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On evolutionary stability in predator–prey models with fast behavioural dynamics

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ABSTRACT

Question: Does optimality in predator–prey models with plastic traits evolving on a fast time-scale imply evolutionary stability?

Mathematical methods: Predator–prey models of population growth described by differential equations with controls and feedback regulation. *G*-function.

Key assumptions: Plastic responses of organisms to changes in environment are adaptive in the sense that they maximize individual fitness. Population dynamics are deterministic and described by the Lotka-Volterra type dynamics.

Predictions: Adaptive plastic responses do not necessarily lead to evolutionary stability. Mutants with a different strategy can invade a monomorphic resident population, but they cannot replace residents.

Keywords: adaptive foraging, evolutionarily stable strategies, *G*-function, game theory, ideal free distribution, population dynamics, predator–prey games.

INTRODUCTION

A central challenge in ecology is to develop models that faithfully capture those important mechanistic details of natural systems that are required to make reliable predictions about population community structure and dynamics. This requires integration of processes that run on three different time-scales: individual, population, and evolutionary. The individual time-scale comprises phenotypic plasticity that produces behaviourally flexible phenotypes as a response to changing environment (Miner *et al.*, 2005). The population time-scale is concerned with population dynamics that manifest on a slower time-scale than behavioural responses. The evolutionary time-scale focuses on slow trait changes due to mutation and selection processes. This trichotomy led to separation of these three research programmes that currently correspond to behavioural ecology, population ecology, and evolutionary

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ecology. To unify these programmes, several theoretical approaches that are based on time-scale separation have been developed. One of the first approaches to use time-scale separation is the early work on the functional response that integrates some details of animal behaviour (e.g. pursuit and capture of a prey by predator) with population dynamics (Holling, 1966). This work still treats animal behaviour in a very rudimentary way, as it only implicitly defines behavioural mechanisms by which predators select their prey. More explicit treatments of behavioural effects on population dynamics focused on diet selection, habitat selection, and activity budget (for a review, see Bolker *et al.*, 2003). These works assume that animal behaviour maximizes fitness at the current population densities. Similarly, there is a long line of research on the interface between the population and evolutionary time-scale. For instance, Vincent and Brown (2005) use a separation of population vs. evolutionary time-scale for their Darwinian dynamics (that assumes population densities are at stable equilibrium given the current phenotype distribution) to examine the evolutionary stability of population behaviours through their *G*-function approach (see also Cohen *et al.*, 1999). Similarly, the adaptive dynamics approach (e.g. Dieckmann and Law, 1996; Geritz *et al.*, 1997, 1998; Abrams, 2005) produces a canonical equation to model trait evolution at population equilibrium.

In this article, we are interested in combining these three time-scales. We study some predator–prey models in which individual behaviour can change rapidly within a single generation, since these behaviours are given by strategies such as habitat choice or foraging/predating activity levels that individuals may change many times during their lifetime. In fact, we assume that changes in behaviour run on a much faster time-scale than changes in population density. At the behavioural time-scale, fitness is instantaneously maximized, which leads to the Nash equilibrium (Nash, 1951) or, if it exists, the evolutionarily stable strategy (ESS) (Maynard Smith and Price, 1973). The Nash equilibrium is the optimal strategy that maximizes individual fitness in the sense that, if all individuals in a given population use this strategy, then an individual with another strategy cannot get a higher fitness. In addition to being a Nash equilibrium, the ESS requires that any other strategy that does as well as the resident strategy cannot invade the resident population and must die. We remark that the ESS was originally defined for a single species only, while the Nash equilibrium can be applied to any number of interacting populations. The extension of the evolutionary stability concept to the multiple species setting is more complicated and was introduced only recently (e.g. Cressman, 1992; Vincent and Brown, 2005). Population dynamics are assumed to operate on an intermediate time-scale and are modelled by a set of differential equations. Population dynamics together with behavioural dynamics correspond to a resident-trait dynamics. The question of primary interest to us is on the evolutionary stability of the resident-trait system, i.e. whether mutants playing a different strategy can invade the resident system or not. To this end, we analyse several Lotka-Volterra predator–prey models with adaptive predator and/or prey strategies.

Our first general conclusion is that, although mutant strategies can survive, they cannot drive out the residents. Second, the combined resident–mutant system displays the same long-term behaviour as the resident system when this latter system has a globally stable attractor (e.g. a stable equilibrium or family of limit cycles). This yields a dynamic interpretation of the evolutionary stability of adaptive systems even in the case when these systems periodically fluctuate.

Our models fall in the category of systems that we call ‘population game models’. This name emphasizes the fact that these models combine game-theoretical approaches with population dynamics. In other words, these models aim to unify three major ecological

disciplines: behavioural ecology, population ecology, and evolutionary ecology. In connection with our previous results (Cressman *et al.*, 2004; Abrams *et al.*, 2007), our models clearly show that a complex feedback loop exists between these three different time-scale processes. In particular, animal behaviour can have strong effects on population dynamics, which in turn influences animal behaviour and evolutionary processes.

EVOLUTIONARY STABILITY IN DENSITY-DEPENDENT POPULATION MODELS

In this article, we explore evolutionary stability of strategies in multiple populations that undergo population dynamics. If $x = (x_1, \dots, x_n)$ denotes the vector of population densities of n populations, then typically these models have the form

$$\dot{x}_i = x_i f_i(x, u), \quad i = 1, \dots, n \quad (1)$$

where $u = (u_1, \dots, u_k) \in U = U^1 \times \dots \times U^k \subset \mathbb{R}^m$ is a control vector given in terms of phenotypically plastic traits (Miner *et al.*, 2005) with values in given sets U^i and $f_i(x, u)$ is individual fitness in species i (i.e. it is the per capita population growth rate of this species). Such traits can correspond to changes in species' behaviour, physiology, morphology, life-history, and so on.

We assume throughout that each population has at most one plastic trait. In this section, without loss of generality, we then order populations in model (1) so that the first k populations are those with plastic traits. Thus, when $k < n$, there are some populations without plastic traits. It is also assumed in this article that these traits respond to the current environment (i.e. to population density x) in such a way that individual fitness maximizes, i.e. u_i is a trait for species i for which $f_i(x, u)$ is maximized.

In frequency-dependent models, optimality is understood in the sense of evolutionarily stable strategies (Maynard Smith and Price, 1973), i.e. a strategy that is resistant to invasion of mutants that use a different strategy. Model (1) is then called the monomorphic resident system where all individuals are using their current optimal strategy. The ESS was defined for a single population only and its extension to multiple species is more difficult (but see Cressman, 1992; Křivan *et al.*, 2008). Instead, in our multiple species context, optimality will be understood in the sense of the Nash equilibrium. If all resident individuals use this strategy, no individuals have an incentive to switch to another strategy. To calculate these optimal strategies, it is useful to follow the terminology of Vincent and Brown (2005), who defined, for those populations that show adaptive traits, the so-called G -function that satisfies $G_i(u_i; u, x) = f_i(x, u)$ for every species $i = 1, \dots, k$. Then, for every population density vector x , fitness maximization provides us with a set of Nash equilibria:

$$N(x) = \{u \in U \mid G_i(u_i; u, x) \geq G_i(v; u, x) \text{ for any } v \in U^i, i = 1, \dots, k\}. \quad (2)$$

Thus, together with model (1) we consider trait dynamics

$$u \in N(x) \quad (3)$$

and call (1) combined with (3) the resident population-trait dynamics. It is important to note that this concept involves two time-scales. As (3) assumes that the optimal trait value changes instantaneously with changing population densities, trait dynamics are assumed to be infinitely faster than population dynamics (1). As the map that associates to every population density the corresponding optimal strategy $N(x)$ is multi-valued, the question arises if solutions to resident population-trait dynamics exist. Because $N(x)$ is upper

semi-continuous and convex valued (Aubin and Cellina, 1984) for continuous G -functions, resident population-trait dynamics have solutions for every initial population density (Aubin and Cellina, 1984; Filippov, 1988; Colombo and Křivan, 1993).¹

For models that we consider in the following sections, the map $N(x)$ is typically set-valued for some population densities. In a single species context, if there are several Nash equilibria, finding ESSs corresponds to a selection procedure that chooses only those that are stable with respect to possible invasions of monomorphic mutants. This selection procedure is based on frequency dependence of the fitness function. However, in our examples, there is no direct frequency dependence of the fitness function on the resident strategy. In particular, for our predator–prey models, the resident predator population sets the resource level, which in turn defines the fitness function of a predator mutant that uses a different strategy. In other words, the resident strategy does not explicitly appear in the mutant fitness function. This excludes the possibility of selection of some strategies (such as those that are evolutionarily stable) on frequency-dependent grounds. On the other hand, we show that it is often possible to reduce the set of Nash equilibria on the basis of density dependence. It turns out that, at those points where $N(x)$ is set-valued in our examples, trajectories of the resident population-trait dynamics are constrained to stay on a lower dimensional manifold described by continuous maps $g_i: R^n \mapsto R, i = 1, \dots, l$

$$M = \{x \in R^n \mid g_1(x) = 0, \dots, g_l(x) = 0\}. \quad (4)$$

Invariance of this manifold under the resident population-trait dynamics selects a subset $S(x)$ of $N(x)$ that provides us with a single strategy in many cases.

In this article, we concentrate on the evolutionary stability of predator–prey systems. That is, in analogy with the evolutionary stability of a single-species ESS at fixed population density, we investigate whether mutants can successfully invade the residents. In what follows, we will assume that every population with an adaptive trait can be invaded by a single mutant only, but the analysis can be extended to the case of multiple mutants. The population dynamics of our resident–mutant system then have the form

$$\begin{aligned} \frac{dx_i}{dt} &= x_i G_i(u_i; u, x, \tilde{u}, \tilde{x}), \quad i = 1, \dots, k \\ \frac{d\tilde{x}_i}{dt} &= \tilde{x}_i G_i(\tilde{u}_i; u, x, \tilde{u}, \tilde{x}), \quad i = 1, \dots, k \\ \frac{dx_i}{dt} &= x_i f_i(x, \tilde{x}, u, \tilde{u}), \quad i = k + 1, \dots, n \end{aligned} \quad (5)$$

where $\tilde{x} = (\tilde{x}_1, \dots, \tilde{x}_k)$ is the density vector of the mutant populations that use some given strategy $\tilde{u} = (\tilde{u}_1, \dots, \tilde{u}_k)$ (that may also depend on current densities x, \tilde{x}). Together with these population dynamics, we consider trait dynamics that now depend also on mutant trait and density, i.e.

$$u \in N(x, \tilde{x}, \tilde{u}) = \{u \in U \mid G_i(u_i; u, x, \tilde{u}, \tilde{x}) \geq G_i(v; u, x, \tilde{u}, \tilde{x}) \text{ for any } v \in U^i, i = 1, \dots, k\}. \quad (6)$$

¹ We remark that in this article we do not need to use the Filippov concept of a solution for a differential equation with a discontinuous right-hand side, as our resident population-trait dynamics have a solution in the usual sense.

As in the resident-only system, the set of all Nash equilibria for given population densities and mutant strategy can be reduced if population dynamics are to stay on a set M , which eventually leads to the resident strategy set $S(x, \tilde{x}, \tilde{u})$.

A priori, there are several possibilities for general multi-species resident–mutant population-trait dynamics (5) and (6). The resident–mutant system can converge to a population equilibrium, or the attractor can be more complex. Whether or not population dynamics settle on an equilibrium, there are three possibilities: (1) mutants die out; (2) both mutants and residents of some species co-exist and no residents die out, which leads to an extended polymorphism; or (3) some mutants replace residents, which corresponds to evolutionary instability. The fact that population dynamics of the resident–mutant system may not converge to an equilibrium, or strategies that maximize fitness are not unique, considerably complicate the analysis and immediately bring up the problem of what is the meaning of evolutionary stability (as strategies that are stable with respect to invasion) in these situations. We postpone a discussion of these issues until the following section where concrete predator–prey examples are introduced and analysed.

However, we can answer already one question for these general models; namely, whether mutants can spread in the population and replace the residents. From (5), it is straightforward to show that

$$\frac{d(\tilde{x}_i/x_i)}{dt} = \frac{\tilde{x}_i}{x_i} (G_i(\tilde{u}_i; u, x, \tilde{u}, \tilde{x}) - G_i(u_i; u, x, \tilde{u}, \tilde{x})) \leq 0 \quad (7)$$

for $i = 1, \dots, k$ when $u \in S(x, \tilde{x}, \tilde{u})$ is the optimal strategy. Thus, the proportion of mutants in species i never increases for $i = 1, \dots, k$ and so this proportion can never be higher than it is initially. In particular, mutants cannot replace residents who use an optimal strategy. However, the above inequality does not exclude the possibility that mutants survive in the system or that the presence of mutants fundamentally alters how the multi-species system evolves (that is, the resident–mutant population-trait dynamics may be qualitatively different from the resident population-trait dynamics). We examine both these issues in the following predator–prey examples.

PREDATOR–PREY MODELS WHERE THE PREDATOR HAS AN ADAPTIVE PLASTIC TRAIT

In this section, we study two predator–prey models where adaptive predators make a choice of habitat or a choice of diet respectively. We again are most interested in the evolutionary stability of the optimal strategies in the two models.

Two-patch predator–prey model where predators are adaptive foragers

Following the model developed by Křivan (1997), the monomorphic resident Lotka–Volterra predator–prey model with only predators moving between two patches is

$$\begin{aligned} \frac{dx_1}{dt} &= x_1(r_1 - \lambda_1 v_1 x_3) \\ \frac{dx_2}{dt} &= x_2(r_2 - \lambda_2 v_2 x_3) \\ \frac{dx_3}{dt} &= x_3(e_1 v_1 x_1 + e_2 v_2 x_2 - m). \end{aligned} \quad (8)$$

Here x_i is the density of prey species i ($i = 1, 2$) that inhabit patch i exclusively; x_3 is the density of the predator population whose members are all using the foraging strategy $v = (v_1, v_2)$, where v_i is the proportion of time each predator forages in patch i ($v_1 + v_2 = 1$).² In fact, for our adaptive residents, the optimal foraging strategy v is for all predators to inhabit the better patch from their perspective (i.e. the patch with higher $e_i x_i$). Thus, the optimal predator strategy satisfies

$$v_1 \in N(x) = \begin{cases} \{1\} & \text{if } e_1 x_1 > e_2 x_2 \\ \{0\} & \text{if } e_1 x_1 < e_2 x_2 \\ \{u_1 \mid 0 \leq u_1 \leq 1\} & \text{if } e_1 x_1 = e_2 x_2. \end{cases} \quad (9)$$

In particular, when both patches are equally profitable for predators, any resident predator distribution is possible. Thus, the map $N(x)$ at these prey densities is an interval $[0, 1]$.

These results can also be seen from the game-theoretic perspective in terms of the predator's G -function. Here, the fitness of an individual predator with strategy $v = (v_1, v_2)$ in a resident population with strategy $u = (u_1, u_2)$ is $G(v; u, x) = e_1 v_1 x_1 + e_2 v_2 x_2 - m = (e_1 x_1 - m)v_1 + (e_2 x_2 - m)v_2$. G does not depend directly on the mean strategy u of the resident population, or on its own species density. The dependence is indirect through prey population densities that depend on the resident predator strategy through the resident population dynamics (8). Thus, at fixed population density $x = (x_1, x_2, x_3)$, we have a 'game against nature' (Maynard Smith, 1982) with $G(v; u, x) = \langle v, B(x) \rangle = v_1 B_1 + v_2 B_2$ where $B(x) = (B_1, B_2) = (e_1 x_1 - m, e_2 x_2 - m)$. The optimal strategy in a game against nature is the strategy corresponding to the largest B_i . To examine the evolutionary stability of this optimal strategy, we consider the resident–mutant system.

First, for the resident population–trait dynamics (8, 9), it was proven by Boukal and Křivan (1999) that the global attractor is located in plane $M = \{x = (x_1, x_2, x_3) \mid e_1 x_1 = e_2 x_2\}$. That is, when $N(x)$ is multiple-valued, the manifold described in (4) becomes the hyperplane M in this two-patch model (i.e. the single constraint in (4) becomes $g(x) = 0$ where $g(x) = e_1 x_1 - e_2 x_2$). In fact, if the first patch has a higher intrinsic prey growth rate when compared with the second patch (i.e. if $r_1 > r_2$, which we will assume from now on), then they show that the attractor is the subset of M formed by the family of closed Lotka–Volterra cycles of

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 \left(\frac{r_1 \lambda_2 + r_2 \lambda_1 - \lambda_1 \lambda_2 x_3}{\lambda_1 + \lambda_2} \right) \\ \frac{dx_3}{dt} &= x_3 (e_1 x_1 - m) \end{aligned} \quad (10)$$

for which all points on the trajectory satisfy $x_3 \geq (r_1 - r_2)/\lambda_1$ (see Figure 1A in Křivan and Eisner, 2006). Note that the dynamics for the second prey species need not be specified here since $dx_2/dt = (e_1/e_2) (dx_1/dt)$ on the attractor. Substituting the expressions from (8) for these

² Alternatively, both prey species inhabit a single patch and there is no direct competition between these species. Then v_i is the proportion of time each predator forages for prey species i .

derivatives implies that $r_1 - \lambda_1 v_1 x_3 = r_2 - \lambda_2 v_2 x_3$ when $e_1 x_1 = e_2 x_2$ and so the optimal predator strategy on the attractor can be computed explicitly as:³

$$v_1 = \frac{r_1 - r_2 + \lambda_2 x_3}{(\lambda_1 + \lambda_2)x_3}. \tag{11}$$

That is, although any strategy v_1 that satisfies (9) is optimal in the sense that it obtains the highest possible payoff at each point along a trajectory, on the attractor the strategies must satisfy (11). Thus, v_1 depends not only on x_1, x_2 as in (9) but also on the predator density x_3 through (11). It is interesting to note that, on the attractor, predator fitness ($G = e_1 v_1 x_1 + e_2 v_2 x_2 - m$) seems to depend explicitly through (11) on the predator population density. However, substituting v_1 from (11) into this formula shows that the actual value of $G = e_1 x_1 - m$ is independent of x_3 at all points of M for which $x_3 \geq (r_1 - r_2)/\lambda_1$.

Thus, for the monomorphic predator–prey system with adaptive residents, the predator habitat selection game combined with population dynamics selects the optimal strategy (11) among infinitely many possible optimal strategies given by (9) when $e_1 x_1 = e_2 x_2$. The primary question of interest to us is if, and in which sense, this optimal strategy is stable with respect to invasions by mutants using a different strategy.

The fact that the resident population dynamics periodically fluctuate on the attractor causes problems when applying the classical game theory that assumes either fixed population sizes or exponentially growing populations (Cressman, 1992). Instead, we analyse stability of the optimal strategy by assuming that the predator population is split into residents (with density x_3 and optimal strategy v) and mutants (with density \tilde{x}_3 and strategy \tilde{v}) that differ from residents only in their strategy, and then study the resultant resident–mutant population dynamics:⁴

$$\begin{aligned} \frac{dx_1}{dt} &= x_1(r_1 - \lambda_1 v_1 x_3 - \lambda_1 \tilde{v}_1 \tilde{x}_3) \\ \frac{dx_2}{dt} &= x_2(r_2 - \lambda_2 v_2 x_3 - \lambda_2 \tilde{v}_2 \tilde{x}_3) \\ \frac{dx_3}{dt} &= x_3(e_1 v_1 x_1 + e_2 v_2 x_2 - m) \\ \frac{d\tilde{x}_3}{dt} &= \tilde{x}_3(e_1 \tilde{v}_1 x_1 + e_2 \tilde{v}_2 x_2 - m). \end{aligned} \tag{12}$$

³ In general, if the attractor is contained in the manifold $M = \{x \in R^n \mid g_1(x) = 0, \dots, g_l(x) = 0\}$ as in (4), invariance implies the additional constraint that

$$v \in S(x) = \{u \in N(x) \mid \langle \nabla g_i(x), f(x, u) \rangle = 0, \quad i = 1, \dots, l\}$$

where ∇g_i is the gradient of partial derivatives of g_i and $f = (f_1, \dots, f_n)$. For $g(x) = e_1 x_1 - e_2 x_2$, this constraint yields (11). Although we do not use the Filippov concept of a solution, it turns out that (11) coincides with the definition of the Filippov solution for the control system (8, 9), by the so-called ‘equivalent control method’ (Filippov, 1988; Vincent and Grantham, 1997; Dercole *et al.*, 2007).

⁴ We will assume that strategy $\tilde{v} = (\tilde{v}_1, \tilde{v}_2)$ depends only on x_1, x_2, x_3 , and \tilde{x}_3 and is such that the resident–mutant system (12) has a solution for all initial conditions and for all $t \geq 0$ (for example, this will be the case if \tilde{v}_1 depends continuously on x_1, x_2, x_3 , and \tilde{x}_3). In particular, the resident–mutant population dynamics is autonomous in that the vector field on the right-hand side of (12) has no explicit time dependence.

It follows from (7) that mutants cannot spread (i.e. no mutant strategy \tilde{u} can ‘strictly’ invade the resident system in that the proportion of invading predator strategies is never larger than it is initially). Indeed, along any trajectory of (12), \tilde{x}_3/x_3 monotonically decreases to a limiting value $k^* \geq 0$ that depends on initial conditions.

It is shown in Appendix 1 that all trajectories of the resident–mutant system (12) converge to a global attractor that is contained in the hyperplane $M = \{(x_1, x_2, x_3, \tilde{x}_3) \mid e_1 x_1 = e_2 x_2\}$. The attractor is formed by closed cycles⁵ of the Lotka–Volterra system

$$\begin{aligned}\frac{dx_1}{dt} &= x_1 \frac{r_1 \lambda_2 + r_2 \lambda_1 - (x_3 + \tilde{x}_3) \lambda_1 \lambda_2}{\lambda_1 + \lambda_2} \\ \frac{dx_3}{dt} &= x_3 (e_1 x_1 - m)\end{aligned}\tag{13}$$

for which all points on the trajectory satisfy the following constraints for some $k^* \geq 0$:

$$x_3 \geq \max \left\{ \frac{r_1 - r_2}{\lambda_1 + k^*(\lambda_1 \tilde{v}_1 - \lambda_2 \tilde{v}_2)}, \frac{r_2 - r_1}{\lambda_2 - k^*(\lambda_1 \tilde{v}_1 - \lambda_2 \tilde{v}_2)} \right\}.$$

It is also shown there that the optimal strategy of the resident on the attractor is of the form

$$v_1 = \frac{r_1 - r_2 + x_3(\lambda_2 + k^*(\lambda_2 \tilde{v}_2 - \lambda_1 \tilde{v}_1))}{(\lambda_1 + \lambda_2)x_3},\tag{14}$$

which generalizes the optimal foraging strategy (11) of the resident system [i.e. in the absence of mutants ($k^* = 0$), the optimal strategy (14) on the attractor is again given by (11)].

It is interesting to analyse what happens when the mutant strategy \tilde{v} is constant (i.e. when all mutants spend fixed proportions of their time in each habitat regardless of the prey density there). If residents adjust their strategy (11) to the overall population size $x_3 + \tilde{x}_3$, i.e. if

$$v_1 = \frac{r_1 - r_2 + \lambda_2(x_3 + \tilde{x}_3)}{(\lambda_1 + \lambda_2)(x_3 + \tilde{x}_3)}\tag{15}$$

on the attractor, then (14) implies that either $\tilde{x}_3 = 0$ there or that the ‘mutant’ strategy is identical to the resident strategy ($\tilde{v}_1 = v_1$). Thus, mutants that use a constant strategy must die out as documented in Fig. 1 (left panels).

As formula (15) holds only when the trajectory is on the attractor, i.e. in the plane $e_1 x_1 = e_2 x_2$, while off this plane the optimal strategy is either equal to 1 or to 0, it may seem that preferences given by (15) are unlikely to be observed in simulations due to numerical errors. However, this is not so, because in these cases the average value of the optimal strategy converges to v_1 given by (15) (Aubin and Cellina, 1984; Filippov, 1988) as the trajectory fluctuates in the vicinity of the attractor from one side to the other.

At another extreme, if residents do not adjust their strategy to the presence of mutants but continue to use (11), then from (14) mutants must use strategy $\tilde{v}_1 = \lambda_2/(\lambda_1 + \lambda_2)$ on the attractor to survive. In this case, the resident–mutant system is polymorphic with mutants

⁵ Note that we do not include dx_2/dt or $d\tilde{x}_3/dt$ in this system (13), since $e_1 x_1 = e_2 x_2$ and $\tilde{x}_3 = k^* x_3$.

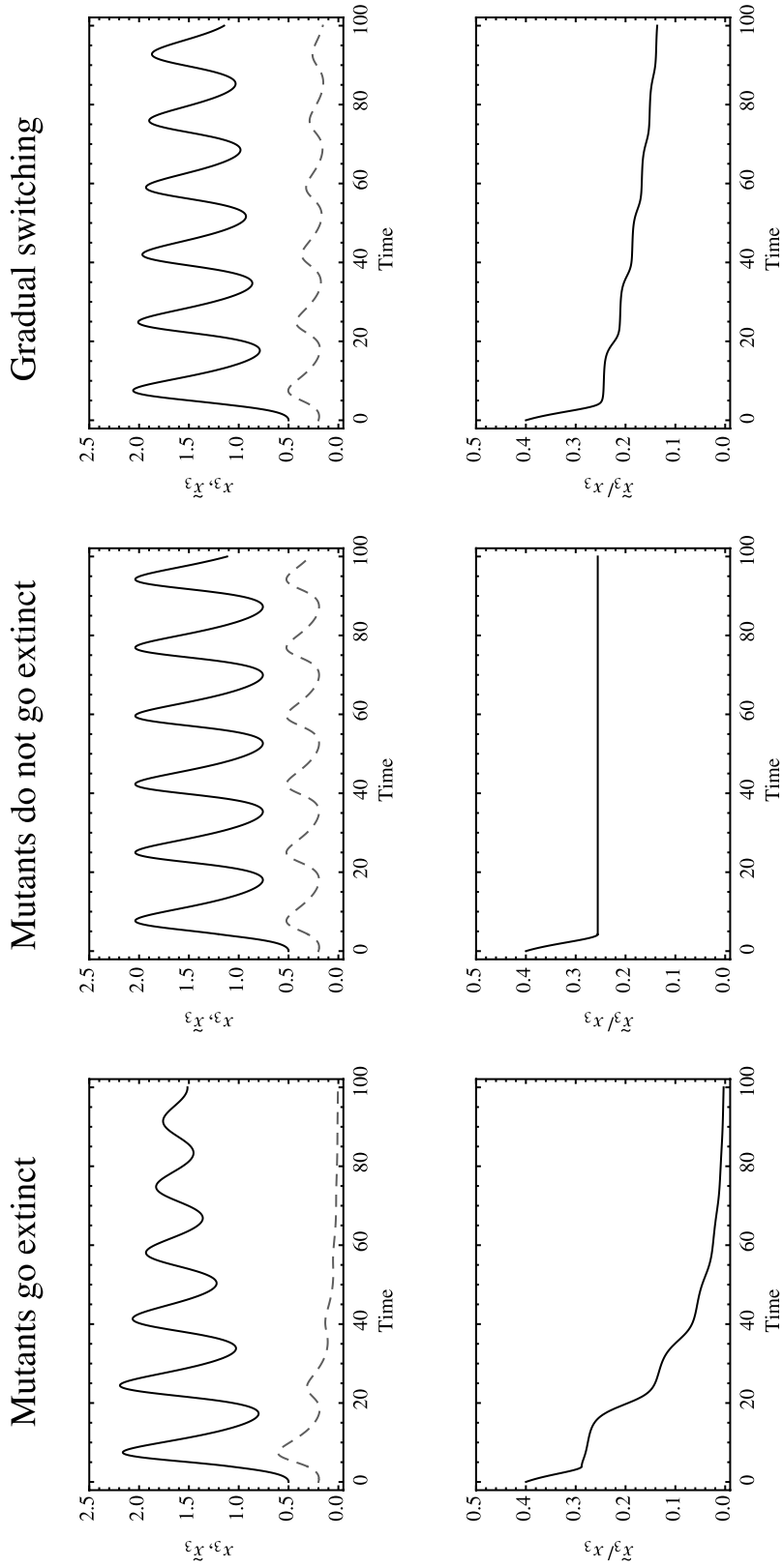


Fig. 1. Simulation of the resident-mutant system (12) with $\tilde{v}_1 = \lambda_2 / (\lambda_1 + \lambda_2)$. In the left-hand panels, v_1 is given by (9) and (15). In this case, condition (14) does not hold with a positive k^* since $\tilde{v}_1 \neq v_1$ on the attractor and mutants die out. In the middle panels, v_1 is given by (9) and (11). Now condition (14) holds with a positive k^* and mutants survive in the system. The right-hand panels show simulations where predator strategy changes gradually with changing population densities according to the formula $u_1 = (e_1 \lambda_1 x_1 / e_2 \lambda_2 x_2)^{\mu} / (1 + (e_1 \lambda_1 x_1 / e_2 \lambda_2 x_2)^{\mu})$ with the switching precision $\mu = 5$. Parameters used for simulations: $r_1 = 1$, $r_2 = 0.5$, $\lambda_1 = 1$, $\lambda_2 = 0.8$, $m = 0.2$, $e_1 = e_2 = 0.1$.

and residents eventually cycling in phase and in constant proportions (Fig. 1, middle panels) along Lotka-Volterra trajectories on the attractor. In fact, for the parameters used in Fig. 1, the lower middle panel indicates that this stable polymorphic cyclic state already emerges on a population time-scale (i.e. in the medium term) before $t = 10$. On the evolutionary time-scale, further decrease in the proportion of mutants is possible only through fluctuations that perturb the system away from the attractor when residents use optimal strategies. On the other hand, if residents switch strategies between 0 and 1 more gradually on either side of the attractor, mutants tend to extinction on a population time-scale (Fig. 1, right panels).

In summary, the introduction of mutant predator strategists does not alter the fundamental properties of the limiting trajectories as Lotka-Volterra cycles adjusted to the overall population size $x_3 + \tilde{x}_3$. It is in this sense that the existence of residents playing the optimal strategy (as a function of the current population distribution) produces an evolutionarily stable state that resists invasion by mutant strategists. Furthermore, polymorphism can evolve, although, for this to occur here, the combined resident–mutant predator strategy on the attractor must satisfy (14) with $k^* > 0$. If resident predators use the strategy given by (11) adjusted to the overall number of predators, no polymorphism will evolve unless we are in the case where $\tilde{v}_1 = \lambda_2 / (\lambda_1 + \lambda_2)$.

At first glance, this latter case might seem very unlikely. However, if mutants disperse from patch 1 to patch 2 with rate λ_1 and from patch 2 to patch 1 with λ_2 , which corresponds to their search rates in either patch, then the proportion of mutants in patch 1 will be given exactly by this formula. For example, if the search rate in both patches is the same $\lambda_1 = \lambda_2$, this formula predicts equal preferences of ‘naive’ mutants for either patch. Then the two strategies, one which maximizes predator payoff and another which leads to undirected predator movement, co-exist.

Optimal diet selection model

In this subsection, there is again one predator species foraging on two prey species, but in contrast to our previous foraging model, we assume that the environment is homogeneous. This means that a searching predator encounters individual prey sequentially and upon each encounter it has to decide whether to accept the encountered prey type or to search for a new one. Here the trade-off is not where to forage but whether to accept or to reject a prey. Acceptance of a prey means that there is an associated cost to handle this prey type, called the handling time, that plays an important role. Thus, the underlying linear functional response in the foraging model of the previous subsection must be replaced by the Holling type II functional response for multiple prey types. Following van Baalen *et al.* (2001), we will consider a situation where a predator has a preferred prey type (prey type 1) on which it always feeds, but there is also an alternative (allochthonous) prey type. We assume that the alternative prey type density x_2 is constant in the environment, i.e. not influenced by predation. This leads to the preferred predator–prey resident dynamics

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 \left(r_1 - \frac{\lambda_1 u_1 x_3}{1 + h_1 \lambda_1 u_1 x_1 + h_2 \lambda_2 u_2 x_2} \right) \\ \frac{dx_3}{dt} &= x_3 \left(\frac{e_1 \lambda_1 u_1 x_1 + e_2 \lambda_2 u_2 x_2}{1 + h_1 \lambda_1 u_1 x_1 + h_2 \lambda_2 u_2 x_2} - m \right). \end{aligned} \tag{16}$$

Here $h_i > 0$ are handling times (i.e. the time a predator needs to process and consume a prey item) and u_i is the probability of accepting a prey of species i when encountered. That is, the strategy space for the predator species is the two-dimensional unit square $U \equiv \{(u_1, u_2) \mid 0 \leq u_1 \leq 1 \text{ and } 0 \leq u_2 \leq 1\}$. The meaning of other parameters and variables is the same as in the previous subsection.

The fitness function for an individual predator using strategy $v = (v_1, v_2)$ when all predators in the monomorphic resident system use $u = (u_1, u_2)$ is given by the G -function:⁶

$$G(v; u, x_1, x_2) = \frac{e_1 \lambda_1 v_1 x_1 + e_2 \lambda_2 v_2 x_2}{1 + h_1 v_1 \lambda_1 x_1 + h_2 \lambda_2 v_2 x_2} - m. \quad (17)$$

It is a well-known result in optimal foraging theory (Charnov, 1976; Stephens and Krebs, 1986; Houston and McNamara, 1999) that the strategy that maximizes the resident fitness always accepts the better prey type, which we assume is prey species 1 (the prey type with the higher e_i/h_i ratio is the better type and so we assume that $e_1/h_1 > e_2/h_2$), upon each encounter ($u_1 = 1$), while the alternative prey type will be accepted only when the density of prey type 1 is below the threshold level $x_1^* = e_2/(\lambda_1(e_1 h_2 - e_2 h_1))$. Specifically, the optimal strategy is

$$N(x) = \begin{cases} (1, 1) & \text{if } x_1 < \frac{e_2}{\lambda_1(e_1 h_2 - e_2 h_1)} \\ (1, 0) & \text{if } x_1 > \frac{e_2}{\lambda_1(e_1 h_2 - e_2 h_1)} \\ \{(1, u_2) \mid 0 \leq u_2 \leq 1\} & \text{if } x_1 = \frac{e_2}{\lambda_1(e_1 h_2 - e_2 h_1)}. \end{cases} \quad (18)$$

It has been shown (van Baalen *et al.*, 2001; Křivan and Eisner, 2003; Křivan and Schmitz, 2003) that the resident population–trait dynamics combining (16) with (18) can promote species co-existence without stabilizing it at an equilibrium. Indeed, model (16) with fixed preferences u_1 and u_2 is not persistent, because the Holling type II functional response destabilizes population dynamics. However, when predators' diet choice is optimal, a locally asymptotically stable limit cycle emerges (the small amplitude limit cycle in Fig. 2A). This locally stable limit cycle is partly formed by the 'switching' line $x_1 = x_1^*$. Local stability of this limit cycle implies that there is only one possible value of the optimal predator strategy on this line due to the forward invariance of the cycle. That is, this strategy can be determined by considering the population dynamics exactly as for the two-patch predator–prey model [the explicit formula for u_2 when $x_1 = x_1^*$ was given in van Baalen *et al.* (2001)].

Once again, we can ask if such a strategy is evolutionarily stable. We introduce a mutant with a strategy that is different from the resident strategy. The mutant–resident system is

⁶ Note that the G -function again does not depend on the resident strategy or on the predator density. However, unlike our first foraging model, $G(v; u, x_1, x_2)$ is not a linear function of v and so cannot be expressed in the form of a matrix game. Nevertheless, maximization methods can be used to obtain the optimal predator strategy in this game against nature.

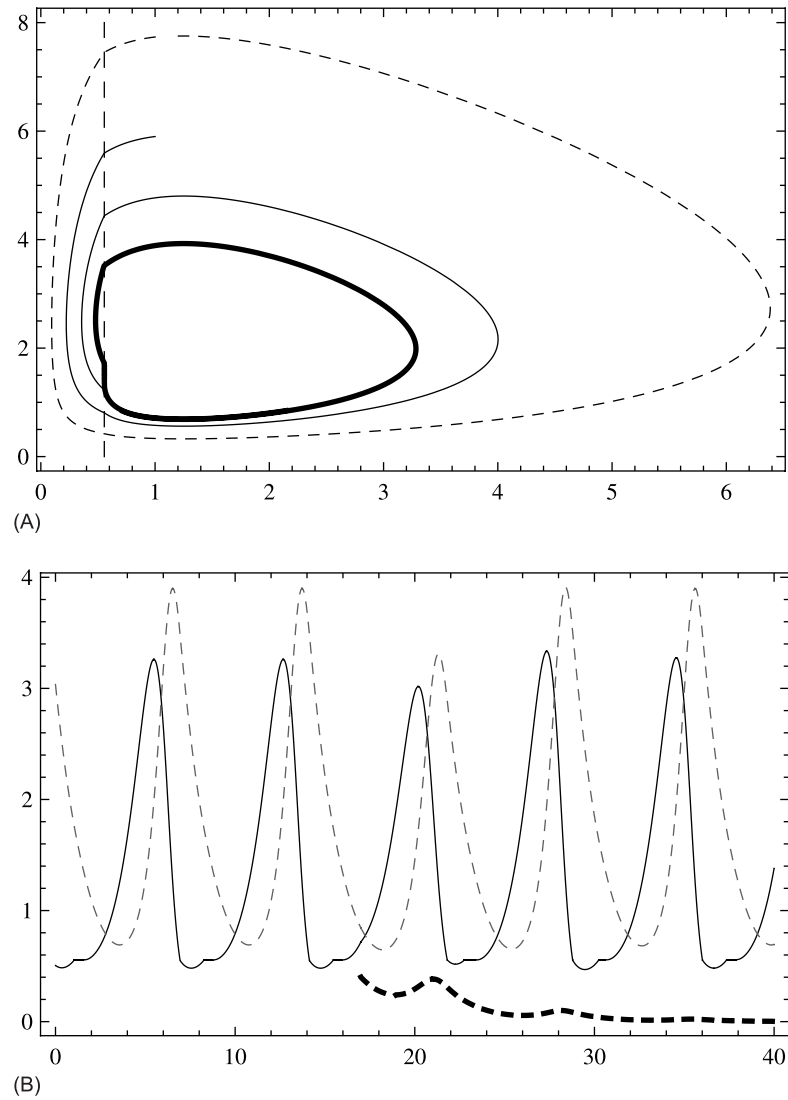


Fig. 2. Simulation of the resident-mutant system (19). Panel (A) shows resident-trait dynamics. There are two limit cycles. The small amplitude limit cycle (the inner cycle of the solid line) is locally stable while the large amplitude limit cycle (dashed line) is unstable. Panel (B) shows that when mutants (\tilde{x}_3 , thick dashed line) are introduced in small quantity at time $t = 17$ when the resident-trait dynamics are on the attractor, mutants die out. The solid line is the resident prey density (x_1), while the dashed line is the resident predator density (x_3). Here mutant predators use strategy $\tilde{u}_1 = \tilde{u}_2 = 1$. Parameters used in simulations: $x_2 = 5$, $r_1 = 1.2$, $\lambda_1 = \lambda_2 = 1$, $e_1 = 1$, $e_2 = 0.1$, $h_1 = h_2 = 0.2$, $m = 1$.

$$\begin{aligned}
\frac{dx_1}{dt} &= x_1 \left(r_1 - \frac{\lambda_1 u_1 x_3}{1 + h_1 u_1 \lambda_1 x_1 + h_2 u_2 x_2} - \frac{\lambda_1 \tilde{u}_1 \tilde{x}_3}{1 + h_1 \tilde{u}_1 \lambda_1 x_1 + h_2 \lambda_2 \tilde{u}_2 x_2} \right) \\
\frac{dx_3}{dt} &= x_3 \left(\frac{e_1 \lambda_1 u_1 x_1 + e_2 \lambda_2 u_2 x_2}{1 + h_1 u_1 \lambda_1 x_1 + h_2 \lambda_2 u_2 x_2} - m \right) \\
\frac{d\tilde{x}_3}{dt} &= \tilde{x}_3 \left(\frac{e_1 \lambda_1 \tilde{u}_1 x_1 + e_2 \lambda_2 \tilde{u}_2 x_2}{1 + h_1 \tilde{u}_1 \lambda_1 x_1 + h_2 \lambda_2 \tilde{u}_2 x_2} - m \right).
\end{aligned} \tag{19}$$

Note that the predator G -function for the resident–mutant system is identical to that of the resident system (i.e. $G(v; u, \tilde{u}, x, \tilde{x}) = G(v; u, x)$ in (17)) and so does not depend on the mutant’s strategy or its density. Thus, the optimal strategy remains (18).

Due to (7) applied to x_3 , the proportion of mutant predators will be strictly decreasing at those times when mutants use a different strategy than predators (Fig. 2B). If the mutant strategy is different than the resident’s optimal strategy off the switching line $x_1 = x_1^*$, then at every part of the limit cycle of the resident–mutant system that is not on the switching line, we have \tilde{x}_3/x_3 is strictly decreasing. In fact, the proportion of mutants in the system approaches 0 (i.e. the mutants go extinct). Moreover, introduction of mutant predators can qualitatively change the evolutionary behaviour in this model even though they go extinct. The reason for this is that the resident system also contains a large amplitude unstable limit cycle (Fig. 2A), outside of which the system spirals outwards. The introduction of mutants into a resident system that is initially inside the large unstable limit cycle can evolve to population densities outside this cycle, which leads to instability. However, for this to happen when the resident system is near the inner stable limit cycle, the number of mutants cannot be too low initially.

PREDATOR–PREY MODELS WHERE BOTH SPECIES HAVE A PLASTIC TRAIT

The previous section considered games where only one species showed adaptive plasticity. Now we will consider two predator–prey games where both predators and prey have an adaptive plastic trait. Two different ‘escape’ strategies of prey under predation risk were observed (reviewed in Schmitz *et al.*, 2004). First, prey try to avoid predators by moving to less riskier patches (e.g. Peacor and Werner, 2000). Second, prey reduce their encounter rate with predators by reducing their activity level (e.g. Sih, 1980; Lima and Dill, 1990; Werner, 1992; Kotler *et al.*, 2004). In this section, we study evolutionary stability of optimal escape strategies.

Two-patch predator–prey model when both species are mobile

The two-patch foraging model of the previous section assumed that only predators are mobile while prey are not. Following Křivan (1997), we consider now the case where both species are mobile and residents are monomorphic. Suppose that the resident predators with population density y use strategy $v = (v_1, v_2)$ and resident prey with density x use strategy $u = (u_1, u_2)$.⁷ The corresponding population dynamics for residents are

⁷ Both $u_1 + u_2$ and $v_1 + v_2 = 1$, since u_i and v_i give the respective proportions of their time that prey and predators spend in patch i .

$$\begin{aligned}\frac{dx}{dt} &= (r_1 - \lambda_1 v_1 y) u_1 x + (r_2 - \lambda_2 v_2 y) u_2 x \\ \frac{dy}{dt} &= (e_1 u_1 x - m_1) v_1 y + (e_2 u_2 x - m_2) v_2 y.\end{aligned}\tag{20}$$

That is, in terms of G -functions, we have

$$\begin{aligned}G_1(\tilde{u}; u, v, x, y) &= (r_1 - \lambda_1 v_1 y) \tilde{u}_1 + (r_2 - \lambda_2 v_2 y) \tilde{u}_2 \\ G_2(\tilde{v}; u, v, x, y) &= (e_1 u_1 x - m_1) \tilde{v}_1 + (e_2 u_2 x - m_2) \tilde{v}_2.\end{aligned}$$

Our first task is to determine the set of optimal strategies $N(x, y)$ defined in (2) for these G -functions of the resident system. We assume that, in this resident system, both prey and predators choose optimal foraging strategies. Since the fitness of individual prey and individual predators in (20) are both linear in u and in v , we can again use game-theoretic methods based on payoff matrices to determine these optimal strategies. However, in contrast to our previous models, now the predator's payoff depends on the prey strategy u as well as on the total prey density x . Similarly, prey payoff depends on the predator's strategy v and density y . For fixed densities x and y , these payoffs can now be represented through the bimatrix game (Hofbauer and Sigmund, 1998) given by matrices A (for prey) and B (for predator) respectively. For example, to obtain matrix A , prey fitness is written as

$$(r_1 - \lambda_1 v_1 y) u_1 + (r_2 - \lambda_2 v_2 y) u_2 = (r_1 - \lambda_1 y) u_1 v_1 + r_1 u_1 v_2 + r_2 u_2 v_1 + (r_2 - \lambda_2 y) u_2 v_2.$$

The individual entries in matrix A are then the appropriate coefficients in the right-hand side expansion. Combined with a similar calculation using predator fitness, we find that

$$A = \begin{pmatrix} r_1 - \lambda_1 y & r_1 \\ r_2 & r_2 - \lambda_2 y \end{pmatrix} \text{ and } B = \begin{pmatrix} e_1 x - m_1 & -m_1 \\ -m_2 & e_2 x - m_2 \end{pmatrix}.$$

The two matrices A and B are often written in the game-theoretic literature as a bimatrix

$$[A, B^T] = \begin{bmatrix} r_1 - \lambda_1 y, e_1 x - m_1 & r_1, -m_2 \\ r_2, -m_1 & r_2 - \lambda_2 y, e_2 x - m_2 \end{bmatrix},$$

where B^T is the transpose of matrix B . That is, the rows in this bimatrix correspond to prey strategy (first row means prey are in patch 1, second row means prey are in patch 2) and similarly columns represent predator strategy. The first of the two expressions in the entries of the bimatrix is the payoff for prey, while the second is payoff for predators. For example, if prey are in patch 1 and predators in patch 2, the corresponding payoffs are given in the upper right corner of the bimatrix. With this notation, the resident population dynamics (20) can be rewritten in matrix form as

$$\begin{aligned}\frac{dx}{dt} &= x \langle u, Av \rangle \\ \frac{dy}{dt} &= y \langle v, Bu \rangle.\end{aligned}\tag{21}$$

From now on, assume that predator mortality in patch 1 is higher than in patch 2 ($m_1 > m_2$) and prey intrinsic per capita growth rate in patch 1 is higher than that in patch 2 ($r_1 > r_2$).⁸

⁸ For the other cases, see Křivan (1997).

From standard techniques for bimatrix games (Hofbauer and Sigmund, 1998), $[A, B^T]$ has a unique Nash equilibrium pair (u, v) unless $x = (m_1 - m_2)/e_1$ or $y = (r_1 - r_2)/\lambda_1$. Specifically, if prey density is so low that $x < (m_1 - m_2)/e_1$, then it is always better for predators to be in patch 2 because the higher predator mortality rate in patch 1 cannot be compensated for by a higher growth rate there even if all prey stay in patch 1 (i.e. $e_1 u_1 x - m_1 < e_2 u_2 x - m_2$ for all $0 \leq u_1 \leq 1$). This then implies that all prey are better off in patch 1, as their growth rate is higher there and there are no predators (since $r_1 > r_2 - \lambda_2 y$). That is, the only Nash equilibrium is (u, v) with $u_1 = 1$ and $v_1 = 0$. On the other hand, if $x \geq (m_1 - m_2)/e_1$, then both predators and prey will be in patch 1 (i.e. $u_1 = v_1 = 1$) if predator density is so low that $y < (r_1 - r_2)/\lambda_1$. Finally, if both population densities are high enough [i.e. when $x \geq (m_1 - m_2)/e_1$ and $y \geq (r_1 - r_2)/\lambda_1$ with one of these a strict inequality], predators and prey will distribute themselves between the two patches according to the unique Nash equilibrium (u, v) given by

$$u_1 = \frac{m_1 - m_2 + e_2 x}{(e_1 + e_2)x}, v_1 = \frac{r_1 - r_2 + \lambda_2 y}{(\lambda_1 + \lambda_2)y}. \quad (22)$$

At this distribution, prey in patch 1 receive the same payoff as prey in patch 2 (and likewise for predators). It is interesting to note that the optimal predator strategy v_1 in (22) is exactly the same when prey are immobile and the population dynamics are on the attractor (see 11). This shows that prey movement does not influence the optimal predator distribution.

There are several reasons to assert that this Nash equilibrium is the foraging strategy chosen by each species at fixed densities x and y . First, (u, v) is the optimal strategy in the sense that it is the only strategy pair where individuals of each species maximize their per capita growth rate given the current distribution of the other species. Second, since (u, v) is a weak evolutionarily stable strategy, (u, v) is globally asymptotically stable for the continuous-time best response dynamics (Křivan *et al.*, 2008) that model dispersal behaviour whereby individuals move to the patch with the higher payoff. Thus, if dispersal occurs on a much faster time-scale than changes in population size (i.e. dispersal is effectively instantaneous), then we expect that each species strategy is at its Nash equilibrium.

To summarize these results for the resident system from the game-theoretic perspective, we have (Křivan, 1997)

$$N(x, y) = \left\{ \begin{array}{ll} (v_1^*, u_1^*) & \text{if } x > \frac{m_1 - m_2}{e_1 \lambda_1}, y > \frac{r_1 - r_2}{\lambda_1}, \\ (1, 1) & \text{if } x > \frac{m_1 - m_2}{e_1 \lambda_1}, y < \frac{r_1 - r_2}{\lambda_1}, \\ (1, 0) & \text{if } x < \frac{m_1 - m_2}{e_1 \lambda_1}, \\ \{(1, u_1) \mid u_1 \in [0, u_1^*]\} & \text{if } x = \frac{m_1 - m_2}{e_1 \lambda_1}, y > \frac{r_1 - r_2}{\lambda_1}, \\ \{(1, u_1) \mid u_1 \in [0, 1]\} & \text{if } x = \frac{m_1 - m_2}{e_1 \lambda_1}, y \leq \frac{r_1 - r_2}{\lambda_1}, \\ \{(v_1, 1) \mid v_1 \in [v_1^*, 1]\} & \text{if } x > \frac{m_1 - m_2}{e_1 \lambda_1}, y = \frac{r_1 - r_2}{\lambda_1}. \end{array} \right.$$

The resident population dynamics (20) was analysed by Boukal and Křivan (1999) when residents use the above optimal foraging strategy. They show that the dynamics converge to a global attractor formed by solutions of the Lotka-Volterra model

$$\begin{aligned}\frac{dx}{dt} &= x \left(\frac{r_1 \lambda_2 + r_2 \lambda_1}{\lambda_1 + \lambda_2} - \frac{\lambda_1 \lambda_2}{\lambda_1 + \lambda_2} y \right) \\ \frac{dy}{dt} &= y \left(\frac{e_1 e_2}{e_1 + e_2} x - \frac{e_1 m_2 + e_2 m_1}{e_1 + e_2} \right)\end{aligned}\quad (23)$$

that are contained in the region of the population density phase space where $x \geq (m_1 - m_2)/e_1$ and $y \geq (r_1 - r_2)/\lambda_1$. In particular, u_1 and v_1 given by (22) satisfy $0 \leq u_1 \leq 1$ and $0 \leq v_1 \leq 1$ on the attractor.

We now study invasibility of this resident system by a subpopulation of rare mutants for both species. The corresponding resident–mutant population dynamics when residents using the optimal strategy pair (u, v) are invaded by mutants of both species using \tilde{u} and \tilde{v} respectively is

$$\begin{aligned}\frac{dx}{dt} &= (r_1 - \lambda_1 v_1 y - \lambda_1 \tilde{v}_1 \tilde{y}) u_1 x + (r_2 - \lambda_2 v_2 y - \lambda_2 \tilde{v}_2 \tilde{y}) u_2 x \\ \frac{dy}{dt} &= (e_1 u_1 x + e_1 \tilde{u}_1 \tilde{x} - m_1) v_1 y + (e_2 u_2 x + e_2 \tilde{u}_2 \tilde{x} - m_2) v_2 y \\ \frac{d\tilde{x}}{dt} &= (r_1 - \lambda_1 v_1 y - \lambda_1 \tilde{v}_1 \tilde{y}) \tilde{u}_1 \tilde{x} + (r_2 - \lambda_2 v_2 y - \lambda_2 \tilde{v}_2 \tilde{y}) \tilde{u}_2 \tilde{x} \\ \frac{d\tilde{y}}{dt} &= (e_1 u_1 x + e_1 \tilde{u}_1 \tilde{x} - m_1) \tilde{v}_1 \tilde{y} + (e_2 u_2 x + e_2 \tilde{u}_2 \tilde{x} - m_2) \tilde{v}_2 \tilde{y}.\end{aligned}\quad (24)$$

Here, x and y are the densities of the resident prey and predator populations respectively and \tilde{x} and \tilde{y} are those of the mutant populations. The bimatrix game faced by the residents is now

$$\begin{bmatrix} r_1 - \lambda_1 y - \lambda_1 \tilde{v}_1 \tilde{y}, e_1 x + e_1 \tilde{u}_1 \tilde{x} - m_1 & r_1 - \lambda_1 \tilde{v}_1 \tilde{y}, -m_2 + e_2 \tilde{u}_2 \tilde{x} \\ r_2 - \lambda_2 \tilde{v}_2 \tilde{y}, -m_1 + e_1 \tilde{u}_1 \tilde{x} & r_2 - \lambda_2 y - \lambda_2 \tilde{v}_2 \tilde{y}, e_2 x + e_2 \tilde{u}_2 \tilde{x} - m_2 \end{bmatrix}.$$

That is, the residents will adjust their optimal strategy to the overall population size. In place of (22), the unique Nash equilibrium for this adjusted bimatrix game is

$$\begin{aligned}u_1 &= \frac{m_1 - m_2 + e_2(x + \tilde{x}) - \tilde{u}_1 \tilde{x}(e_1 + e_2)}{(e_1 + e_2)x} \\ v_1 &= \frac{r_1 - r_2 + \lambda_2(y + \tilde{y}) - \tilde{v}_1 \tilde{y}(\lambda_1 + \lambda_2)}{(\lambda_1 + \lambda_2)y}\end{aligned}\quad (25)$$

provided $0 \leq u_1, v_1 \leq 1$. The corresponding population dynamics for the overall prey and predator densities is

$$\begin{aligned}\frac{d(x + \tilde{x})}{dt} &= (x + \tilde{x}) \left(\frac{r_1 \lambda_2 + r_2 \lambda_1}{\lambda_1 + \lambda_2} - \frac{\lambda_1 \lambda_2}{\lambda_1 + \lambda_2} (y + \tilde{y}) \right) \\ \frac{d(y + \tilde{y})}{dt} &= (y + \tilde{y}) \left(\frac{e_1 e_2}{e_1 + e_2} (x + \tilde{x}) - \frac{e_1 m_2 + e_2 m_1}{e_1 + e_2} \right),\end{aligned}\tag{26}$$

the same dynamics as on the global attractor of the resident system (23). Thus, if mutant strategies are such that the adjusted Nash equilibrium satisfies $0 \leq u_1, v_1 \leq 1$ along the entire trajectory, then the introduction of mutants will not qualitatively change the resident dynamics. Moreover, from (24), along this trajectory

$$\begin{aligned}\frac{d\tilde{y}/y}{dt} &= \frac{\tilde{y}}{y} ((e_1 u_1 x + e_1 \tilde{u}_1 \tilde{x} - m_1)(\tilde{v}_1 - v_1) + (e_2 u_2 x + e_2 \tilde{u}_2 \tilde{x} - m_2)(\tilde{v}_2 - v_2)) \\ &= \frac{\tilde{y}}{y} ((e_1 u_1 x + e_1 \tilde{u}_1 \tilde{x} - m_1) - (e_2 u_2 x + e_2 \tilde{u}_2 \tilde{x} - m_2))(\tilde{v}_1 - v_1) = 0,\end{aligned}$$

since $e_1 u_1 x + e_1 \tilde{u}_1 \tilde{x} - m_1 = e_2 u_2 x + e_2 \tilde{u}_2 \tilde{x} - m_2$. Similarly, $(d\tilde{x}/x)/dt = 0$. In other words, the proportion of mutants in both species remains constant along this Lotka–Volterra trajectory and, on the attractor, both residents and mutants will follow Lotka–Volterra cycling dynamics. Thus, the mutants will not die out on a population time-scale, although their proportion in the population will not increase either. On an evolutionary time-scale, continued perturbations away from the attractor can again eventually lead to extinction of the mutants as in our previous two-patch foraging model where only the resident predators are adaptive.

The question remains as to how the resident–mutant system (24) evolves when u_1 or v_1 in (25) does not satisfy $0 \leq u_1, v_1 \leq 1$. In this case, the only Nash equilibrium will be such that at least one of the two populations will occupy one patch only. For example, if $u_1 > 1$ in (25), then $e_1 x + e_1 \tilde{u}_1 \tilde{x} - m_1 < -m_2 + e_2 \tilde{u}_2 \tilde{x}$ and $-m_1 + e_1 \tilde{u}_1 \tilde{x} < e_2 x + e_2 \tilde{u}_2 \tilde{x} - m_2$. In other words, patch 2 strictly dominates patch 1 for predators (i.e. predators are better off in patch 2 no matter what strategy u_1 the resident prey use in that $e_1 u_1 x + e_1 \tilde{u}_1 \tilde{x} - m_1 < e_2 u_2 x + e_2 \tilde{u}_2 \tilde{x} - m_2$ for all $0 \leq u_1 \leq 1$). Thus, the unique Nash equilibrium has $v_1 = 0$ and so

$$\frac{d\tilde{y}/y}{dt} = \frac{\tilde{y}}{y} ((e_1 u_1 x + e_1 \tilde{u}_1 \tilde{x} - m_1) - (e_2 u_2 x + e_2 \tilde{u}_2 \tilde{x} - m_2)) \tilde{v}_1 \leq 0$$

with equality if and only if $\tilde{v}_1 = 0$. That is, along this part of the trajectory, the proportion of mutant predators strictly decreases unless \tilde{v}_1 is the same as the resident predator strategy. The last statement can also be shown if $u_1 < 0$ in (25).

In summary, $(d\tilde{y}/y)/dt \leq 0$ along every trajectory and so \tilde{y}/y approaches a limit $k^* \geq 0$. Similarly, \tilde{x}/x approaches a limit $l^* \geq 0$. Moreover, the limiting behaviour of the system is the same as the resident system with x and y replaced by $(1 + l^*)x$ and $(1 + k^*)y$ respectively. Thus, the combined resident–mutant dynamics approaches the global attractor formed by Lotka–Volterra cycles of (26) contained in the region where $(1 + l^*)x \geq (m_1 - m_2)/e_1$ and $(1 + k^*)y \geq (r_1 - r_2)/\lambda_1$. Again, we find that the existence of residents playing their optimal strategy yields an evolutionarily stable state on a population time-scale comprised of a fixed proportion of mutants in each species.

A predator–prey model with adaptive activity levels

In this subsection, we consider evolutionary stability of a predator–prey model in a homogeneous environment where both prey and predators change their activity levels to maximize their fitness. Following Křivan (2007), the monomorphic resident dynamics is

$$\begin{aligned}\frac{dx}{dt} &= (r_1u + r_2 - (\lambda_1u + \lambda_2v)y) x = x \langle (u, 1 - u), A(v, 1 - v) \rangle \\ \frac{dy}{dt} &= (e(\lambda_1u + \lambda_2v)x - (m_1 + m_2v)) y = y \langle (v, 1 - v), B(u, 1 - u) \rangle,\end{aligned}\tag{27}$$

where $0 \leq u \leq 1$ ($0 \leq v \leq 1$) denotes prey (predator) activity. This dynamics models the foraging–predation risk trade-offs undertaken by both species. In particular, with all parameters positive (except possibly r_2), increased prey activity (u) increases prey growth rate ($r_1u + r_2$) but it also increases the encounter rate with predators ($\lambda_1u + \lambda_2v$). Similarly, increasing predator activity (v) increases both predator growth rate ($e(\lambda_1u + \lambda_2v)x$) and mortality rate ($m_1 + m_2v$).⁹

The bimatrix $[A, B^T]$ of the underlying predator–prey game is

$$\begin{bmatrix} r_1 + r_2 - (\lambda_1 + \lambda_2)y, e\lambda_2x - m_2 + e\lambda_1x - m_1 & r_1 + r_2 - \lambda_1y, e\lambda_1x - m_1 \\ r_2 - \lambda_2y, e\lambda_2x - m_2 - m_1 & r_2, -m_1 \end{bmatrix},$$

where rows describe the strategy of prey and columns the strategy of predators. That is, the first row (column) corresponds to strategy $u = 1$ (respectively, $v = 1$) where prey (predator) is fully active while the second row (column) is for completely inactive prey (predator) with $u = 0$ (respectively, $v = 0$).

For each fixed prey and predator densities that are different from $x_s = m_2/(e\lambda_2)$ and $y_s = r_1/\lambda_1$, the unique Nash equilibrium (u, v) is at a vertex of the unit square. Specifically, we have

$$u = \begin{cases} 1 & \text{if } y < \frac{r_1}{\lambda_1} \\ 0 & \text{if } y > \frac{r_1}{\lambda_1} \end{cases} \quad \text{and} \quad v = \begin{cases} 1 & \text{if } x > \frac{m_2}{e\lambda_2} \\ 0 & \text{if } x < \frac{m_2}{e\lambda_2} \end{cases}.\tag{28}$$

When $x = x_s$ ($y = y_s$), the optimal strategy of predators (prey) is not uniquely defined and can be anywhere between 0 and 1. In this case, there are infinitely many Nash equilibria (if $x = x_s$ and $y = y_s$, all points in the unit square are Nash equilibria). If residents use their optimal strategy, the long-term evolution of (5) can be quite complex, depending on

⁹ Model (27) assumes that the encounter rate between prey and predators is a linear function of prey and predator activity. Several other functional dependencies have been considered in the literature (Yapp, 1955; Skellam, 1958; Werner and Anholt, 1993; Křivan and Siroť, 2004). For example, Yapp (1955) considered prey and predators moving at characteristic velocities u and v in a two-dimensional space. Assuming that these animals have a circular perceptual field and that the direction of predator movement is randomly and uniformly distributed with respect to prey movement direction, he derived that the encounter rate of a prey individual with a predator is proportional to $\sqrt{u^2 + v^2}$. In our model (27), this formula was approximated by a linear relationship for mathematical tractability.

the choice of parameters (see Figure 3 of Křivan, 2007). However, when $\lambda_2/m_2 < \lambda_1/m_1$, $r_1/\lambda_1 > r_2/\lambda_2$, and $r_2 > 0$ (conditions that we will assume from now on), the resident population dynamics converge to the equilibrium $E = (x_s, y_s)$ (for a corresponding Lyapunov function, see Appendix 2) and at this equilibrium the species preferences are $u^* = (m_1\lambda_2)/(m_2\lambda_1)$ and $v^* = (r_2\lambda_1)/(r_1\lambda_2)$.

Once again we ask whether adaptive residents can resist invasion by mutants playing different strategies \tilde{u} and \tilde{v} for prey and predator respectively. Now, the resident–mutant population dynamics is

$$\begin{aligned} \frac{dx}{dt} &= (r_1u + r_2 - (\lambda_1u + \lambda_2v)y - (\lambda_1u + \lambda_2\tilde{v})\tilde{y}) x = x\langle(u, 1 - u), A(v, 1 - v)\rangle \\ \frac{dy}{dt} &= (e(\lambda_1u + \lambda_2v)x + e(\lambda_1\tilde{u} + \lambda_2v)\tilde{x} - (m_1 + m_2v)) y = y\langle(v, 1 - v), B(u, 1 - u)\rangle \\ \frac{d\tilde{x}}{dt} &= (r_1\tilde{u} + r_2 - (\lambda_1\tilde{u} + \lambda_2v)y - (\lambda_1\tilde{u} + \lambda_2\tilde{v})\tilde{y}) \tilde{x} = \tilde{x}\langle(\tilde{u}, 1 - \tilde{u}), A(v, 1 - v)\rangle \\ \frac{d\tilde{y}}{dt} &= (e(\lambda_1u + \lambda_2\tilde{v})x + e(\lambda_1\tilde{u} + \lambda_2\tilde{v})\tilde{x} - (m_1 + m_2\tilde{v})) \tilde{y} = \tilde{y}\langle(\tilde{v}, 1 - \tilde{v}), B(u, 1 - u)\rangle. \end{aligned} \quad (29)$$

That is, the bimatrix $[A, B^T]$ from the adaptive residents' perspective is adjusted by the mutants according to

$$\begin{aligned} A &= \begin{pmatrix} r_1 + r_2 - (\lambda_1 + \lambda_2)y - \lambda_1\tilde{y} - \lambda_2\tilde{v}\tilde{y} & r_1 + r_2 - \lambda_1y - \lambda_1\tilde{y} - \lambda_2\tilde{v}\tilde{y} \\ r_2 - \lambda_2y - \lambda_2\tilde{v}\tilde{y} & r_2 - \lambda_2\tilde{v}\tilde{y} \end{pmatrix} \\ B &= \begin{pmatrix} e\lambda_2x - m_2 + e\lambda_1x - m_1 + e\lambda_1\tilde{u}\tilde{x} + e\lambda_2\tilde{x} & e\lambda_2x - m_2 - m_1 + e\lambda_1\tilde{u}\tilde{x} + e\lambda_2\tilde{x} \\ e\lambda_1x - m_1 + e\lambda_1\tilde{u}\tilde{x} & -m_1 + e\lambda_1\tilde{u}\tilde{x} \end{pmatrix}. \end{aligned}$$

The unique Nash equilibrium is given by (28) with x and y replaced by $x + \tilde{x}$ and $y + \tilde{y}$ respectively [see (34) in Appendix 2]. That is, adaptive residents simply base their decision on the overall population numbers including mutants. From Appendix 2, mutants cannot increase their proportion of the population (i.e. $(d\tilde{x}/x)/dt \leq 0$ and $(d\tilde{y}/y)/dt \leq 0$) and all trajectories of (29) converge to the set where $x + \tilde{x} = m_2/(e\lambda_2)$ and $y + \tilde{y} = r_1/\lambda_1$.

In summary, the existence of adaptive residents forces the overall population sizes to their equilibrium values (x_s, y_s) . It is in this sense that the existence of residents using optimal behaviour implies that the system is evolutionarily stable.

DISCUSSION

This article addresses a complex relationship between plasticity, population dynamics, and evolutionary stability in predator–prey Lotka–Volterra type models. Static evolutionary stability conditions for multiple species are much more difficult than for a single species. For instance, suppose that prey fitness depends only on the strategy used by predators as the classical Lotka–Volterra model assumes (i.e. there is no prey density dependence). It is then unclear why, when the prey population departs from its equilibrium strategy, it should return to this equilibrium, as its fitness does not depend on its own strategy. In this article, we have adopted the approach that the adaptive resident system will be stable at current

population densities in that residents must have no incentive to change their strategy. From this assumption, it is then clear the residents, who all use an optimal strategy, must maximize their own fitness given these densities. This then makes the resident's strategy a (possibly multivalued) function of population densities. This function is then fed back to the population dynamics, which produces a resident population dynamics and we ask whether this system can be invaded by mutant strategists.

In these predator–prey models that consider explicit resident–mutant population dynamics, there is yet another complication in that the resident system on its own often evolves to periodic fluctuations. Since we can no longer expect a single evolutionarily stable state in such circumstances, we examine instead whether the introduction of mutants into these fluctuating environments fundamentally alters this qualitative behaviour. Our main results show that, again in this setting, the mutant population cannot increase relative to residents and that, furthermore, the combined resident–mutant population dynamics eventually follow the same periodic fluctuations when the resident system has a globally stable equilibrium or a global attractor consisting of a family of limit cycles. It is in this latter sense that the existence of adaptive residents in our optimal foraging predator–prey models produces an evolutionarily stable system.

Our modelling approach to optimal adaptive foraging assumes that individual residents change their behaviour on a much faster time-scale than the population dynamics changes species densities. This is reasonable for our models where individual behaviour is typically characterized by choice of habitat or activity levels. Several experimental set-ups in which distance between patches is relatively small or prey rapidly change their behaviour under predation risk (e.g. Murdoch, 1969; Milinski, 1979; Fraser and Huntingford, 1986; Holbrook and Schmitt, 1988; Brown and Alkon, 1990; Brown, 1998; Lima, 1998a, 1998b; Sih, 1998; Peacor and Werner, 2001; Werner and Peacor, 2003; Berec *et al.*, 2006) conform to this assumption. There are also examples of rapid morphological and physiological adaptations in some prey species (e.g. Wikelski and Thom, 2000; Yalden, 2000; Relyea and Auld, 2004; Losos *et al.*, 2006). Evolution of phenotypes that are behaviourally flexible and that require changes in genotype [i.e. evolution of phenotypic plasticity (e.g. Schlichting and Pigliucci, 1998; Miner *et al.*, 2005)] runs on an evolutionary (slow) time-scale. For such systems, the adaptive dynamics method (e.g. Dieckmann and Law, 1996; Geritz *et al.*, 1998; Abrams, 2001; Cressman and Hofbauer, 2005; Vincent and Brown, 2005; Dercole and Rinaldi, 2008) seems more suitable. Here, population densities quickly attain stable equilibrium values for current phenotypes and the main point of interest is the dynamics of population behaviour that is often described by the canonical equation of adaptive dynamics. Equilibria of this dynamics are then tested for their evolutionary stability by confirming that they cannot be successfully invaded by rare mutants (e.g. Mylius and Dieckmann, 1995; Metz *et al.*, 2008) and that evolutionary branching does not occur (Geritz *et al.*, 1997; Claessen and Dieckmann, 2002). In most of our models based on the time-scales reversed, population densities cycle on an attractor rather than converge to equilibrium and, although mutants can survive in our predator–prey systems on a population time-scale, their survival does not qualitatively change the population dynamics.

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APPENDIX 1: ON THE ATTRACTOR OF MODEL (12)

To prove that the trajectories of model (12) converge to the global attractor contained in the hyperplane $M = \{(x_1, x_2, x_3, \tilde{x}_3) \mid e_1 x_1 = e_2 x_2\}$, we generalize the method of Boukal and Křivan (1999) by introducing the function

$$V(x_1, x_2, x_3, \tilde{x}_3) = \lambda_2 \left(e_1 x_1 - m - m \ln \left(\frac{e_1 x_1}{m} \right) \right) + \lambda_1 \left(e_2 x_2 - m - m \ln \left(\frac{e_2 x_2}{m} \right) \right) \\ + \lambda_1 \lambda_2 x_3 - (r_1 \lambda_2 + r_2 \lambda_1) - (r_1 \lambda_2 + r_2 \lambda_1) \ln \left(\frac{\lambda_1 \lambda_2 x_3}{r_1 \lambda_2 + r_2 \lambda_1} \right) + \lambda_1 \lambda_2 \tilde{x}_3.$$

We obtain the following two properties of V . First, $V(x_1, x_2, x_3, \tilde{x}_3) > 0$ except at equilibrium E where

$$V\left(\frac{m}{e_1}, \frac{m}{e_2}, \frac{r_1\lambda_2 + r_2\lambda_1}{\lambda_1\lambda_2}, 0\right) = 0.$$

Second, from (12), the derivative of V along trajectories of the resident–mutant system is

$$\frac{dV}{dt}(x_1, x_2, x_3, \tilde{x}_3) = -(e_1x_1 - e_2x_2)((r_1\lambda_2 + r_2\lambda_1)v_1 - r_1\lambda_2). \quad (30)$$

Since $v_1 = 1$ when $e_1x_1 > e_2x_2$ and $v_1 = 0$ when $e_1x_1 < e_2x_2$, $dV/dt < 0$ except at points with $e_1x_1 = e_2x_2$ (where it is 0). That is, V is a (non-strict) Lyapunov function. Thus, the omega-limit set of any trajectory of (12) (i.e. the global attractor of (12)) is contained in the hyperplane M . Due to the LaSalle invariance principle (Shevitz and Paden, 1994), the omega-limit set of model (12) is contained in the largest invariant subset of M . Thus, we will study now invariant subsets of M .

Points on a trajectory of (12) in an invariant subset of M must satisfy $(d/dt)(e_1x_1) = (d/dt)(e_2x_2)$ when $e_1x_1 = e_2x_2$. Substituting these conditions into (12) yields

$$v_1 = \frac{r_1 - r_2 + \lambda_2x_3 + \tilde{x}_3(\lambda_2\tilde{v}_2 - \lambda_1\tilde{v}_1)}{(\lambda_1 + \lambda_2)x_3} \quad (31)$$

on the attractor. Since $\tilde{x}_3 = k^*x_3$ for some k^* there, we have (14). Moreover, since $0 \leq v_1 \leq 1$, we obtain the constraint

$$x_3 \geq \max \left\{ \frac{r_1 - r_2}{\lambda_1 + k^*(\lambda_1\tilde{v}_1 - \lambda_2\tilde{v}_2)}, \frac{r_2 - r_1}{\lambda_2 - k^*(\lambda_1\tilde{v}_1 - \lambda_2\tilde{v}_2)} \right\}.$$

Conversely, if v_1 in (14) is outside the interval $0 \leq v_1 \leq 1$, then the trajectory is at a point in M where $(d/dt)(e_1x_1) \neq (d/dt)(e_2x_2)$. That is, such points do not belong to an invariant subset of M and the trajectory must leave M .

Substituting the strategy (14) into model (12) leads to the following population dynamics on the attractor:

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 \frac{r_1\lambda_2 + r_2\lambda_1 - (x_3 + \tilde{x}_3)\lambda_1\lambda_2}{\lambda_1 + \lambda_2} \\ \frac{dx_3}{dt} &= x_3(e_1x_1 - m). \end{aligned} \quad (32)$$

It follows that trajectories of (32) are closed Lotka-Volterra cycles. Therefore, the attractor is formed by a family of these cycles that are contained in M .

APPENDIX 2: ON THE ATTRACTOR OF MODEL (27)

Here we show that the resident population dynamics (27) when both species are adaptive converges to the equilibrium $(x_s, y_s) = (m_2/(e\lambda_2), r_1/\lambda_1)$ when $r_1/\lambda_1 > r_2/\lambda_2$, $\lambda_2/m_2 < \lambda_1/m_1$ and $r_2 > 0$. To see this, consider the following function for $x > 0$ and $y > 0$:

$$V(x, y) = x - x_s - x_s \ln\left(\frac{x}{x_s}\right) + \frac{1}{e} \left(y - y_s - y_s \ln\left(\frac{y}{y_s}\right) \right). \quad (33)$$

$V(x, y) = 0$ at the point (x_s, y_s) and is positive otherwise. From (27),

$$\frac{dV}{dt} = \frac{(r_2\lambda_1 - r_1\lambda_2v)(e\lambda_2x - m_2) + (\lambda_1y - r_1)(m_2u\lambda_1 - \lambda_2m_1)}{e\lambda_1\lambda_2}.$$

Substitution of the optimal strategy (u, v) given by (28) yields $dV/dt < 0$ if $(x, y) \neq (x_s, y_s)$. Thus v is a strict Lyapunov function for the system and so (x_s, y_s) is globally asymptotically stable.

Next, we show that all trajectories of (29) converge to the set where $x + \tilde{x} = m_2/(e\lambda_2)$ and $y + \tilde{y} = r_1/\lambda_1$. From this resident–mutant system, we calculate

$$\frac{d\tilde{x}/x}{dt} = \frac{\tilde{x}}{x}(\tilde{u} - u)(r_1 - \lambda_1(y + \tilde{y}))$$

and

$$\frac{d\tilde{y}/y}{dt} = \frac{\tilde{y}}{y}(\tilde{v} - v)(e\lambda_2(x + \tilde{x}) - m_2).$$

Since residents use the strategies

$$u = \begin{cases} 1 & \text{if } y + \tilde{y} < \frac{r_1}{\lambda_1} \\ 0 & \text{if } y + \tilde{y} > \frac{r_1}{\lambda_1} \end{cases} \quad \text{and } v = \begin{cases} 1 & \text{if } x + \tilde{x} > \frac{m_2}{e\lambda_2} \\ 0 & \text{if } x + \tilde{x} < \frac{m_2}{e\lambda_2} \end{cases}, \quad (34)$$

$(d\tilde{x}/x)/dt \leq 0$ and $(d\tilde{y}/y)/dt \leq 0$. Thus $\lim_{t \rightarrow \infty} \tilde{x}/x = k^* \geq 0$ and $\lim_{t \rightarrow \infty} \tilde{y}/y = l^* \geq 0$.

The Lyapunov function (33) can be extended to the resident–mutant model by redefining V as

$$V(x, y, \tilde{x}, \tilde{y}) = x + \tilde{x} - x_s - x_s \ln\left(\frac{x}{x_s}\right) + \frac{1}{e}\left(y + \tilde{y} - y_s - y_s \ln\left(\frac{y}{y_s}\right)\right),$$

which satisfies $V(x_s, y_s, 0, 0) = 0$ and is positive otherwise. The derivative of V along trajectories of model (29) is

$$\frac{dV}{dt} = \frac{(r_2\lambda_1 - r_1\lambda_2v)(e\lambda_2(x + \tilde{x}) - m_2) + (\lambda_1(y + \tilde{y}) - r_1)(m_2u\lambda_1 - \lambda_2m_1)}{e\lambda_1\lambda_2}.$$

Since $r_2\lambda_1 - r_1\lambda_2 < 0$ and $m_2\lambda_1 - m_1\lambda_2 > 0$, $dV/dt < 0$ by (34) except at points where $x + \tilde{x} = m_2/(e\lambda_2)$ and $y + \tilde{y} = r_1/\lambda_1$. Thus, the attractor of (29) is contained in the latter set. In fact, since both \tilde{x}/x and \tilde{y}/y approach a limit as $t \rightarrow \infty$, each trajectory converges to a single limit point in this set.

