x, \theta_y) = (0, 1)$) or when one or both populations are not monomorphic (e.g. there are some mobile and some sessile predators corresponding to a mixed equilibrium predator population $0 < \theta_y < 1$ for which $W_M = W_S$). If one of these equilibria is stable,² it will predict the eventual foraging mode of the predator-prey system. Otherwise, we can expect more complicated non equilibrium behavior whereby predator and/or prey strategies oscillate over time.

3. The Lotka-Volterra model. For the LV model, substituting $F_{AB}(x) = \alpha_{AB}x$ into (1), (2) and (3) yields the following population density dynamics

$$\dot{x} = rx\left(1 - \frac{x}{K}\right) - \alpha_{MM}\theta_{y}y\theta_{x}x - \alpha_{MS}\theta_{y}y\left(1 - \theta_{x}\right)x$$

$$-\alpha_{SM}\left(1 - \theta_{y}\right)y\theta_{x}x - \alpha_{SS}\left(1 - \theta_{y}\right)y\left(1 - \theta_{x}\right)x$$

$$\dot{y} = -\mu y + c\alpha_{MM}\theta_{y}y\theta_{x}x + c\alpha_{MS}\theta_{y}y\left(1 - \theta_{x}\right)x$$

$$+c\alpha_{SM}\left(1 - \theta_{y}\right)y\theta_{x}x + c\alpha_{SS}\left(1 - \theta_{y}\right)y\left(1 - \theta_{x}\right)x$$
(6)

and (replicator) strategy dynamics

$$\dot{\theta}_x = u\theta_x \left(1 - \theta_x\right) \left(-\alpha_{MM}\theta_y y - \alpha_{SM} \left(1 - \theta_y\right) y + \alpha_{MS}\theta_y y + \alpha_{SS} \left(1 - \theta_y\right) y\right) \dot{\theta}_y = v\theta_y \left(1 - \theta_y\right) \left(c\alpha_{MM}\theta_x x + c\alpha_{MS} \left(1 - \theta_x\right) x - c\alpha_{SM}\theta_x x - c\alpha_{SS} \left(1 - \theta_x\right) x\right).$$

$$\tag{7}$$

For fixed positive densities x and y, (7) corresponds to a two-strategy zero-sum evolutionary game between two species [22] with payoff matrix given by Table 1. We first analyze this strategy dynamics in the following section before considering the four-dimensional co-evolutionary coupled system (6) and (7) in Section 3.2.

3.1. The strategy dynamics. The general analysis of a two-strategy zero-sum evolutionary game between two species can be classified into two types, depending on the relative sizes of the entries in Table 1 (specifically, on the comparison of the diagonal entries to the off diagonal entries).

If the off diagonal entries α_{MS} and α_{SM} are both larger than both diagonal entries α_{MM} and α_{SS} , then neither the predator nor the prey has a winning (also called a "dominant") strategy. In particular, the predator forages more efficiently if it has the opposite strategy to its prey and, conversely, prey are better able to avoid predation if they have the same strategy as the predator. Thus, if all prey are sessile, then it is optimal for the predator to be mobile and this, in turn, implies the prey should be mobile and so the predator is better off being sessile, etc. In game-theoretic terms, no pure strategy of either population is dominated, in which case the strategy-dynamics (7) is expected to cycle (as we will see below).

A similar argument shows that there is no dominated strategy when the off diagonal entries of Table 1 are both smaller than the diagonal entries (i.e. α_{MS} and α_{SM} are both smaller than α_{MM} and α_{SS}). This case is mathematically equivalent to the previous paragraph (e.g. the strategy-dynamics again cycle but in the opposite direction) but is of little interest biologically since it models such unrealistic scenarios as when sessile predators have a better chance of encountering sessile prey than

 $^{^{2}}$ In this article, "stability" refers to local asymptotic stability under the relevant dynamics.

mobile predators do.³ For this reason, the LV model where there is no dominated strategy will refer to the situation where

$$\alpha_{MS}$$
 and α_{SM} are both larger than α_{MM} and α_{SS} (8)

for the remainder of the paper. In this case, game theory predicts that evolution will lead to polymorphism, i.e., a mixture of sessile and mobile individuals.

The second type of evolutionary game is when there is a dominated strategy.⁴ We will concentrate on one particular case of a dominated strategy in what follows since there are analogous effects in the LV model (6) and (7) whenever there is a dominated strategy. For example, in all cases, the evolutionary outcome of the strategy dynamics will be a pure strategy for both predator and prey. As will become apparent in what follows, these results are also true when the smoothed best response strategy dynamics (11) replaces the replicator equation in (7).

3.1.1. The effect of a dominated strategy. Suppose a mobile predator has higher foraging efficiency than a sessile predator independent of the strategy of the prey (i.e. mobility is the dominant strategy for predators in that $\alpha_{MM} > \alpha_{SM}$ and $\alpha_{MS} > \alpha_{SS}$). From (7), the proportion of mobile predators is increasing (i.e. $\dot{\theta}_y \ge 0$) and will evolve to 1. Now, once θ_y is sufficiently close to 1, $\dot{\theta}_x$ is always positive (if $\alpha_{MM} < \alpha_{MS}$) or $\dot{\theta}_x$ is always negative (if $\alpha_{MM} > \alpha_{MS}$). These results are also true when the smoothed best response strategy dynamics replaces the replicator equation in (7).

Suppose $\alpha_{MM} > \alpha_{MS}$. We are then in the situation considered by Yapp [41] where it is argued that predator-prey encounter rates increase whenever the predator or prey (or both) become more mobile. From the preceding paragraph, the only possible outcome of the strategy dynamics are that all predators are mobile and all prey are sessile (i.e. $\theta_y = 1$ and $\theta_x = 0$), agreeing with the conclusion reached in [41]. This conclusion also follows from the game-theoretic method called the iterated elimination of strictly dominated strategies. Here the sessile predator strategy is eliminated first by domination and then, in the remaining system where there are only mobile predators, the mobile prey are eliminated by strict domination. The strategy pair of mobile predators and sessile prey is called a strict Nash equilibrium (NE) of this game.

Unless otherwise specified, the model with a dominated strategy will refer to the situation where

$$\alpha_{MM} > \alpha_{SM}, \alpha_{MS} > \alpha_{SS} \text{ and } \alpha_{MM} > \alpha_{MS}, \tag{9}$$

i.e. where the winning strategy combination has all predators being mobile and all prey being sessile.

3.1.2. No dominated strategy. When foraging efficiencies satisfy (8), there are five equilibria of the replicator equation (7). These are the four pure-strategy pairs plus the equilibrium where both strategic behaviors are present for each species. In mathematical terms, the latter is an interior equilibrium $E = (\theta_x^*, \theta_y^*)$, with

³A more realistic assumption is that α_{SS} is the smallest entry in Table 1.

⁴It can be shown that, if none of the foraging efficiencies in Table 1 are equal (a condition we assume throughout the paper), then either there is no dominated strategy or at least one of the pure strategies of the predator or prey will be dominated.

 $0 < \theta_x^*, \theta_y^* < 1.$ From (7),

$$\theta_x^* = \frac{\alpha_{MS} - \alpha_{SS}}{\alpha_{SM} - \alpha_{MM} + \alpha_{MS} - \alpha_{SS}} \text{ and } \theta_y^* = \frac{\alpha_{SM} - \alpha_{SS}}{\alpha_{SM} - \alpha_{MM} + \alpha_{MS} - \alpha_{SS}}.$$
 (10)

In fact, (θ_x^*, θ_y^*) is the only NE for this frequency-dependent evolutionary game between predators and prey. In particular, with densities fixed at (x, y), no individual can increase its fitness by altering its strategy when the proportions of mobile prey and predators are given by θ_x^* and θ_y^* , respectively. However, the replicator strategy dynamics (7) does not converge to this NE. Instead, trajectories form neutrally stable cycles around (10) in the unit square ([22]; see also Figure 1a).

The smoothed best response dynamics

$$\dot{\theta}_x = \frac{\theta_x e^{m(-\alpha_{MM}\theta_y y - \alpha_{SM}(1 - \theta_y)y)}}{\theta_x e^{m(-\alpha_{MM}\theta_y y - \alpha_{SM}(1 - \theta_y)y) + (1 - \theta_x)e^{m(-\alpha_{MS}\theta_y y - \alpha_{SS}(1 - \theta_y)y)}} - \theta_x$$

$$\dot{\theta}_y = \frac{\theta_y e^{n(c\alpha_{MM}\theta_x x + c\alpha_{MS}(1 - \theta_x)x)}}{\theta_y e^{n(c\alpha_{MM}\theta_x x + c\alpha_{MS}(1 - \theta_x)x) + (1 - \theta_y)e^{n(c\alpha_{SM}\theta_x x + c\alpha_{SS}(1 - \theta_x)x)}} - \theta_y$$

$$(11)$$

has the same equilibria as (7) but now trajectories spiral inward to E at fixed population densities (Figure 1b). The intuition here is that the smoothed best response strategy dynamics has a more stabilizing effect than the replicator equation and this is reflected in the comparison of the trajectories shown in Figures 1a and 1b for the respective systems.⁵

3.2. The Lotka-Volterra system with strategy evolution. In this section, we analyze how the results of Section 3.1 for the strategy dynamics affect the four-dimensional co-evolutionary system where population densities are also evolving according to (6). That is, we analyze the four-dimensional dynamical system (6) and (7) when there is a dominated strategy first (Section 3.2.1) and then when there is not (Section 3.2.2).

3.2.1. The effect of a dominated strategy. From Section 3.1.1 where game-theoretic methods predict mobile predators and sessile prey, the proportion of mobile predators is increasing (i.e. $\dot{\theta}_y \geq 0$ if $0 < \theta_y < 1$) if there are prey present. In fact, x cannot evolve to 0 if there are some prey initially $(x \to 0 \text{ implies } (x, y) \to (0, 0)$ and this is impossible since (0, 0) is a saddle point equilibrium of (6)). Thus $\theta_y \to 1$. Once θ_y is sufficiently close to 1, $\dot{\theta}_x$ is always negative since $\alpha_{MM} > \alpha_{MS}$ and so either θ_x evolves to 0 or else y evolves to 0 (in which case x evolves to the carrying capacity K from (6)).⁶ These results are also true when the smoothed best response strategy dynamics replaces the replicator equation in (7).

From the preceding paragraph, the only possible outcomes of the population density and strategy dynamics (6) and (7) are either that all predators are mobile and all prey are sessile or else that the predators go extinct and the prey evolve to their carrying capacity.⁷ In the first case, any trajectory approaches one on the

⁵The global asymptotic stability of E under the smoothed best response is not surprising given that the same result holds for the perturbed best response [20].

⁶Now, y can in fact evolve to 0 as we see in Figure 2b. This is a common phenomenon of evolutionary games that include density effects (see, for example, [5]) in which event we cannot expect θ_x to evolve to 0.

⁷In the latter case, the limiting value of θ_y is irrelevant since there are no predators and the limiting value of θ_x can be anywhere between 0 and 1 depending on initial conditions.



FIGURE 1. Trajectories of the decoupled LV strategy and density dynamics when there is no dominant strategy. Panels (a) and (b) show clockwise trajectories of the replicator equation (7) and the smoothed best response dynamics (11) respectively with densities fixed at (x^*, y^*) given by E_1 in (15). Panel (c) shows the counterclockwise trajectory of the density dynamics (6) with strategies fixed at (θ_x^*, θ_y^*) given by E in (10). Parameters: $\alpha_{SM} = 1.3$, $\alpha_{MS} = 1.5$, $\alpha_{SS} = 0.2$, $\alpha_{MM} = 0.2$, r = 2, K = 6, $\mu = 0.3$, c = 1, u = v = 1 and m = n = 20.

face with $\theta_x = 0$ and $\theta_y = 1$ where the dynamics is

$$\dot{x} = rx\left(1 - \frac{x}{K}\right) - \alpha_{MS}yx$$
$$\dot{y} = -\mu y + c\alpha_{MS}yx.$$

Clearly, this system has an interior equilibrium $(x, y) = \left(\frac{\mu}{c\alpha_{MS}}, \frac{r(c\alpha_{MS}K-\mu)}{c\alpha_{MS}^2K}\right)$ if and only if $\frac{\mu}{cK} < \alpha_{MS}$. Moreover, it is well-known [21] that this equilibrium is globally asymptotically stable if it exists; otherwise, (x, y) evolves to (K, 0).

In terms of our four-dimensional density-strategy dynamics (6) and (7), the equilibrium $(x, y, \theta_x, \theta_y) = \left(\frac{\mu}{c\alpha_{MS}}, \frac{r(c\alpha_{MS}K - \mu)}{c\alpha_{MS}^2K}, 0, 1\right)$ is globally asymptotically stable if it exists (i.e. if $\frac{\mu}{cK} < \alpha_{MS}$);⁸ otherwise, (x, y) evolves to (K, 0) and (θ_x, θ_y) evolves to a single point of the form $(\theta'_x, 1)$. In summary, when the mobile predator strategy dominates the sessile strategy (i.e. $\alpha_{MM} > \alpha_{SM}$ and $\alpha_{MS} > \alpha_{SS}$) and the sessile prey strategy does better than the mobile prey strategy when predators are mobile (i.e. $\alpha_{MM} > \alpha_{MS}$), the outcome of the predator-prey system is either the globally asymptotically stable equilibrium $\left(\frac{\mu}{c\alpha_{MS}}, \frac{r(c\alpha_{MS}K-\mu)}{c\alpha_{MS}^2K}, 0, 1\right)$ if it exists (Figure 2a) or, if not, a unique point on the equilibrium line with no predators and prey at carrying capacity (see Figure 2c and 2d). From the figure, we see that these results hold whether the replicator equation or the smoothed best response is used for the strategy dynamics. Analogous results emerge whenever there is a dominated strategy for either predator or prey.

That is, the behavioral effects and density effects can be separated to predict the eventual outcome no matter what the time scales of these two processes are (cf. [12]). Specifically, first fix the population densities and then the strategy dynamics evolves to the strategy found by game theory through the iterated elimination of dominated strategies (i.e. the strategy where all predators are mobile and all prey sessile, $(\theta_x, \theta_y) = (0, 1)$). Substitution of the strategy into the density dynamics results in a standard LV two-dimensional predator-prey system that evolves to an interior equilibrium if it exists or else to predator extinction. This final step (i.e. the analysis of the density dynamics) is the approach used by Křivan [26] who obtained the same result when prey logistic growth and predator mortality rates are independent of mobility.

The technical reason that the method of time scale separation determines the coevolutionary outcome is that the linearization of the four-dimensional LV system in Appendix A is upper block diagonal. However, as shown by Cressman and Křivan [12], a similar independence of time scales also emerges for two-patch LV predatorprey systems with dispersal (where strategies correspond to species' distributions between the patches) even though their linearizations are not upper block diagonal. What is common for both the dispersal model and the mobility model of this paper is that, for fixed population sizes, there is a unique stable strategy that specifies the behaviour of each species. This intuition is further strengthened by the analysis of a two-patch LV competitive system [12] where there is strategy bistability and time-scale separation does not work.

3.2.2. No dominated strategy. In this section, the equilibrium of most interest now is one where both strategic behaviors are present for each species. Biologically, there are two possible explanations. First, both populations become polymorphic with some individuals mobile and some sessile. This can be an onset of a speciation process leading eventually to the emergence of different species. Alternatively, proportions θ_x and θ_y can refer to animal behavioral modes, where these proportions are interpreted as the proportion of animal lifetime the individual is moving. In mathematical terms, this is an interior equilibrium $E_1 = (x^*, y^*, \theta_x^*, \theta_y^*)$, with $x^*, y^* > 0$ and (θ_x^*, θ_y^*) given by (10) as the interior NE of the frequency-dependent evolutionary game between predators and prey of Section 3.1.2 with densities fixed at (x^*, y^*) .⁹

Conversely, with the mobile proportions fixed at their equilibrium values θ_x^* and θ_y^* , $\alpha_{MM}\theta_x^*\theta_y^* + \alpha_{SM}\theta_x^* (1-\theta_y^*) + \alpha_{MS} (1-\theta_x^*) \theta_y^* + \alpha_{SS} (1-\theta_x^*) (1-\theta_y^*) =$

⁸See equilibrium E_2 in Section 3.2.2.

⁹This equilibrium cannot exist in Section 3.2.1 due to dominance.



FIGURE 2. Trajectories of the four-dimensional LV system when there is a dominated strategy. In panel (a), E_2 given by (17) exists since $\frac{\mu}{cK} < \alpha_{MS}$ (K = 6, $\mu = 0.3$, c = 1). In panels (b,c,d), E_2 does not exist since $\alpha_{MS} < \frac{\mu}{cK}$ (K = 1, $\mu = 0.9$, c = 0.4). Trajectories are shown for the system (6) with replicator strategy dynamics (7) for the projection on the x - y plane (a); the time history of y (b); the projection on the $x_1 - x_2$ plane (c). Here x_1 (respectively, x_2) is the number of mobile (respectively, sessile) prey. The trajectory of the LV system (6) with smoothed best response strategy dynamics (11) projected on the $x_1 - x_2$ plane (d). Other parameters: $\alpha_{SM} = 1.3$, $\alpha_{MS} = 1.5$, $\alpha_{SS} = 0.2$, $\alpha_{MM} = 1.6$, r = 2, u = v = 1 and m = n = 20.

 $\frac{\alpha_{MS}\alpha_{SM}-\alpha_{SS}\alpha_{MM}}{\alpha_{SM}-\alpha_{MM}+\alpha_{MS}-\alpha_{SS}}$. Thus, the population dynamics (6) becomes the following standard Lotka-Volterra predator-prey system

$$\dot{x} = rx\left(1 - \frac{x}{K}\right) - \alpha^* xy$$

$$\dot{y} = -\mu y + c\alpha^* xy$$
(12)

where

$$\alpha^* \equiv \frac{\alpha_{MS} \alpha_{SM} - \alpha_{SS} \alpha_{MM}}{\alpha_{SM} - \alpha_{MM} + \alpha_{MS} - \alpha_{SS}} > 0.$$
(13)

Provided the equilibrium prey density $x^* = \frac{\mu}{c\alpha^*}$ is less than the prey carrying capacity K, i.e.

$$\frac{\mu}{cK} < \alpha^*,\tag{14}$$

the interior equilibrium E_1 exists. Moreover, substitution of $\alpha^*, \theta_x^*, \theta_y^*$ and x^* into (12) yields

$$x^{*} = \frac{\mu}{c\alpha^{*}},$$

$$y^{*} = \frac{r}{\alpha^{*}} \left(1 - \frac{\mu}{cK\alpha^{*}}\right),$$

$$\theta^{*}_{x} = \frac{\alpha_{MS} - \alpha_{SS}}{\alpha_{SM} - \alpha_{MM} + \alpha_{MS} - \alpha_{SS}},$$

$$\theta^{*}_{y} = \frac{\alpha_{SM} - \alpha_{SS}}{\alpha_{SM} - \alpha_{MM} + \alpha_{MS} - \alpha_{SS}}.$$
(15)

It is well-known ([21]; see also Figure 1c) that the equilibrium E_1 is globally asymptotically stable for (12) with the mobile proportions fixed at their equilibrium values θ_x^* and θ_y^* in each population. When E_1 exists, the question is then whether the asymptotic stability of the density dynamics combined with the neutral stability of the replicator strategy dynamics in Section 3.1 leads to stability of the coupled system (6) and (7). The standard stability analysis through the linearized dynamics at E_1 is inconclusive since there are purely imaginary eigenvalues as shown in Appendix A1. This is not surprising given the neutrally stable cycles (Figure 1a) around (θ_x^*, θ_y^*) when densities are fixed at (x^*, y^*) . However, from extensive numerical simulations of the system, it appears that E_1 is globally asymptotically stable under the coupled system (6) and (7), although the convergence to E_1 can be quite slow (see the first four panels of Figure 3).¹⁰ Further evidence of the global asymptotic stability of E_1 is given in Appendix A2 where it is shown analytically that prey density must converge to x^* when u = v = 1 (i.e. when density and strategy dynamics evolve on the same time scale).

It is also instructive to consider the coupled system (6) and (11) with strategy dynamics given by the smoothed best response. From Section 3.1.2, when E_1 exists, this dynamics spirals inwards to it at fixed equilibrium densities (Figure 1b). Although the linearized dynamics of the coupled system (6) and (11) at E_1 remains inconclusive (see Appendix A2), simulations again show convergence to a globally asymptotically stable E_1 (see Figure 3e and 3f). The convergence here is faster than for the replicator equation since m = n = 20 was chosen in Figure 3e and 3f as compared to u = v = 1 (in the corresponding panels Figure 3b and 3c).

The coupled system (6) and (7) may also have equilibria where both predators and prey are present but the populations adopt pure strategies. Specifically, under the condition

$$\frac{\mu}{cK} < \alpha_{MS} \tag{16}$$

the coupled system (6) and (7) has the equilibrium

$$E_2 = \left(\frac{\mu}{c\alpha_{MS}}, \frac{r(c\alpha_{MS}K - \mu)}{c\alpha_{MS}^2 K}, 0, 1\right),$$
(17)

¹⁰The slow convergence to E_1 in our deterministic model means that stochastic effects due to finite population size or small perturbations in parameter values will keep the system from evolving exactly to E_1 . In fact, it is well-known that stochastic effects break the neutral stability when two-dimensional predator-prey systems (that do not include strategy considerations) exhibit cyclic behavior and that one of the species will eventually disappear from the system [6, 30]. Species and/or strategy extinction is also likely to occur in stochastic versions of our four-dimensional system, a topic that is beyond the scope of our paper.



FIGURE 3. Trajectories of the four-dimensional LV system when there is no dominated strategy and E_1 exists. The trajectory for (6) with replicator strategy dynamics (7) is shown as projected on the x - y plane (a); the time history of x (b); the time history of θ_x (c); the time history of θ_y (d). The trajectory of the LV system (6) with smoothed best response strategy dynamics (11) is illustrated by the time history of x (e) and the time history of θ_x (f). Parameters: $\alpha_{SM} = 1.3$, $\alpha_{MS} = 1.5$, $\alpha_{SS} = 0.2$, $\alpha_{MM} = 0.2$, r = 2, K = 6, $\mu = 0.3$, c = 1, u = v = 1 and m = n = 20.

where predators and prey coexist but adopt opposite strategies (i.e. all prey are mobile and all predators are sessile). The equilibrium E_2 is the one considered in Section 3.2.1 where it is globally asymptotically stable if it exists due to the

dominated strategy there. However, when there is no dominated strategy as assumed in this section, E_2 is unstable if it exists. For example, E_2 can be invaded by mobile prey (see Appendix A1). Other possible equilibria where predators and prey coexist are $E_3 = (\frac{\mu}{c\alpha_{SM}}, \frac{r(c\alpha_{SM}K-\mu)}{c\alpha_{SM}^2K}, 1, 0), E_4 = (\frac{\mu}{c\alpha_{SS}}, \frac{r(c\alpha_{SS}K-\mu)}{c\alpha_{SS}^2K}, 0, 0)$ and $E_5 = (\frac{\mu}{c\alpha_{MM}}, \frac{r(c\alpha_{MM}K-\mu)}{c\alpha_{MM}^2K}, 1, 1)$. None of these are stable either.

The only other equilibria of the coupled system (6) and (7) are when the predator population is extinct. These are when the prey population is at carrying capacity; namely,

$$E_{6} = (K, 0, \hat{\theta}_{x}, 0),$$

$$E_{7} = (K, 0, \hat{\theta}_{x}, 1),$$

$$E_{8} = (K, 0, \frac{\alpha_{MS} - \alpha_{SS}}{\alpha_{SM} - \alpha_{MM} + \alpha_{MS} - \alpha_{SS}}, \hat{\theta}_{y}),$$
(18)

where $\hat{\theta}_x$ and $\hat{\theta}_y$ take any value between 0 and 1. Finally, there is also the trivial equilibrium with no prey and predators $E_9 = (0, 0, \hat{\theta}_x, \hat{\theta}_y)$.

When E_1 does not exist, the simulations (see Figure 4) indicate the predators eventually go extinct and the prey evolve to carrying capacity (i.e. (x, y) evolves to (K, 0)) in that each trajectory evolves to one of the points in (18).



FIGURE 4. Trajectories of the LV system when there is no dominated strategy and E_1 does not exist. Projection of the trajectory on the $x_1 - x_2$ plane (where $x_1 = \theta_x x$ and $x_2 = (1 - \theta_x)x$ are the densities of mobile and sessile prey respectively) for the LV system (6) with replicator strategy dynamics (7) (panel (a)) and with smoothed best response strategy dynamics (11) (panel (b)). Parameters: $\alpha_{SM} = 1.3$, $\alpha_{MS} = 1.5$, $\alpha_{SS} = 0.2$, $\alpha_{MM} = 0.2$, r = 2, K = 1, $\mu = 0.6$, c = 0.5, u = v = 1 and m = n = 20.

Based on these analytic and numerical results, the eventual outcome again emerges by separating the behavioral and density effects. In particular, the strategy dynamics cycles inward toward (θ_x^*, θ_y^*) and; if E_1 exists, the density dynamics converges to (x^*, y^*) ; otherwise, it converges to predator extinction and to prey carrying capacity.

All the results of Section 3 for the four-dimensional LV system can be nicely summarized in terms of dominance effects and the strength of the interaction coefficients (i.e. the foraging efficiences). With weak interaction coefficients (i.e. $\alpha < \frac{\mu}{cK}$ where $\alpha = \alpha^*$ (respectively $\alpha = \alpha_{MS}$) without dominance (respectively, with dominance)), the system evolves to predator extinction and prey carrying capacity. For strong interaction coefficients, the system evolves to an equilibrium where predator and prey coexist with strategy distributions given by the stable equilibrium of the strategy dynamics (i.e. a mixed strategy (respectively, pure strategy) for each species without dominance (respectively, with dominance)). These results are also summarized in table form in the final Discussion section (see Table 2 there).

4. The Rosenzweig-MacArthur model. In this section, we consider the game between the prey species and predator species with Holling type II functional (behavioral) response. By substituting $F(x) = \frac{\alpha x}{1+\alpha hx}$, the population density and (replicator) strategy dynamics become

$$\dot{x} = rx\left(1 - \frac{x}{K}\right) - \frac{\alpha_{SM}\theta_x x(1-\theta_y)y}{\alpha_{SM}\theta_x xh+1} - \frac{\alpha_{MS}(1-\theta_x)x\theta_y y}{\alpha_{MS}(1-\theta_x)xh+1} - \frac{\alpha_{MM}\theta_x x\theta_y y}{\alpha_{MM}\theta_x xh+1} - \frac{\alpha_{SS}(1-\theta_x)x(1-\theta_y)y}{\alpha_{SS}(1-\theta_x)xh+1}$$

$$\dot{y} = -\mu y + \frac{c\alpha_{SM}\theta_x x(1-\theta_y)y}{\alpha_{SM}\theta_x xh+1} + \frac{c\alpha_{MS}(1-\theta_x)x\theta_y y}{\alpha_{MS}(1-\theta_x)xh+1} + \frac{c\alpha_{MM}\theta_x x\theta_y y}{\alpha_{MM}\theta_x xh+1} + \frac{c\alpha_{SS}(1-\theta_x)x(1-\theta_y)y}{\alpha_{SS}(1-\theta_x)xh+1}$$

$$(19)$$

$$\dot{\theta}_x = u\theta_x (1-\theta_x) \left(\frac{\alpha_{MS}\theta_y y}{\alpha_{MS}(1-\theta_x)xh+1} - \frac{\alpha_{SM}(1-\theta_y)y}{\alpha_{SM}\theta_x xh+1} + \frac{\alpha_{SS}(1-\theta_y)y}{\alpha_{SS}(1-\theta_x)xh+1} - \frac{\alpha_{MM}\theta_y y}{\alpha_{MM}\theta_x xh+1} \right)$$

$$(20)$$

$$\dot{\theta}_y = v\theta_y(1-\theta_y) \left(\frac{c\alpha_{MS}(1-\theta_x)x}{\alpha_{MS}(1-\theta_x)xh+1} - \frac{c\alpha_{SM}\theta_xx}{\alpha_{SM}\theta_xxh+1} + \frac{c\alpha_{MM}\theta_xx}{\alpha_{MM}\theta_xxh+1} - \frac{c\alpha_{SS}(1-\theta_x)x}{\alpha_{SS}(1-\theta_x)xh+1} \right).$$
(20)

We are particularly interested in the effect that the handling time h has on this four-dimensional co-evolutionary coupled system. For short handling time, the system will be close to that of the LV models of Sections 2 and 3 since, with h = 0, strategic effects are again linear in θ_x and θ_y and so (19) and (20) revert to (6) and (7). We follow the same procedure as in Section 3; namely, we start with the analysis of the strategy dynamics followed by the analysis of coupled system (19) and (20).

4.1. The strategy dynamics. For the strategy dynamics, assume that the prey and predator population sizes are fixed at positive values x and y respectively. We first examine the case of a dominated strategy with domination given by condition (9) where game theory predicts the evolutionary outcome of the LV system is mobile predators and sessile prey.

4.1.1. The effect of a dominated strategy. Since $\alpha_{MM} > \alpha_{SM}$ and $\alpha_{MS} > \alpha_{SS}$, $\frac{c\alpha_{MM}\theta_x x}{\alpha_{MM}\theta_x xh+1} > \frac{c\alpha_{SM}\theta_x x}{\alpha_{SM}\theta_x xh+1}$ and $\frac{c\alpha_{MS}(1-\theta_x)x}{\alpha_{MS}(1-\theta_x)xh+1} > \frac{c\alpha_{SS}(1-\theta_x)x}{\alpha_{SS}(1-\theta_x)xh+1}$ which implies that $\dot{\theta}_y > 0$. Thus, θ_y evolves to 1 (i.e. all predators are mobile). Then, by substituting $\theta_y = 1$ into (20), the strategy of the prey population eventually evolves according to

$$\dot{\theta}_x = u\theta_x \left(1 - \theta_x\right) y \left(\frac{\alpha_{MS}}{\alpha_{MS} \left(1 - \theta_x\right) x h + 1} - \frac{\alpha_{MM}}{\alpha_{MM} \theta_x x h + 1}\right)$$

However, unlike Section 3.1.1, $\alpha_{MM} > \alpha_{MS}$ no longer implies that $\theta_x < 0$ for all $0 < \theta_x < 1$ and so θ_x does not necessarily evolve to 0.

In particular, it depends upon the handling time since $\dot{\theta}_x = 0$ at

$$\widehat{\theta}_x \equiv \frac{\alpha_{MM} - \alpha_{MS} + \alpha_{MM}\alpha_{MS}xh}{2\alpha_{MM}\alpha_{MS}xh} = \frac{1}{2} + \frac{\alpha_{MM} - \alpha_{MS}}{2\alpha_{MM}\alpha_{MS}xh} > \frac{1}{2}.$$

From $\alpha_{MM} - \alpha_{MS} > 0$, $\hat{\theta}_x > 1$ for short handling times and so all prey eventually become sessile (i.e. $\dot{\theta}_x < 0$) and all predators mobile as in Section 3.1.1. However, for $h > \frac{\alpha_{MM} - \alpha_{MS}}{x\alpha_{MM}\alpha_{MS}}$, $\frac{1}{2} < \hat{\theta}_x < 1$. For these handling times, $\dot{\theta}_x > 0$ for $\theta_x > \hat{\theta}_x$ and $\dot{\theta}_x < 0$ for $\theta_x < \hat{\theta}_x$. That is, both $(\theta_x, \theta_y) = (0, 1)$ and $(\theta_x, \theta_y) = (1, 1)$ are stable equilibria. The strategy dynamics evolves to all mobile predators and either all prey are mobile or all prey are sessile.¹¹

This bistable outcome can be understood in terms of the dilution effect generated by the Holling II functional response [13, 16]. When prey density is small, each prey best avoids predation by choosing the strategy with the lower predator foraging efficiency (i.e. by adopting the sessile strategy). However, since the mortality risk of each prey decreases as the number of conspecifics using the same strategy increases, for large prey density, it is better for each prey to adopt the same strategy as the rest of the population.

4.1.2. No dominated strategy. For short handling times and no domination (i.e. condition (8) holds), there is no stable equilibrium of (20) on the boundary of the unit square and a unique equilibrium (θ_x^*, θ_y^*) in the interior since this dynamics is approximated by that of the LV system (7). However, unlike the LV system, all nearby trajectories spiral outward away from $(\theta_x^*, \theta_y^*)^{12}$

For longer handling times, stable boundary equilibria can occur where predator and prey adopt opposite foraging modes (i.e. at $(\theta_x, \theta_y) = (0, 1)$ and $(\theta_x, \theta_y) = (1, 0)$).¹³. For example, when prey density is sufficiently high (specifically, if $\alpha_{MS}(1 - \alpha_{MM}xh) < \alpha_{MM}$ and so $\frac{\alpha_{MS}}{\alpha_{MS}xh+1} < \alpha_{MM}$), then mobile predators and sessile prey form a stable equilibrium of (20). The complete theoretical analysis of the effects of all such possibilities on the four-dimensional RM system is beyond the scope of this paper. Instead, these effects are illustrated through simulations in Section 4.2.2 (see Figure 7 there).

The theoretical analysis here and the beginning of Section 4.2.2 is restricted to the special case when α_{MM} and α_{SS} are both 0 here and in Section 4.2.2 below. In this case, there is a unique equilibrium of (20) (note that (20) simplifies to (27) below) in the interior of the unit square given by

$$\theta_{xh}^* = \frac{\alpha_{MS}}{\alpha_{MS} + \alpha_{SM}}$$
 and $\theta_{yh}^* = \frac{\alpha_{SM}}{\alpha_{MS} + \alpha_{SM}}$.

Here the subscript h indicates "Holling Type II". The behavioral equilibrium $(\theta_{xh}^*, \theta_{yh}^*)$ is the same as for the LV model when there is no dominance (cf. (10)).

However, unlike the LV model, $(\theta_{xh}^*, \theta_{yh}^*)$ is unstable under the strategy dynamics given by the replicator equation (20) at fixed positive prey and predator densities x and y (Appendix B1). In fact, trajectories spiral outwards to the boundary of

¹¹The analysis in this section assumes the strategy dynamics is given by the replicator equation (20). The same results hold when the smoothed best response (see (21) below) is used instead. Moreover, the choice of strategy dynamics does not alter the evolutionary outcome for the fourdimensional RM system when there is a dominated strategy. For this reason, we have omitted the analysis of the smoothed best response in Sections 4.1.1 and 4.2.1.

¹²For small h, the Jacobian will have the same sign structure as J_{Eh1L} in Appendix B1; namely, $\begin{bmatrix} \varepsilon & + \\ - & 0 \end{bmatrix}$ where ε is small but positive. There are then two complex conjugate eigenvalues with

positive real part and so trajectories spiral outward from the interior equilibrium.

¹³On the other hand, it is never stable for predators and prey to adopt the same foraging mode (i.e. the pure-strategy pairs $(\theta_x, \theta_y) = (1, 1)$ and $(\theta_x, \theta_y) = (0, 0)$ are always unstable).

the unit square (Figure 6a below). Interestingly, the situation changes when the strategy dynamics is given by the smoothed best response:

$$\dot{\theta}_x = \frac{\theta_x A}{\theta_x A + (1 - \theta_x)B} - \theta_x$$

$$\dot{\theta}_y = \frac{\theta_y C}{\theta_y C + (1 - \theta_y)D} - \theta_y.$$
(21)

Here

$$A \equiv e^{-\frac{m\alpha_{SM}(1-\theta_y)y}{\alpha_{SM}\theta_x x h+1} - \frac{m\alpha_{MM}\theta_y y}{\alpha_{MM}\theta_x x h+1}},$$

$$B \equiv e^{-\frac{m\alpha_{MS}\theta_y y}{\alpha_{MS}(1-\theta_x) x h+1} - \frac{m\alpha_{SS}(1-\theta_y)y}{\alpha_{SS}(1-\theta_x) x h+1}},$$

$$C \equiv e^{\frac{nc\alpha_{MS}(1-\theta_x)x}{\alpha_{MS}(1-\theta_x) x h+1} + \frac{nc\alpha_{MM}\theta_x x}{\alpha_{MM}\theta_x x h+1}},$$

$$D \equiv e^{\frac{nc\alpha_{SM}\theta_x x}{\alpha_{SM}\theta_x x h+1} + \frac{nc\alpha_{SS}(1-\theta_x)x}{\alpha_{SS}(1-\theta_x) x h+1}}.$$
(22)

Although $(\theta_{xh}^*, \theta_{yh}^*)$ is still unstable under (21) when $\alpha_{MM} = \alpha_{SS} = 0$ (Appendix B2), the trajectories now spiral to a globally stable limit cycle around (θ_x^*, θ_y^*) (Figures 6b), confirming again that the smoothed best response has a more stabilizing effect on the strategy dynamics compared to the replicator equation.

4.2. The Rosenzweig-MacArthur system with strategy evolution. In this section, we analyze the four-dimensional system (19) and (20) in two steps; namely, when there is a dominated strategy (Section 4.2.1) and when there is not (Section 4.2.2).

4.2.1. The effect of a dominated strategy. By Section 4.1.1, there are two possible stable equilibria of the strategy dynamics if the predators do not go extinct. The stable equilibrium with all predators mobile and all prey sessile (i.e. $(\theta_x, \theta_y) = (0, 1)$) always exists. With strategies fixed at $(\theta_x, \theta_y) = (0, 1)$, the density dynamics (19) becomes

$$\dot{x} = rx\left(1 - \frac{x}{K}\right) - \frac{\alpha_{MS}xy}{\alpha_{MS}xh + 1}
\dot{y} = -\mu y + \frac{c\alpha_{MS}xy}{\alpha_{MS}xh + 1}$$
(23)

which is the standard RM predator prey system with foraging efficiency α_{MS} . It is well known [22, 31] that an interior equilibrium (x_{01}^*, y_{01}^*) of (23) exists if and only if $\mu h < c$ and $x_{01}^* = \frac{\mu}{(c-\mu h)\alpha_{MS}} < K$; otherwise, the predators go extinct and the prey population evolves to carrying capacity. Moreover, when (x_{01}^*, y_{01}^*) exists, it is globally asymptotically stable for (23) if and only if

$$\frac{K\alpha_{MS}h - 1}{2\alpha_{MS}h} \le x_{01}^* < K.$$

$$\tag{24}$$

On the other hand, if $0 < x_{01}^* < \frac{K\alpha_{MS}h-1}{2\alpha_{MS}h}$, the equilibrium is unstable and there is a globally stable limit cycle around (x_{01}^*, y_{01}^*) .

These outcomes can be classified intuitively in terms of the foraging efficiency α_{MS} and the handling time h as follows (see also Table 3 in the Discussion). If the predator population goes extinct for the LV model (i.e. if the interaction type is weak in that $\alpha_{MS} < \frac{\mu}{cK}$), it will also go extinct in the RM model since the extra time to handle prevolvers the predator's fitness. The predator will also go extinct

when $\alpha_{MS} > \frac{\mu}{cK}$ if the loss of fitness due to handling is large enough (specifically, if $h > \frac{cK\alpha_{MS} - \mu}{\mu K \alpha_{MS}}$).

For $0 < h < \frac{cK\alpha_{MS}-\mu}{\mu K\alpha_{MS}}$, the equilibrium (x_{01}^*, y_{01}^*) exists. For h in this range, we have the following outcomes. For intermediate interaction strength (specifically for $\frac{\mu}{cK} < \alpha_{MS} < (3+2\sqrt{2})\frac{\mu}{cK})$,¹⁴ (x_{01}^*, y_{01}^*) is globally asymptotically stable. When interaction type is strong $(\alpha_{MS} > 5.82\frac{\mu}{cK})$, (x_{01}^*, y_{01}^*) is globally asymptotically stable for either short or long handling times whereas a globally stable limit cycle around (x_{01}^*, y_{01}^*) emerges for handling times of medium length.¹⁵ These two outcomes are illustrated by the solid black curves in Figure 5.

For the four-dimensional system (19) and (20), simulations indicate corresponding local behavior emerges. Specifically, if $h > \frac{cK\alpha_{MS}-\mu}{\mu K\alpha_{MS}}$, then trajectories that start close to the plane with $(\theta_x, \theta_y) = (0, 1)$ stay close to this plane and evolve to predator extinction and prey carrying capacity. On the other hand, if $0 < h < \frac{cK\alpha_{MS}-\mu}{\mu K\alpha_{MS}}$, then (θ_x, θ_y) evolves to (0, 1) and either the system evolves to the locally asymptotically stable equilibrium $(x_{01}^*, y_{01}^*, 0, 1)$ or to a stable limit cycle around $(x_{01}^*, y_{01}^*, 0, 1)$ in this plane (Figure 5, solid black curves).

From Section 4.1.1, the four-dimensional RM system has a second possible stable equilibrium of the strategy dynamics when h is large enough; namely, all predators and prey are mobile (i.e. $(\theta_x, \theta_y) = (1, 1)$). With strategies fixed at $(\theta_x, \theta_y) = (1, 1)$, the density dynamics corresponding to (23) is

$$\dot{x} = rx\left(1 - \frac{x}{K}\right) - \frac{\alpha_{MM}xy}{\alpha_{MM}xh+1}$$

$$\dot{y} = -\mu y + \frac{c\alpha_{MM}xy}{\alpha_{MM}xh+1}.$$
(25)

The outcome for this dynamics is the same as described above for (23) (where strategies were fixed at $(\theta_x, \theta_y) = (0, 1)$) except that α_{MM} replaces α_{MS} . In particular, the interior equilibrium (x_{11}^*, y_{11}^*) exists with $x_{11}^* = \frac{\mu}{(c-\mu h)\alpha_{MM}}$ if and only if $\mu h < c$ and $x_{11}^* < K$ (i.e. $0 < h < \frac{cK\alpha_{MM} - \mu}{\mu K\alpha_{MM}}$). However, when the handling time is short, the plane with $(\theta_x, \theta_y) = (1, 1)$ is

However, when the handling time is short, the plane with $(\theta_x, \theta_y) = (1, 1)$ is now unstable (i.e., this plane is a repeller since θ_x is decreasing $(\dot{\theta}_x < 0)$ for any trajectory with $\theta_x < 1$ close to this plane). This makes it more difficult to analyze all evolutionary outcomes (in terms of model parameters) for trajectories of the four-dimensional system (19) and (20) that start close to this plane. For weak interactions $(\alpha_{MM} < \frac{\mu}{cK})$ or for long handling times (specifically, for $h > \frac{cK\alpha_{MM} - \mu}{\mu K\alpha_{MM}} > \frac{cK\alpha_{MS} - \mu}{\mu K\alpha_{MS}}$), the predators will still go extinct.

 $h > \frac{cK\alpha_{MM} - \mu}{\mu K \alpha_{MM}} > \frac{cK\alpha_{MS} - \mu}{\mu K \alpha_{MS}}$, the predators will still go extinct. For h in the range $0 < h < \frac{cK\alpha_{MM} - \mu}{\mu K \alpha_{MM}}$, trajectories that start close to the plane with $(\theta_x, \theta_y) = (1, 1)$ may undergo an abrupt change in behavior as h increases.

¹⁴The precise factor $3 + 2\sqrt{2} \approx 5.82$ appears since $\alpha_{MS} < 5.82 \frac{\mu}{cK}$ implies $x_{01}^* > \frac{K\alpha_{MS}h-1}{2\alpha_{MS}h}$ for all handing times. This factor also appears in the classical two-dimensional RM model (23) with α fixed at α_{MS} . Similar thresholds for handing times mentioned in the remainder of this section are also a consequence of the parameters chosen for the classical RM system. They are given for illustrative purpose and are not meant to reflect any specific predator-prey system.

¹⁵In technical terms, a Hopf bifurcation occurs at these transition values of the handling time. Conditions when a Hopf bifurcation occurs for the RM model are usually given in terms of the carrying capacity K [22]. When $K \leq (c + \mu h)/(\alpha_{MS}h(c - \mu h))$ the equilibrium is locally asymptotically stable and for larger values of K a locally stable limit cycle exists. This is known in the ecological literature as the Paradox of Enrichment, because more productive environments tend to destabilize the resource-consumer interactions.

For short handling times, either the predator goes extinct (if $h > \frac{cK\alpha_{MS}-\mu}{\mu K\alpha_{MS}}$) or else all trajectories converge to the plane where $(\theta_x, \theta_y) = (0, 1)$ (in which case, the outcome is the local behavior near this plane as described above). For longer handling times, the trajectories converge to the plane where $(\theta_x, \theta_y) = (1, 1)$ and then either $(x_{11}^*, y_{11}^*, 1, 1)$ is locally asymptotically stable or there is a stable limit cycle around this equilibrium. That is, although all predators are mobile in the long run, there is an abrupt change in behavior of the prey as h increases from all trajectories converging to the plane where prey are sessile to the bistable situation where all prey are sessile or all mobile.

The transitions between these different qualitative behaviors occur at parameter values of the model that depend on both the handling time and the strength of interaction. This is illustrated in Figure 5 where, for h < 0.208, all predators are mobile and all prev sessile at the evolutionary outcome which is the globally stable equilibrium $(x_{01}^*, y_{01}^*, 0, 1)$ (see the black curve in Figure 5). Then, for 0.208 < h < 2.17, the plane $(\theta_x, \theta_y) = (1, 1)$ is locally stable with trajectories that are initially nearby converging to the stable equilibrium $(x_{11}^*, y_{11}^*, 1, 1)$ for 0.208 < h < 0.5 and 1.67 < h < 2.17 and to a stable limit cycle for 0.5 < h < 1.67 (the red curves in Figure 5). Finally, for h > 2.17, the predator goes extinct. For other parameter values, the abrupt change as h increases can occur when there is a stable limit cycle on the other.

4.2.2. No dominated strategy. As pointed out in Section 4.1.2 where α_{MS} and α_{SM} are both larger than α_{MM} and α_{SS} , the strategy dynamics can become quite complicated with stable boundary equilibria existing when handling times are long. For this reason, we will start this section with the theoretical analysis assuming that the mobile (active) predator catches only sessile prey and the sessile (ambush) predator catches only mobile prey (i.e. $\alpha_{MM} = 0$ and $\alpha_{SS} = 0$). One interpretation of this assumption is that it models a specialist predator who is "intentional" ([11]) in that, for a given foraging mode, it has a preferred type of prey and will only attack this type (specifically, a mobile predator only attacks sessile prey and vice versa). From this perspective, predators in the general model with arbitrary foraging efficiencies given in Table 1 are (partially) "opportunistic" in that they will also attack prey of the non preferred type.

With the simplification $\alpha_{MM} = 0$ and $\alpha_{SS} = 0$, the population density and strategy dynamics (19) and (20) becomes

$$\dot{x} = rx\left(1 - \frac{x}{K}\right) - \frac{\alpha_{SM}\theta_x x(1-\theta_y)y}{\alpha_{SM}\theta_x xh+1} - \frac{\alpha_{MS}(1-\theta_x)x\theta_y y}{\alpha_{MS}(1-\theta_x)xh+1}$$

$$\dot{y} = -\mu y + \frac{c\alpha_{SM}\theta_x x(1-\theta_y)y}{\alpha_{SM}\theta_x xh+1} + \frac{c\alpha_{MS}(1-\theta_x)x\theta_y y}{\alpha_{MS}(1-\theta_x)xh+1}$$
(26)

$$\dot{\theta}_{x} = u\theta_{x} \left(1-\theta_{x}\right) \left(\frac{\alpha_{MS}\theta_{y}y}{\alpha_{MS}(1-\theta_{x})xh+1} - \frac{\alpha_{SM}(1-\theta_{y})y}{\alpha_{SM}\theta_{x}xh+1}\right)
\dot{\theta}_{y} = v\theta_{y} \left(1-\theta_{y}\right) \left(\frac{c\alpha_{MS}(1-\theta_{x})x}{\alpha_{MS}(1-\theta_{x})xh+1} - \frac{c\alpha_{SM}\theta_{x}x}{\alpha_{SM}\theta_{x}xh+1}\right).$$
(27)

The equilibrium that we are most interested in is the interior equilibrium where the prey and predator species coexist with both strategies used by each species. The interior equilibrium is given by $E_{h1} = (x_h^*, y_h^*, \theta_{xh}^*, \theta_{yh}^*)$ with $x_h^*, y_h^* > 0$ and $0 < \theta_{xh}^*, \theta_{yh}^* < 1$, where



FIGURE 5. The bifurcation diagram for the four-dimensional RM model with respect to the handling time h when there is a dominated strategy. The diagram is generated by trajectories that start close to the planes where all predators are mobile and prev are either all sessile or all mobile. For a fixed value of h, the local maxima and minima values of x along the trajectory are plotted (solid curves) for sufficiently large times so that transient behavior is not expected to be a factor. Thus, a stable equilibrium corresponds to those values of h for which $\max x = \min x$ (e.g. the solid black curve when h < 0.59 and when h > 1.55). For intermediate values of h, max x and min x are single-valued but unequal (the solid black curves for 0.59 < h < 1.55), indicating the trajectory is periodic with a unique maximum and minimum. The equilibrium of the density dynamics (23) with (θ_x, θ_y) fixed at (0, 1) is shown as the dashed black curve for 0.59 < h < 1.55 and as the solid black curve outside this interval. This shows that the predator goes extinct and prey reach carrying capacity at $x_{01}^* = K$ (i.e. for h > 2.14). The plane $(\theta_x, \theta_y) = (1, 1)$ is only locally stable under (19) and (20) for h > 0.208 where the outcome is then given by the solid red curve; otherwise the system evolves to the plane where $(\theta_x, \theta_y) = (0, 1)$. This abrupt jump in the evolutionary outcome is clear from the change in the stability at h = 0.208 from the unstable dashed red curve to the stable solid red curve. Parameters: $\alpha_{SM} = 0.2, \ \alpha_{MS} = 0.55, \ \alpha_{SS} = 0.1, \ \alpha_{MM} = 0.6, \ r = 2, \ K = 5,$ $\mu = 0.4, c = 1, u = 1, and v = 1.$

$$x_{h}^{*} = \frac{\mu}{\alpha^{*}(c-\mu h)}$$

$$y_{h}^{*} = \frac{rc}{\alpha^{*}(c-\mu h)} \left(1 - \frac{\mu}{(c-\mu h)K\alpha^{*}}\right)$$

$$\theta_{xh}^{*} = \frac{\alpha_{MS}}{\alpha_{MS} + \alpha_{SM}}$$

$$\theta_{yh}^{*} = \frac{\alpha_{SM}}{\alpha_{MS} + \alpha_{SM}}$$
(28)

and $\alpha^* = \frac{\alpha_{MS}\alpha_{SM}}{\alpha_{SM} + \alpha_{MS}} > 0$ (cf. (13)). With the mobile proportions fixed at these equilibrium values, the population dynamics (26) becomes

$$\dot{x} = rx\left(1 - \frac{x}{K}\right) - \frac{\alpha^* xy}{\alpha^* xh + 1}$$

$$\dot{y} = -\mu y + \frac{c\alpha^* xy}{\alpha^* xh + 1}.$$
(29)

This is the same as (23) and (25) with foraging efficiency now given as α^* . Thus, if the interior equilibrium E_{h1} does not exist, the predators go extinct and prey evolve to carrying capacity.

In fact, E_{h1} exists if and only if

$$0 < h < \frac{cK\alpha^* - \mu}{\mu K\alpha^*}.$$
(30)

In this case, (x_h^*, y_h^*) is globally asymptotically stable for the standard RM predator prev system (29) with strong predator-prev interaction (specifically, if $\alpha^* > 5.82 \frac{\mu}{cK}$). For intermediate interaction strength $(\frac{\mu}{cK} < \alpha_{MS} < 5.82 \frac{\mu}{cK})$, (x_h^*, y_h^*) is globally asymptotically stable for either short or long handling times whereas a globally stable limit cycle around (x_h^*, y_h^*) emerges for handling times of medium length.

However, from Section 4.1.2, $(\theta_{xh}^*, \theta_{yh}^*)$ is always unstable under the replicator strategy dynamics at fixed equilibrium densities (x_h^*, y_h^*) . Thus, it is not surprising that E_{h1} is always unstable by evaluating the 4 \times 4 Jacobian matrix (Appendix B1) at this equilibrium for the four-dimensional dynamical system (26) and (27). This instability implies that we can no longer predict the eventual outcome of the four-dimensional RM system by separating behavioral and density effects when E_{h1} exists, as we could for the LV system of Section 3. This is clear from Figure 6 (panels (c) and (d)) where the simulations indicate the dynamics projected onto the density plane is periodic of period 4 or lower when handling time is short (h < 0.14). For handling times of medium length (0.14 < h < 0.86), the system displays rich dynamic behaviors [28] including intervals of period doubling bifurcations for has well as intervals where the dynamics appear to exhibit chaotic behavior. For 0.86 < h < 1.41, trajectories with period two again appear with maximum prey density now close to carrying capacity. A small number of predators maintain oscillations between mobile and sessile prey populations (i.e. $\theta_{x max}$ and $\theta_{x min}$ are essentially 1 and 0 respectively). For 1.41 < h < 3.09, the predators eventually go extinct but not before the prey evolve to their preferred strategy (prey prefer mobility here since foraging efficiency of predators is greater for sessile prey (i.e. $\theta_x = 1$ since $\alpha_{SM} < \alpha_{MS}$). Finally, when E_{h1} does not exist (i.e. for h > 3.09), predator extinction occurs so rapidly that there is no selection for the prey strategy which then evolves to a neutrally stable (mixed) equilibrium that depends on the trajectory's initial conditions.

The situation changes when the strategy dynamics is given by the smoothed best response. Although E_{h1} remains unstable (Appendix B2) under the coupled RM system (26) and (21), the rich dynamic behavior observed for the replicator equation for 0.14 < h < 0.86 no longer occurs. For all handling times where E_{h1} exists (i.e. 0 < h < 3.09), the dynamic behavior more closely resembles periodic motion with a single maximum for the strategy dynamics (Figure 6, panel (f)) and either one or two local maxima for the density dynamics (Figure 6, panel (e)).

In fact, it is clear from Figure 6 that the four-dimensional RM system driven by the replicator equation and the one driven by the smoothed best response dynamics



FIGURE 6. Trajectories of the strategy dynamics and bifurcation diagrams with respect to handling time for the four-dimensional RM system when there is no dominant strategy and E_{h1} exists. Panels (a) and (b) show trajectories of the replicator equation (27)and the smoothed best response (21) respectively when h = 0.25and densities are fixed at (x^*, y^*) given by E_{h1} in (28). Panels (c) and (d) give bifurcation diagrams projected on the density and strategy planes respectively for the RM system (26) and (27) (i.e. the strategy dynamics is given by the replicator equation). Panels (e) and (f) give these same bifurcation diagrams when the strategy dynamics is given by the smoothed best response (21). The (local) maxima (blue) and minima (red) values plotted in panels (c), (d), (e) and (f) are taken along a trajectory (as in Figure 5). The dashed lines in these four panels give the interior equilibrium E_{h1} as a function of h for densities (panels (c) and (e)) and for strategies (panels (d) and (f) where this equilibrium is independent of h). Other parameters: $\alpha_{SM} = 1.3$, $\alpha_{MS} = 1.5$, r = 2, K = 6, $\mu = 0.3$, c = 1, u = 1, v = 1, m = 1 and n = 1.

equation behave significantly differently whenever E_{h1} exists. Under the replicator

equation, the total population size of the predator approaches 0 when h > 1.41. With the extinction of the predator, the prey population reaches its carrying capacity K. However, under the smoothed best response, both the prey and predator species survive when 1.41 < h < 3.09. With the increase of h, the predator species has less time to spend chasing prey. As a result, their abilities to survive and to reproduce decrease. In this case, for the predator species, the ability to adjust behaviors to maximize their fitness is very important. Since, for the same fitness difference, the smoothed best response allows the predator species to react more quickly than under the replicator equation (Appendix B3), the predator species is more likely to survive when its strategy evolution is based on the smoothed best response.

Next we consider the coupled system (26) and (27) when E_{h1} does not exist. In this case, there may be boundary equilibria where predators do not go extinct. For example, (26) and (27) has the biologically feasible pure strategic equilibrium

$$E_{h2} = \left(\frac{\mu}{\alpha_{MS}\left(c-\mu\,h\right)}, \, \frac{rc}{\alpha_{MS}\left(c-\mu\,h\right)} \left(1 - \frac{\mu}{\left(c-\mu\,h\right)K\alpha_{MS}}\right), \, 0, \, 1\right)$$

if and only if $\mu h < c$ and $\frac{\mu}{(c-\mu h)K} < \alpha_{MS}$. However, this equilibrium where all predators are mobile and all prev sessile is now unstable since sessile prev can invade such a system (see also Appendix B). The other possible boundary equilibrium

$$E_{h3} = \left(\frac{\mu}{\alpha_{SM} \left(c - \mu h\right)}, \frac{rc}{\alpha_{SM} \left(c - \mu h\right)} \left(1 - \frac{\mu}{\left(c - \mu h\right) K \alpha_{SM}}\right), 1, 0\right)$$

where all predators are sessile and all prey mobile (which exists if and only if $\mu h < c$ and $\frac{\mu}{(c-\mu h)K} < \alpha_{SM}$) is also unstable. Based on this, we expect the predators will always go extinct and the prey go to carrying capacity just as occurred in the LV system of Section **3** when there is no dominating strategy and the interior equilibrium does not exist. This intuition is illustrated in Figure **6** (panels (c) and (e)) where, for h > 3.09, E_{h1} does not exist and x equals the equilibrium carrying capacity K = 6 since no predators survive. The predator extinction occurs so rapidly for h > 3.09 that the prey strategy approaches a neutrally stable polymorphic equilibrium (Figure **6**, panels (d) and (f)) that depends on the trajectory's initial conditions.¹⁶

The analysis so far in this section assumes that there is no dominance since $\alpha_{MM} = 0$ and $\alpha_{SS} = 0$. When α_{MM} and α_{SS} are not both zero, the interior equilibrium E_{h1} can no longer be determined analytically as in (28) but can be found numerically. This is illustrated in Figure 7 where α_{SS} is taken as 0 and the numerical solution for E_{h1} is shown as the dashed black curves in panels (a), (b), (d) and (e) as α_{MM} increases. For the parameter values chosen there, there is no dominance for $0 < \alpha_{MM} < 1.3$. Figure 7, panels (a) and (b), also shows the rich dynamic behavior of the four-dimensional RM system under the replicator equation (20) compared to that under the smoothed best response (21) given in panels (d) and (e). In fact, there appears to be chaotic behavior under the replicator equation for most choices of α_{MM} in this parameter range whereas trajectories are often of period two or four under the smoothed best response. These results are consistent with the maximum Lyapunov exponent being mostly positive for the replicator

¹⁶This contrasts with prey strategies either oscillating or approaching a pure strategy for h < 3.09. Simulations of prey population size for h > 3.09 (not shown) indicate that prey evolve to their carrying capacity in similar fashion to those shown in Figure 4 for the LV system (i.e. to a single point on the line where $x_1 + x_2 = K$).



equation (panel (c)) compared to intervals where it is negative for the smoothed best response (panel (f)).

FIGURE 7. Bifurcation diagrams for the RM system showing the dependence of the long-run behavior on α_{MM} when E_{h1} exists and there is no dominance (i.e. $0 < \alpha_{MM} < 1.3$). The numerical solution for E_{h1} is shown as the dashed black curve. The longrun local maxima (blue) and minima (red) values of the prey density (respectively, strategy) along trajectories are plotted under the replicator equation in panel (a) (respectively, panel (b)) and under the smoothed best response in panel (d) (respectively, panel (e)). (The exception is in panel (a) where only the local maxima are plotted since the diagram becomes too hard to decipher if local minima are also included.) The maximum Lyapunov exponents under the replicator equation (panel (c)) and under the smoothed best response (panel (f)) are also given for these trajectories. The horizontal line at height 0 is provided in these panels to emphasize where the Lyapunov exponent is positive and where it is negative. Parameters: $\alpha_{SM} = 1.3$, $\alpha_{MS} = 1.5$, $\alpha_{SS} = 0$, r = 2, K = 6, $h = 0.3, \mu = 0.3, c = 1, u = 1, v = 1, m = 1$ and n = 1.

The above analysis of how the four-dimensional RM system depends on α_{MM} can be extended beyond the range where there is no dominance. Specifically, for $\alpha_{MM} > \min\{\alpha_{SM}, \alpha_{MS}\}$, there is dominance. Thus, when the other parameters are those used in Figure 7, we are back to the situation of a dominant strategy as discussed in Sections 4.1.1 and 4.2.1 when $\alpha_{MM} > 1.3$ since $\alpha_{MM} > \alpha_{SM}$ and $\alpha_{MS} > \alpha_{SS}$. The simulations, which are not provided here, show that the system evolves to a mobile predator population and that either all prey become mobile or all sessile (as predicted in Section 4.2.1). In fact, for these parameters, there are stable limit cycles on the corresponding $\theta_x = 0, \theta_y = 1$ and the $\theta_x = 1, \theta_y = 1$ boundary planes since we are in the middle range of handling times as in Figure 5.

Here, however, the simulated limit cycles show the two species take turns getting quite close to extinction.

5. **Discussion.** To study co-evolution in predator-prey systems, it is important to understand how behavioral (i.e. strategy) evolution in each species can influence population dynamics (and vice versa). In particular, it is important to know when these two factors can be analyzed separately when studying such co-evolutionary systems. Two complementary approaches based on the assumption of complete time scales separation have been developed. The first approach assumes that the behavioral process acts on a fast time scale and instantaneously reaches its equilibrium for any given population sizes, which we use to solve for the stable equilibrium of the resulting population dynamics [25, 26]. The second approach, called adaptive dynamics, assumes that population dynamics are at a population equilibrium at the current trait value and then solves for the trait dynamics (e.g., [14, 15, 19]).

However, it is often the case that behavioral and density evolutionary processes do not operate on different time scales [12] or that one (or both) of these processes do not evolve to equilibrium. A general framework for dealing with such systems was developed by Vincent and Brown [39]. It is such circumstances that are the

Interaction	Interaction	Foraging	Population
Type	Strength	Mode	Dynamics
Dominant	Strong	Predator Mobile	Globally Stable
Strategy	$\frac{\mu}{cK} < \alpha_{MS}$	Prey Sessile	Predator-Prey Coexistence
Prey Sessile	Weak		Prey at Carrying Capacity
Predator Mobile	$\frac{\mu}{cK} > \alpha_{MS}$		Predator Extinct
No Dominant	Strong $\frac{\mu}{cK} < \alpha^*$	Stable Coexistence of Mobile and Sessile Predator and Prey	Globally Stable Predator-Prey Coexist
Strategy	$\frac{\text{Weak}}{\frac{\mu}{cK} > \alpha^*}$		Prey at Carrying Capacity Predator Extinct

TABLE 2. How the evolutionary outcome of the Lotka-Volterra model with interspecific strategic effects depends on strategy dominance and the strength of predator-prey interaction. When interactions are weak (i.e. predator foraging efficiency α is small compared to other model parameters, $\alpha < \frac{\mu}{cK}$), the prey evolve to carrying capacity and predators go extinct. The foraging mode of the predator and prey is then irrelevant as indicated by the two blank entries in this column. For strong interactions, the foraging mode either evolves to the dominant strategy (which is mobile predator and sessile prey when dominance is given by condition (9) with corresponding foraging efficiency α_{SM}) or to the stable coexistence equilibrium of both strategy types when there is no dominant strategy (with corresponding foraging efficiency α^* given by (13)). In both cases, there is a globally stable equilibrium where predators and prey coexist.

subject of our investigation. For the predator-prey models we consider, we assume that each species can adopt either mobile or sessile behaviors. Our results are most complete when the density dynamics is given through a Lotka-Volterra model. We then show that, independent of time scales, the evolutionary outcome depends only on whether one of the species has a dominant strategy. For example, if mobile predators do better than sessile predators no matter what behavior their prey adopt, then the co-evolutionary outcome will be given by assuming that all predators are mobile and prey adopt their best choice against such predators. Depending on the predator foraging efficiency (i.e. the interaction strength) when the species use these two behaviors, either there is predator-prey coexistence or the predators go extinct. This is reported in the top half of Table 2 where it is assumed that prey are better off being sessile if predators are mobile. When there is no dominant strategy (bottom half of Table 2), neither species should use one strategy all the time. In fact, a specific mixed strategy (i.e. a mixture for each species) is best and then there is stable predator-prey coexistence at this stable mixed strategy or the predators go extinct.

Interaction Strength	Foraging	Population Dynamics			
versus Handing Time	Mode	1 5			
Very Weak		Prey at Carrying Capacity			
$\alpha_{MM}K(c-\mu h) < \mu$		Predator Extinct			
Weak		Prey at Carrying Capacity			
$\alpha_{MS}K(c-\mu h) < \mu$		Predator Extinct			
$< \alpha_{MM} K(c - \mu h)$	Predator Mobile	Locally Stable Equilibrium			
$< \min\{\frac{c+\mu h}{h}, Kc\alpha_{MS}\}$	Prey Mobile	Predator-Prey Coexistence			
Intermediate	Produtor Mobile	Locally Stable Equilibrium			
	Prov. Mobile on Socie	or Locally Stable Limit Cycle			
	riey mobile of Sessile	Predator-Prey Coexistence			
Strong					
$c\alpha_{MS} < \alpha_{MM} \left(c - \mu h \right)$	Predator Mobile	Globally Stable Equilibrium			
$< \frac{c+\mu h}{Kh},$	Prey Sessile	Predator-Prey Coexistence			
$\mu < \alpha_{MS} \overline{K}(c - \mu h)$					

TABLE 3. How the evolutionary outcome of the Rosenzweig-MacArthur model with interspecific strategic effects depends on handling time h and the strength of predator-prey interaction α_{MS} and/or α_{MM} when there is a dominant strategy. For very weak interaction strength compared to handling time (i.e. $\alpha_{MM}K(c-\mu h) < \mu$), the predator goes extinct and the preview evolve to carrying capacity (first row). This outcome also occurs for weak interaction strength (second row) or else predator and prey coexist with a locally asymptotically stable equilibrium when they are both mobile. For intermediate interaction strength (third row), the predator is always mobile and there are locally stable coexistence equilibrium or locally stable limit cycle with prey either mobile or sessile. Finally, there is a globally stable coexistence equilibrium with predator mobile and prey sessile when interaction strength compared to handling time is strong (row 4).

The results in Table 2 show that the co-evolutionary system can be understood by first finding the stable evolutionary outcome of the behavioral dynamics and then solving the density dynamics at these fixed behaviors. It is important to emphasize here that these results do not assume behavioral evolution operates on a different time scale than changes in population sizes. Table 2 is then useful for biologists to predict observed behavior in predator-prey systems. What is needed from these observations is the dominance relationship among strategies and estimates of the foraging efficiencies.

Table 3 summarizes the corresponding results (which now depend on interaction strength compared to handling time) for the Rosenzweig-MacArthur model when there is the dominant strategy given by mobile predator and sessile prey (with corresponding foraging efficiency α_{MS}) in that condition (9) holds. If biologists suspect there is a dominance relationship among the strategy types, Table 3 can be used to predict the observed outcome of the predator-prey system once foraging efficiency and handling times have been estimated.

If there is no dominance among strategies (i.e. when the game theory predicts polymorphism), the evolutionary outcome is more difficult to describe in the Rosenzweig-MacArthur model. The analysis of the important special case when a predator never catches a prey that adopts the same movement strategy (i.e. $\alpha_{MM} = \alpha_{SS} = 0$) (e.g. the predator's foraging behavior is intentional [11]) is most complete. There will then be predator-prey coexistence if and only if there is a polymorphic equilibrium in both species (e.g. some predators will adopt the mobile strategy and others the sessile). The coexistence equilibrium is now never stable; instead, either periodic motion (with amplitude depending on both the type of strategy dynamics and on the handling time) around this equilibrium emerges, or there is "rich" dynamic behavior that includes chaos and period-doubling bifurcations. Otherwise, the predator goes to extinction and the prey to carrying capacity, which occurs when interaction strength at the polymorphic equilibrium is weak compared to handling time (i.e. $\alpha^*(c - \mu h)K < \mu$).

The strategic outcomes for foraging modes in Tables 2 and 3 should shape the way ecologists think about the evolution of movement in predator-prey systems. The results summarized there suggest that, if there is a dominance relation among strategies, then most individuals in a given species can expected to be mobile (or most sessile). That is, either observing a stable mixture of foraging modes in one species or observing fluctuations in foraging modes in a predator-prey system indicates that there is no dominance among the strategies of either predators or prey and that foraging efficiencies are relatively high in order to avoid predator extinction.¹⁷

Finally, when there is no dominance but predators are not strictly intentional, monomorphic foraging modes with predator-prey coexistence can appear in the evolutionary outcome of Rosenzweig-MacArthur models as discussed at the end of Section 4 (cf. Figure 7). Furthermore, dominance relations among strategies may change as population sizes evolve as environmental factors alter (situations that are beyond the scope of this paper). These possibilities should also be kept in mind when biologists consider the effects of strategies on interspecific interactions for real predator-prey systems. The analyses of such models are important topics for future research.

¹⁷Our analysis also indicates that fluctuating foraging modes means that the predator-prey system is not of LV type. For us, we then have an RM system based on the Holling II functional response. Interestingly, the rich dynamic behavior tends to occur for the replicator equation rather than for the smoothed best response dynamics.

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Appendix A. The Lotka-Volterra Model.

Appendix A1. The stability of the Lotka-Volterra model when there is no dominated strategy. First, we study the stability of the interior equilibrium E_1 when it exists in Section 3.2.2 for the coupled system (6) and (7) (i.e. the strategy dynamics is given by the replicator equation). The linearization at the equilibrium E_1 is the following Jacobian matrix:

$$J_{E1} = \begin{bmatrix} -\frac{rx^*}{K} & -\alpha^*x^* & 0 & 0 \\ c\alpha^*y^* & 0 & 0 & 0 \\ 0 & 0 & 0 & uy^* (\alpha_{SM} - \alpha_{MM}) \theta^*_x \\ 0 & 0 & -cvx^* (\alpha_{MS} - \alpha_{MM}) \theta^*_y & 0 \end{bmatrix}.$$
(31)

To obtain these entries for J_{E1} (e.g. these in the first row) from (6), note that

$$\dot{x} = x \left[r \left(1 - \frac{x}{K} \right) - \alpha_{MM} \theta_y y \theta_x - \alpha_{MS} \theta_y y \left(1 - \theta_x \right) - \alpha_{SM} \left(1 - \theta_y \right) y \theta_x - \alpha_{SS} \left(1 - \theta_y \right) y \left(1 - \theta_x \right) \right],$$
(32)

where the expression in the square bracket is 0 at E_1 . These entries, in order, are thus

$$\frac{\partial \dot{x}}{\partial x} = x^* \left(-\frac{r}{K}\right),$$

$$\frac{\partial \dot{x}}{\partial y} = -x^* r \left(1 - \frac{x^*}{K}\right) / y^* = -\alpha^* x^*,$$

$$\frac{\partial \dot{x}}{\partial \theta_x} = -x^* y^* \left(\alpha_{MM} \theta_y^* - \alpha_{MS} \theta_y^* + \alpha_{SM} \left(1 - \theta_y^*\right) - \alpha_{SS} \left(1 - \theta_y^*\right)\right) = 0,$$

$$\frac{\partial \dot{x}}{\partial \theta_y} = 0.$$
(33)

Similar calculations are done to find the rest of the entries of J_{E1} as well as the other Jacobians in Appendices A and B.

The eigenvalues of the block diagonal matrix J_{E1} can be obtained from its upper main diagonal block matrix

$$J_{E1U} = \begin{bmatrix} -\frac{rx^*}{K} & -\alpha^*x^* \\ c\alpha^*y^* & 0 \end{bmatrix},$$

and its lower main diagonal block matrix

$$J_{E1L} = \begin{bmatrix} 0 & uy^* \left(\alpha_{SM} - \alpha_{MM}\right) \theta_x^* \\ -cvx^* \left(\alpha_{MS} - \alpha_{MM}\right) \theta_y^* & 0 \end{bmatrix}$$

That is, the eigenvalues emerge by linearizing the density dynamics (6) about E_1 holding the frequencies fixed (i.e. the dynamics (12)) to yield J_{E1U} and vice versa to yield J_{E1L} . Under the assumption (8), if the interior equilibrium E_1 is biologically feasible, we have

$$\operatorname{tr}(J_{E1U}) = -\frac{rx^*}{K},$$

and

$$\det(J_{E1U}) = c (\alpha^*)^2 x^* y^* > 0$$

The eigenvalues of matrix J_{E1U} both have negative real parts since this 2 × 2matrix has negative trace and positive determinant. That is, (x^*, y^*) is a locally asymptotically stable equilibrium of the dynamics (12), as is well-known for the linearization method.

Next we consider the eigenvalues of matrix J_{E1L} . Since the diagonal entries of J_{E1L} are both 0 and

$$\det(J_{E1U}) = cuvx^*y^* \left(\alpha_{SM} - \alpha_{MM}\right) \left(\alpha_{MS} - \alpha_{MM}\right) \theta_x^* \theta_y^* > 0,$$

the two eigenvalues of matrix J_{E1U} are purely imaginary. This is also well-known for the strategy dynamics given by the replicator equation [22].

Secondly, consider the coupled system (6) and (11) (i.e. the strategy dynamics is given by the smoothed best response), which share the same equilibria as (6) and (7). Assuming that the interior equilibrium E_1 exists, the linearization at E_1 is now the Jacobian matrix

$$J_{E1} = \begin{bmatrix} -\frac{rx^*}{K} & -\alpha^* x^* & 0 & 0 \\ c\alpha^* y^* & 0 & 0 & 0 \\ 0 & 0 & 0 & my^* (\alpha_{SM} - \alpha_{MM}) \theta_x^* \\ 0 & 0 & -ncx^* (\alpha_{MS} - \alpha_{MM}) \theta_y^* & 0 \end{bmatrix}.$$
(34)

That is, by comparing (31) with (34), we see that m and n play the same role for the smoothed best response that u and v play for the replicator equation as mentioned in the main text. In particular, the stability analysis of E_1 through linearization is the same for both strategy dynamics. That is, since the matrix J_{E1} has two eigenvalues with negative real parts and two purely imaginary eigenvalues in both cases, the stability analysis of E_1 through linearization is inconclusive as claimed in the main text.

Finally, we study the stability of the equilibrium $E_2 = \left(\frac{\mu}{c\alpha_{MS}}, \frac{r(c\alpha_{MS}K-\mu)}{c\alpha_{MS}^2K}, 0, 1\right)$ when it exists. For the coupled system (6) and (7), the corresponding Jacobian at E_2 is given by

$$J_{E2} = \begin{bmatrix} -\frac{\mu r}{c\alpha_{MS}K} & -\frac{\mu}{c} & \frac{r(c\alpha_{MS}K-\mu)\mu (\alpha_{MS}-\alpha_{MM})}{c^2\alpha_{MS}^3 K} & \frac{r(c\alpha_{MS}K-\mu)\mu (\alpha_{SS}-\alpha_{MS})}{c^2\alpha_{MS}^3 K} \\ \frac{r(c\alpha_{MS}K-\mu)}{\alpha_{MS}K} & 0 & \frac{r(c\alpha_{MS}K-\mu)\mu (\alpha_{MM}-\alpha_{MS})}{c\alpha_{MS}^3 K} & \frac{r(c\alpha_{MS}K-\mu)\mu (\alpha_{MS}-\alpha_{MS})}{c\alpha_{MS}^3 K} \\ 0 & 0 & \frac{ur(c\alpha_{MS}K-\mu)(\alpha_{MS}-\alpha_{MM})}{c\alpha_{MS}^2 K} & 0 \\ 0 & 0 & 0 & \frac{v\mu (\alpha_{SS}-\alpha_{MS})}{\alpha_{MS}} \end{bmatrix}.$$

The eigenvalues of J_{E2} can be obtained by calculating the eigenvalues of the following two 2×2 block matrices due to the 2×2 zero matrix in the lower left corner:

$$J_{E2U} = \begin{bmatrix} -\frac{\mu r}{c\alpha_{MS}K} & -\frac{\mu}{c} \\ \frac{r(c\alpha_{MS}K-\mu)}{\alpha_{MS}K} & 0 \end{bmatrix},$$
$$ur(c\alpha_{MS}K-\mu)(\alpha_{MS}-\alpha_{MM}) = 0$$

and

$$J_{E2L} = \begin{bmatrix} \frac{ur(c\alpha_{MS}K - \mu)(\alpha_{MS} - \alpha_{MM})}{c \ \alpha_{MS}^2 K} & 0\\ 0 & \frac{v\mu(\alpha_{SS} - \alpha_{MS})}{\alpha_{MS}} \end{bmatrix}$$

The two eigenvalues of matrix J_{E2U} both have negative real parts, corresponding to the stability of the density dynamics when strategies are fixed as $(\theta_x, \theta_y) = (0, 1)$. On the other hand, the eigenvalues of J_{E2L} depend on whether there is a dominant strategy. When the mobile predator strategy is dominant (Section 3.2.1, $\alpha_{MM} > \alpha_{MS}$ and $\alpha_{MS} > \alpha_{SS}$), both eigenvalues of J_{E2L} are negative and so E_2 is locally asyptotically stable (in fact, it is globally asyptotically stable as shown in the main text since (0,1) emerges from the iterated elimination of dominated strategies). However, in Section 3.2.2 where there is no dominant strategy, the eigenvalue $\frac{ur(c\alpha_{MS}K-\mu)(\alpha_{MS}-\alpha_{MM})}{c \alpha_{MS}^2 K} > 0$ and so E_2 is unstable. This instability of E_2 is also clear from the fact that when all prey are sessile and predators are mobile (i.e. at $(\theta_x, \theta_y) = (0, 1)$), mobile prey have higher fitness due to predation than sessile prey (i.e. $-\alpha_{MM} > -\alpha_{MS}$) and so can invade the system at this equilibrium. The stability analysis of each of the boundary equilibria E_2, E_3, E_4, E_5 are all similar.

For the coupled system (6) and (11) (i.e. the strategy dynamics is given by the smoothed best response), the corresponding Jacobian matrix at E_2 is



Since e $\frac{mr(\alpha_{MS}-\alpha_{MM})(c\alpha_{MS}K-\mu)}{c\alpha_{MS}^2K} - 1 > 0$ if and only if $\frac{mr(\alpha_{MS}-\alpha_{MM})(c\alpha_{MS}K-\mu)}{c\alpha_{MS}^2K} > 0$ and e $\frac{n\mu(\alpha_{SS}-\alpha_{MS})}{\alpha_{MS}} - 1 > 0$ if and only if $\frac{n\mu(\alpha_{SS}-\alpha_{MS})}{\alpha_{MS}} > 0$, the eigenvalues of this Jacobian have the same properties as those of J_{E2} . Thus, when E_2 exists, it is unstable under (6) and (11) when there is no dominated strategy and stable when there is.

Appendix A2. An alternative Lotka-Volterra model and convergence to E_1 . The Lotka-Volterra predator-prey dynamics with strategic mobility effects (6) and (7) can also be developed in terms of the densities of mobile and of sessile individuals in each population. This equivalent formulation will prove quite useful in the analysis below. Specifically, let x_1 and x_2 be the densities of mobile and sessile prey respectively (i.e. $x_1 = \theta_x x$ and $x_2 = (1 - \theta_x) x$) and y_1 and y_2 be the densities of mobile and sessile prey respectively (i.e. $y_1 = \theta_y y$ and $y_2 = (1 - \theta_y) y$). A lengthy but straightforward calculus exercise yields the system

$$\dot{x}_{1} = rx_{1} \left(1 - \frac{x_{1} + x_{2}}{K}\right) - \alpha_{SM}x_{1}y_{2} - \alpha_{MM}x_{1}y_{1} \\ + \frac{x_{1}x_{2}(u-1)(\alpha_{MS}y_{1} + \alpha_{SS}y_{2} - \alpha_{SM}y_{2} - \alpha_{MM}y_{1})}{x_{1} + x_{2}} \\ \dot{x}_{2} = rx_{2} \left(1 - \frac{x_{1} + x_{2}}{K}\right) - \alpha_{MS}x_{2}y_{1} - \alpha_{SS}x_{2}y_{2} \\ + \frac{x_{1}x_{2}(u-1)(\alpha_{SM}y_{2} + \alpha_{MM}y_{1} - \alpha_{MS}y_{1} - \alpha_{SS}y_{2})}{x_{1} + x_{2}} \\ \dot{y}_{1} = -\mu y_{1} + c\alpha_{MS}x_{2}y_{1} + c\alpha_{MM}x_{1}y_{1} \\ + \frac{y_{1}y_{2}(v-1)(c\alpha_{MS}x_{2} + c\alpha_{MM}x_{1} - c\alpha_{SS}x_{2})}{y_{1} + y_{2}} \\ \dot{y}_{2} = -\mu y_{2} + c\alpha_{SM}x_{1}y_{2} + c\alpha_{SS}x_{2}y_{2} \\ + \frac{y_{1}y_{2}(v-1)(c\alpha_{SM}x_{1} + c\alpha_{SS}x_{2} - c\alpha_{MM}x_{1})}{y_{1} + y_{2}}.$$
(35)

The equilibrial listed above can also be given in terms of the equivalent formulation of the model (35). Specifically, the interior equilibrium E_1 corresponds to

$$x_{1}^{*} = \frac{\mu(\alpha_{MS} - \alpha_{SS})}{c(\alpha_{MS}\alpha_{SM} - \alpha_{SS}\alpha_{MM})},$$

$$x_{2}^{*} = \frac{\mu(\alpha_{SM} - \alpha_{MM})}{c(\alpha_{MS}\alpha_{SM} - \alpha_{SS}\alpha_{MM})},$$

$$y_{1}^{*} = \frac{r(\alpha_{SM} - \alpha_{SS})(-\mu\alpha_{MS} + \alpha_{MS}c\alpha_{SM}K + \mu\alpha_{MM} - c\alpha_{SS}K\alpha_{MM} - \mu\alpha_{SM} + \mu\alpha_{SS})}{Kc(\alpha_{MS}\alpha_{SM} - \alpha_{SS}\alpha_{MM})^{2}},$$

$$y_{2}^{*} = \frac{r(-\alpha_{MM} + \alpha_{MS})(-\mu\alpha_{MS} + \alpha_{MS}c\alpha_{SM}K + \mu\alpha_{MM} - c\alpha_{SS}K\alpha_{MM} - \mu\alpha_{SM} + \mu\alpha_{SS})}{Kc(\alpha_{MS}\alpha_{SM} - \alpha_{SS}\alpha_{MM})^{2}},$$
(36)

whereas E_2 , E_3 , E_4 and E_5 correspond to $\left(\frac{\mu}{c\alpha_{SM}}, 0, 0, \frac{r(cK\alpha_{SM}-\mu)}{cK\alpha_{SM}^2}\right)$, $\left(0, \frac{\mu}{c\alpha_{MS}}, \frac{r(\alpha_{MS}cK-\mu)}{cK\alpha_{MS}^2}, 0\right)$, $\left(0, \frac{\mu}{c\alpha_{SS}}, 0, \frac{r(Kc\alpha_{SS}-\mu)}{cK\alpha_{SS}^2}\right)$ and $\left(\frac{\mu}{c\alpha_{MM}}, 0, \frac{r(c\alpha_{MM}K-\mu)}{cK\alpha_{MM}^2}\right)$ respectively. Finally, all the equilibria E_6, E_7 and E_8 correspond to the line $E_K \equiv \{(x_1, x_2, 0, 0) \mid x_1 + x_2 = K\}$ where the prey population is at carrying capacity and there are no predators.

In particular, in the special case that u = v = 1, we obtain

$$\dot{x}_{1} = rx_{1}\left(1 - \frac{x_{1} + x_{2}}{K}\right) - \alpha_{SM}x_{1}y_{2} - \alpha_{MM}x_{1}y_{1}
\dot{x}_{2} = rx_{2}\left(1 - \frac{x_{1} + x_{2}}{K}\right) - \alpha_{MS}x_{2}y_{1} - \alpha_{SS}x_{2}y_{2}
\dot{y}_{1} = -\mu y_{1} + c\alpha_{MS}x_{2}y_{1} + c\alpha_{MM}x_{1}y_{1}
\dot{y}_{2} = -\mu y_{2} + c\alpha_{SM}x_{1}y_{2} + c\alpha_{SS}x_{2}y_{2}.$$
(37)

We note that system (37) has the same equilibria as system (35). Now suppose that there is no dominated strategy (as in Section 3.2) and that E_1 exists. The global asymptotic stability of E_1 for (37) can then be shown by considering the following Lyapunov function

$$V = c \left(x_1 - x_1^* - x_1^* \ln \left(\frac{x_1}{x_1^*} \right) \right) + c \left(x_2 - x_2^* - x_2^* \ln \left(\frac{x_2}{x_2^*} \right) \right) + \left(y_1 - y_1^* - y_1^* \ln \left(\frac{y_1}{y_1^*} \right) \right) \\ + \left(y_2 - y_2^* - y_2^* \ln \left(\frac{y_2}{y_2^*} \right) \right),$$
(38)

which has a unique minimum at E_1 . The derivative of V is obtained as

$$\dot{V} = c \left(x_{1} - x_{1}^{*}\right) \left(r \left(1 - \frac{x}{K}\right) - \alpha_{SM}y_{2} - \alpha_{MM}y_{1}\right) \\
+ c \left(x_{2} - x_{2}^{*}\right) \left(r \left(1 - \frac{x}{K}\right) - \alpha_{MS}y_{1} - \alpha_{SS}y_{2}\right) \\
+ \left(y_{1} - y_{1}^{*}\right) \left(-\mu y_{1} + c\alpha_{MS}x_{2} + c\alpha_{MM}x_{1}\right) \\
+ \left(y_{2} - y_{2}^{*}\right) \left(-\mu + c\alpha_{SM}x_{1} + c\alpha_{SS}x_{2}\right) \\
= -\frac{cr}{K} \left(x_{1} - x_{1}^{*} + x_{2} - x_{2}^{*}\right)^{2}.$$
(39)

Thus, $\dot{V} < 0$ unless $x = x^*$. By LaSalle's invariance principle (LaSalle, 1976), any interior trajectory of (37) must converge to an invariant subset of $\{(x_1, x_2, y_1, y_2) \mid x_1 + x_2 = x^* \text{ and } y \ge 0\}$. That is, prey density converges to x^* as stated in Section 3.2.2.

In fact, it can also be shown that E_1 is an ω -limit point of all these trajectories. To this end, let M be the maximal invariant subset of $\{(x_1, x_2, y_1, y_2) \mid x_1 + x_2 = x^* \text{ and } y \ge 0\}$ under (37). We first show that every interior trajectory of (37) that is initially in M converges to E_1 . For any such trajectory, since $\dot{x} = 0$ and $x = x^*$, $\dot{y} = c\dot{x} + \dot{y} = c\left(rx^*\left(1 - \frac{x^*}{K}\right) - \mu y\right)$ by (37). But $crx^*\left(1 - \frac{x^*}{K}\right) = \mu y^*$ at E_1 and so $\dot{y} = \mu(y^* - y)$. Thus, (x_1, x_2, y_1, y_2) converges to an invariant subset of $\{(x_1, x_2, y_1, y_2) \mid x_1 + x_2 = x^* \text{ and } y_1 + y_2 = y^*\}$. Substituting x^* and y^* from (15) into (6) with $\dot{x} = 0$ yields

$$r\left(1-\frac{x^*}{K}\right)\frac{\left(\alpha_{MS}+\alpha_{SM}-\alpha_{MM}-\alpha_{SS}\right)\mu}{c\left(\alpha_{MM}\alpha_{SS}-\alpha_{MS}\alpha_{SM}\right)^2}Q_1Q_2=0,\tag{40}$$

where

$$Q_1 = \theta_x \left(\alpha_{MM} + \alpha_{SS} - \alpha_{MS} - \alpha_{SM} \right) + \alpha_{MS} - \alpha_{SS}$$

and

$$Q_2 = \theta_y \left(\alpha_{MM} + \alpha_{SS} - \alpha_{MS} - \alpha_{SM} \right) + \alpha_{SM} - \alpha_{SS}.$$

Thus, we have $Q_1 = 0$ or $Q_2 = 0$. That is, either $\theta_x = \theta_x^*$ or $\theta_y = \theta_y^*$ from (10). In the first case, $x_1 = x_1^*$ and $x_2 = x_2^*$, and $\dot{\theta}_x = 0$. Thus, by the first equation of system (7), $y_1 = \theta_y y = y_1^*$ and $y_2 = y_2^*$. Similarly, $\theta_y = \theta_y^*$ implies $y_1 = y_1^*$, $y_2 = y_2^*$ and then the second equation of (7) implies $x_1 = x_1^*$ and $x_2 = x_2^*$. That is, E_1 is the only invariant subset in the interior of $\{(x_1, x_2, y_1, y_2) \mid x_1 + x_2 = x^*$ and $y_1 + y_2 = y^*\}$. Thus, every trajectory of (37) (i.e. of (6) and (7) when u = v = 1) that is initially in the interior of M converges to E_1 . Since every interior trajectory of (37) converges to M (whether it is in M initially or not), it has E_1 as an ω -limit point.

Appendix B. The Rosenzweig-MacArthur model when there is no dominant strategy.

Appendix B1: RM model with replicator equation. To investigate the stability of E_{h1} , we consider the Jacobian matrix of (26) and (27) at E_{h1} , which is obtained as

$$J_{Eh1} = \begin{bmatrix} \frac{rx_h^*(K\alpha^*h - 1 - 2\alpha^*x_h^*h)}{K(\alpha^*x_h^*h + 1)} & -\frac{\mu}{c} & 0 & 0\\ \frac{\alpha^*y_h^*}{(\alpha^*x_h^*h + 1)^2} & 0 & 0 & 0\\ 0 & 0 & \frac{ur\mu h}{c} \left(1 - \frac{x_h^*}{K}\right) & ur\left(1 - \frac{x_h^*}{K}\right)\\ 0 & 0 & \frac{v\mu\left(\mu h - c\right)}{c} & 0 \end{bmatrix}$$

We notice that the eigenvalues of the following matrices,

$$J_{Eh1U} = \begin{bmatrix} \frac{rx_h^*(K\alpha^*h - 1 - 2\alpha^*x_h^*h)}{K(\alpha^*x_h^*h + 1)} & -\frac{\mu}{c} \\ \frac{c\alpha^*y_h}{(\alpha^*x_h^*h + 1)^2} & 0 \end{bmatrix}$$
(41)

and

$$J_{Eh1L} = \begin{bmatrix} \frac{ur\mu h}{c} \left(1 - \frac{x_h^*}{K}\right) & ur\left(1 - \frac{x_h^*}{K}\right) \\ \frac{v\mu \left(\mu h - c\right)}{c} & 0 \end{bmatrix}$$
(42)

are also the eigenvalues of matrix J_{Eh1} . Thus, linearization shows that J_{Eh1} is locally asymptotically stable if and only if J_{Eh1U} and J_{Eh1L} both have negative trace and positive determinant. We note that $\det(J_{Eh1U}) > 0$, and $\det(J_{Eh1L}) = \frac{v\mu ur}{c} (c - \mu h) (1 - \frac{x_h^*}{K}) > 0$ when E_{h1} exists. Also, notice that $\operatorname{tr}(J_{Eh1U}) < 0$ if and only if $\frac{K\alpha^*h-1}{2\alpha^*h} < x_h^* < K$ as stated in the main text. Finally, we consider the trace of matrix J_{Eh1L} . It is easy to verify that $\operatorname{tr}(J_{Eh1L}) = \frac{ur\mu h}{c} (1 - \frac{x_h^*}{K}) > 0$. Thus J_{Eh1L} has an eigenvalue with positive real part and so E_{h1} is unstable.

Next we consider the stability of the biologically realistic pure strategy equilibrium $E_{h2} = \left(\frac{\mu}{\alpha_{MS}(c-\mu h)}, \frac{rc}{\alpha_{MS}(c-\mu h)} \left(1 - \frac{\mu}{(c-\mu h)K\alpha_{MS}}\right), 0, 1\right) = (x_{h2}^*, y_{h2}^*, \theta_{xh2}^*, \theta_{yh2}^*).$ The Jacobian matrix of systems(26) and (27) at E_{h2} is given by

$$J_{Eh2} = \begin{bmatrix} \frac{hr\mu}{c} + \frac{(-c-\mu h)rx_{h2}^*}{cK} & -\frac{\mu}{c} & -\frac{r\mu x_{h2}^*}{\alpha_{MS}Kc} + \frac{r\mu}{\alpha_{MS}c} & \frac{r(x_{h2}^*)^2}{K} - rx_{h2}^* \\ -\frac{r\mu}{\alpha_{MS}K} + (c-\mu h)r & 0 & -\frac{r\mu}{\alpha_{MS}} + \frac{r\mu x_{h2}^*}{\alpha_{MS}K} & rcx_{h2}^* - \frac{rc(x_{h2}^*)^2}{K} \\ 0 & 0 & ru\left(1 - \frac{x_{h2}^*}{K}\right) & 0 \\ 0 & 0 & 0 & -\mu v \end{bmatrix}$$

Due to the structure of matrix J_{Eh2} , its eigenvalues can be obtained by calculating the eigenvalues of the following two 2×2 matrices

$$J_{Eh2U} = \begin{bmatrix} \frac{hr\mu}{c} + \frac{(-c-\mu\,h)rx_{h2}^*}{cK} & -\frac{\mu}{c} \\ -\frac{r\mu}{\alpha_{MS}K} + (-\mu\,h+c)\,r & 0 \end{bmatrix},$$

and

$$J_{Eh2L} = \begin{bmatrix} ru\left(1 - \frac{x_{h2}^*}{K}\right) & 0\\ 0 & -\mu v \end{bmatrix}.$$

Since the eigenvalues of the diagonal matrix J_{Eh2L} are $ru\left(1-\frac{x_{h2}^*}{K}\right) > 0$ and $-\mu v$, E_{h2} is unstable when it exists.

The instabilities of the other boundary equilibria where predator and prey coexist can be proved in a similar way.

Appendix B2: RM model with smoothed best response strategy dynamics. For the Rosenzweig-MacArthur model, the game between the prey species and predator species can also be described using the smoothed best response:

$$\dot{x} = rx\left(1 - \frac{x}{K}\right) - \frac{\alpha_{SM}\theta_x x(1 - \theta_y)y}{\alpha_{SM}\theta_x xh + 1} - \frac{\alpha_{MS}(1 - \theta_x)x\theta_y y}{\alpha_{MS}(1 - \theta_x)xh + 1}$$

$$\dot{y} = -\mu y + \frac{c\alpha_{SM}\theta_x x(1 - \theta_y)y}{\alpha_{SM}\theta_x xh + 1} + \frac{c\alpha_{MS}(1 - \theta_x)x\theta_y y}{\alpha_{MS}(1 - \theta_x)xh + 1},$$
(43)

$$\dot{\theta}_x = \frac{\theta_x e^{-\frac{m\alpha_{SM}(1-\theta_y)y}{\alpha_{SM}\theta_x x h+1}}}{\theta_x e^{-\frac{m\alpha_{SM}(1-\theta_y)y}{\alpha_{SM}\theta_x x h+1} + (1-\theta_x)e^{-\frac{m\alpha_{MS}\theta_y y}{\alpha_{MS}(1-\theta_x) x h+1}}} - \theta_x$$

$$\dot{\theta}_y = \frac{\theta_y e^{\frac{n\alpha_{MS}(1-\theta_x)x}{\alpha_{MS}(1-\theta_x) x h+1} + (1-\theta_y)e^{-\frac{n\alpha_{MS}\theta_y x}{\alpha_{MS}(1-\theta_x) x h+1}}}}{\theta_y e^{\frac{n\alpha_{MS}(1-\theta_x)x}{\alpha_{MS}(1-\theta_x) x h+1} + (1-\theta_y)e^{\frac{n\alpha_{MS}\theta_y x}{\alpha_{MS}(1-\theta_x) x h+1}}} - \theta_y.$$

$$(44)$$

We notice that systems (26), (27) and systems (43), (44) share the same equilibria.

We first consider the stability of the interior equilibrium E_{h1} of systems (43) and (44). Linearizing systems (43) and (44) at E_{h1} yields the corresponding Jacobian given by

$$J_{Sh1} = \begin{bmatrix} \frac{rx_h^*(K\alpha^*h - 1 - 2\alpha^*x_h^*h)}{K(\alpha^*x_h^*h + 1)} & -\frac{\mu}{c} & 0 & 0\\ \frac{c\alpha^*y_h^*}{(\alpha^*x_h^*h + 1)^2} & 0 & 0 & 0\\ 0 & 0 & \frac{mr\mu h}{c} \left(1 - \frac{x_h^*}{K}\right) & rm\left(1 - \frac{x_h^*}{K}\right)\\ 0 & 0 & \frac{n\mu(h\mu - c)}{c} & 0 \end{bmatrix}$$

This is the same matrix as J_{Eh1} for the replicator equation with m and n taking the place of u and v. Thus, the interior equilibrium E_{h1} of the four dimensional RM system with smoothed best response (43) and (44) is unstable.

Next we consider the stability of the pure strategic equilibrium E_{h2} . Linearizing systems (43) and (44) at E_{h2} , we obtain

$$J_{Sh2} = \begin{bmatrix} \frac{hr\mu}{c} + \frac{(-c-\mu h)rx_{h2}^*}{cK} & -\frac{\mu}{c} & -\frac{r\mu x_{h2}^*}{\alpha_{MS}Kc} + \frac{r\mu}{\alpha_{MS}c} & \frac{r(x_{h2}^*)^2}{K} - rx_{h2}^* \\ -\frac{r\mu}{\alpha_{MS}K} + (c-\mu h)r & 0 & -\frac{r\mu}{\alpha_{MS}} + \frac{r\mu x_{h2}^*}{\alpha_{MS}K} & rcx_{h2}^* - \frac{rc(x_{h2}^*)^2}{K} \\ 0 & 0 & e^{rm\left(1 - \frac{x_{h2}^*}{K}\right)} - 1 & 0 \\ 0 & 0 & 0 & e^{-\mu n} - 1 \end{bmatrix}$$

The stability of matrix J_{Sh2} is determined by the eigenvalues of the following two matrices

$$J_{Sh2U} = \begin{bmatrix} \frac{hr\mu}{c} + \frac{(-c-\mu\,h)rx_{h2}^{*}}{cK} & -\frac{\mu}{c} \\ -\frac{r\mu}{\alpha_{MS}K} + (c-\mu\,h)r & 0 \end{bmatrix},$$

and

$$J_{Sh2L} = \begin{bmatrix} e^{rm\left(1 - \frac{x_{h2}^*}{K}\right)} - 1 & 0 \\ 0 & e^{-\mu n} - 1 \end{bmatrix}$$

Since the eigenvalues of matrix J_{Sh2L} are $e^{rm\left(1-\frac{x_{h2}^*}{K}\right)} - 1 > 0$ and $e^{-\mu n} - 1 < 0$, the pure strategic equilibrium E_{h2} is unstable. The other boundary equilibria of systems (43) and (44) where predator and prey coexist can also be shown to be unstable by a similar analysis.

Appendix B3: Predator reaction time in the RM model. Let ΔW denote the fitness difference $W_M - W_S$ of the predator species, i.e.,

$$\Delta W = \frac{c\alpha_{MS}(1-\theta_x)x}{\alpha_{MS}(1-\theta_x)xh+1} - \frac{c\alpha_{SM}\theta_xx}{\alpha_{SM}\theta_xxh+1} + \frac{c\alpha_{MM}\theta_xx}{\alpha_{MM}\theta_xxh+1} - \frac{c\alpha_{SS}(1-\theta_x)x}{\alpha_{SS}(1-\theta_x)xh+1}.$$

The predator strategy dynamics can then be written as

$$\dot{\theta}_y = v\theta_y \left(1 - \theta_y\right) \Delta W,\tag{45}$$

for the replicator equation (20) and as

$$\dot{\theta}_y = \frac{\theta_y \mathrm{e}^{n\Delta W}}{\theta_y \mathrm{e}^{n\Delta W} + (1 - \theta_y)} - \theta_y \tag{46}$$

for the smoothed best response dynamics (21).

If we assume that most predators are sessile (i.e., $\theta_y \approx 0$), then most prey will also be sessile (i.e., $\theta_x \approx 0$) to avoid being caught. In this case, the fitness of the predators is minimized since $\alpha_{MM} = \alpha_{SS} = 0$. In order to survive, the predators must increase their per capita growth rate by reacting to the fitness difference ΔW . Partial differentiation of (45) and (46) with respect to ΔW yields

$$\frac{\partial \theta_y}{\partial \Delta W} = v \theta_y \left(1 - \theta_y \right), \tag{47}$$

and

$$\frac{\partial \dot{\theta}_y}{\partial \Delta W} = n\theta_y \left(1 - \theta_y\right) \frac{\mathrm{e}^{n\Delta W}}{\left(\theta_y \mathrm{e}^{n\Delta W} + 1 - \theta_y\right)^2},\tag{48}$$

respectively.

Since $\frac{e^{n\Delta W}}{(\theta_y e^{n\Delta W} + 1 - \theta_y)^2} > 1$ for $\theta_y \to 0$, $\frac{\partial \dot{\theta}_y}{\partial \Delta W}$ is greater for the smoothed best response dynamics than for the replicator equation. Thus, the predator species reacts more quickly and has a higher chance to survive under the smoothed best response. The same conclusion is reached using a similar analysis if we assume most predators are mobile (i.e. $\theta_y \approx 1$).

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