

Evolutionary branching and long-term coexistence of cycling predators: Critical function analysis

Stefan A.H. Geritz, Éva Kisdi*, Ping Yan

Department of Mathematics and Statistics, University of Helsinki, FIN-00014, Finland

Received 7 April 2006

Available online 24 March 2007

Abstract

It is well known that two predators with different functional responses can coexist on one prey when the system exhibits nonequilibrium dynamics. In this paper, we investigate under which conditions such coexistence is evolutionarily stable, and whether the two predators may evolve from a single ancestor via evolutionary branching. We assume that predator strategies differ in handling time, and hence in the shape of their Holling type II functional response. Longer handling times are costly in terms of lost foraging time, but allow the predator to extract more nutrients from the prey and therefore to produce more offspring per consumed prey. In the analysis, we apply a new method to accommodate arbitrary trade-off functions between handling time and offspring production. Contrary to previous results obtained assuming a particular trade-off [Kisdi, E. and Liu, S., 2006. *J. Evol. Biol.* 19, 49–58], we find that evolutionary branching of handling time is possible, although it does not appear to be very likely and can be excluded for a class of trade-offs. Evolutionarily stable coexistence of two predators occurs under less restrictive conditions, which are always satisfied when the trade-off function has two strongly concave parts connected by a convex piece.

© 2007 Elsevier Inc. All rights reserved.

Keywords: Adaptive dynamics; Critical function analysis; Evolutionary branching; Evolutionarily stable polymorphism; ESS; Geometric analysis; Handling time; Holling type II functional response; Nonequilibrium coexistence; Predator–prey system; Trade-off

1. Introduction

It is well known that several predator species can coexist utilising a single prey, provided that the system exhibits nonequilibrium dynamics such as limit cycles or chaos (Koch, 1974; McGehee and Armstrong, 1977; Hsu et al., 1978a, b; Levins, 1979; Armstrong and McGehee, 1980; Muratori and Rinaldi, 1989; Huisman and Weissing, 1999; Abrams and Holt, 2002; Abrams et al., 2003; Liu et al., 2003; Wilson and Abrams, 2005). Further, many models have addressed the question whether evolution will lead to cyclic population dynamics in systems with a single predator and prey (see Abrams, 2000 for a review). It is, however, far less understood whether evolution can lead to the coexistence of several cycling predators feeding on the same prey. The ecological models that demonstrate nonequilibrium coexistence do not address evolutionary stability,

whereas the evolutionary models that show the emergence of cycles do not consider coexistence.

For nonequilibrium coexistence, it is necessary that the instantaneous growth rate of the predator is a nonlinear function of prey abundance; otherwise the predator type that minimises the average prey density will outcompete every other type. This non-linearity can be due to different forms of functional or numerical responses. The simplest and best studied possibility, on which we focus in this article, is that the predator needs a nonnegligible amount of time to handle (attack, kill, consume, and digest) each item of prey, and hence the number of prey consumed by one predator per unit of time saturates with prey density according to the Holling type II functional response. The same functional response can destabilise the dynamics of the predator–prey system, because saturated predators cannot stop the prey growing when prey density is already high, and conversely unsaturated predators further reduce the prey when prey density is already low. Predator–prey systems with Holling type II functional response thus

*Corresponding author. Fax: +358 9 1915 1400.

E-mail address: eva.kisdi@helsinki.fi (E. Kisdi).

exhibit both non-linearity in the predator growth rate and cycles in the population dynamics, and thereby can maintain the coexistence of several predators (Armstrong and McGehee, 1980).

The most important condition for coexistence by the Armstrong–McGehee mechanism is that the predators have sufficiently large differences in the shape of their functional responses (Abrams and Holt, 2002). The shape of the Holling type II functional response depends on the predator's handling time such that the longer time the predator spends by handling, the faster its functional response saturates. In this article, we study the evolution of coexistence by studying the evolution of the predator's handling time.

If handling time were independent of every other trait that influences the population dynamics, then natural selection would obviously favour the shortest handling time and thereby exclude coexistence: Everything else being equal, the more time the predator spends by searching for prey rather than handling, the more prey it finds and the more offspring it can produce. However, predators with very short handling times will likely not be able to extract much of the nutrients from the captured prey. For this reason, we assume that the conversion factor between the number of prey consumed and the number of new predators produced is an increasing function of handling time. All possible predator types within a model share the same trade-off relationship. We also assume that the predators have the same prey capture rates and death rates, i.e., they differ only in their handling time and in the associated conversion factor.

We investigate the evolution of handling time using the framework of adaptive dynamics (Metz et al., 1996; Geritz et al., 1998). In particular, we address two questions: Firstly, can a single predator evolve into two coexisting types with different handling times by evolutionary branching? Secondly, can two different handling strategies form an evolutionarily stable coexistence?

Kisdi and Liu (2006) studied the evolution of handling time in the standard predator–prey model with Holling type II functional response (Koch, 1974; Hsu et al., 1978a, b; Armstrong and McGehee, 1980; Muratori and Rinaldi, 1989; Abrams and Holt, 2002; Abrams et al., 2003; Liu et al., 2003; Wilson and Abrams, 2005), assuming that the conversion factor between consumed prey and the number of new predators (γ) increases with handling time (h) according to the hyperbolic function

$$\gamma(h) = \left(c \frac{h - h_0}{h + \theta} \right)_+, \quad (1)$$

where c is the total amount of nutrients present in a prey item, h_0 is the minimum handling time necessary to extract any nutrients, and θ controls the speed of saturation. With the assumption of Eq. (1), the answers to the above two questions are both negative. Evolutionary branching is not possible in this model. Although two predators that differ only in their handling strategy but share the same

hyperbolic trade-off can coexist on an ecological time scale, no such coexistence is stable on an evolutionary time scale, because the handling times of initially different, coexisting predators always evolve to a single ESS. These results have been derived analytically and hold also if mutations can be of large effect; the proofs, however, are valid only for the specific trade-off function given by Eq. (1). This trade-off is biologically reasonable, but it is not the only reasonable choice possible. Note that the choice of the particular trade-off function in Eq. (1) is the least supported assumption of the model.

In this article, we investigate the evolution of handling time in the same model, but without a priori committing ourselves to a specific form of the trade-off function $\gamma(h)$. Instead, we use a technique we call *critical function analysis*. This technique has been developed by de Mazancourt and Dieckmann (2004) and Bowers et al. (2005; see also Rueffler et al. (2004) for closely related results), and it has been extended to study the coevolution of two species by Kisdi (2006). Briefly, we work out the local properties of $\gamma(h)$ in the neighbourhood of a given handling strategy h^* that are necessary for h^* to be an evolutionarily singular strategy. From this, we construct a family of critical functions such that if the trade-off function $\gamma(h)$ is tangential to a critical function at h^* , then h^* is singular. Convergence stability (Eshel, 1983; Christiansen, 1991) can be judged from the curvature of the trade-off function relative to the critical function. Evolutionary stability is investigated separately. Using these results, we can establish what types of evolutionary singularities are possible, construct concrete examples of $\gamma(h)$ for any of them, and discuss whether the conditions for evolutionary branching (or other types of singularities) are likely to be met. Next, we investigate systems with two predators, and construct examples where two different handling strategies coexist in an evolutionarily stable manner. Throughout, we rely on geometrical considerations that are easy to visualise.

2. The model

We assume that there is a single prey species with logistic population growth, and possibly more than one predator types with Holling II functional response. Several predator types, henceforth called strategies, can coexist when the system exhibits nonequilibrium dynamics. The predator strategies differ in their handling times (h_i), which determine the shape of their functional response and also determine how much nutrient they can extract from each captured prey individual. The latter affects the number of new predators produced per prey item consumed, i.e., the conversion factor $\gamma(h_i)$. The population dynamics are given by the well-known equations

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K} \right) - \sum_i \frac{\beta x}{1 + \beta h_i x} y_i,$$

$$\frac{dy_i}{dt} = \left(\gamma(h_i) \frac{\beta x}{1 + \beta h_i x} - d \right) y_i, \tag{2}$$

where x and y_i are, respectively, the population densities of the prey and of predator i ($i = 1, \dots, n$), r and K are the parameters of logistic population growth, β is the capture rate per searching time, and d is the death rate of predators. We emphasise that this model covers only closely related predators, because it assumes that all predators have the same capture and death rates, and also share the trade-off function $\gamma(h)$.

By introducing the dimensionless quantities $\tilde{x} = x/K$, $\tilde{y}_i = \beta y_i/r$, $\tilde{t} = rt$, $\tilde{h}_i = \beta K h_i$, $\tilde{\gamma}(\tilde{h}_i) = \beta K \gamma(\tilde{h}_i/\beta K)/r$, and $\tilde{d} = d/r$ and then dropping the tildes, we arrive at the scaled model equations

$$\begin{aligned} \frac{dx}{dt} &= x(1-x) - \sum_i \frac{x}{1+h_i x} y_i, \\ \frac{dy_i}{dt} &= \left(\gamma(h_i) \frac{x}{1+h_i x} - d \right) y_i. \end{aligned} \tag{3}$$

This model is the same as the one used by [Kisdi and Liu \(2006\)](#), except that here we do not assume any particular shape for the function $\gamma(h)$. Biological considerations, however, dictate the following properties of $\gamma(h)$ (cf. [Kisdi and Liu, 2006](#)):

- (i) $\gamma(h)$ should be a continuous and nondecreasing function, because handling a prey item longer will not result in less nutrient obtained. We assume that the predator handles the prey in a fixed way such that the amount of extracted nutrients is uniquely determined by the length of handling time.
- (ii) $\gamma(0) = 0$ because no nutrient can be extracted without handling. The conversion factor $\gamma(h)$ may be zero also on some interval $0 \leq h \leq h_0$ if some initial handling is necessary before nutrient extraction can commence.
- (iii) $\gamma(h)$ must saturate at some finite value c , which corresponds to the total nutrient content of a prey individual.

The population dynamical properties of Eqs. (3) are well known for the case of a single predator. The predator is viable if and only if $\gamma(h) > d(h+1)$. The system has a unique nontrivial fixed point at $\hat{x}(h) = d/(\gamma(h) - hd)$ and $\hat{y}(h) = (1 - \hat{x})(1 + h\hat{x})$, which is stable irrespectively of the value of $\gamma(h)$ if $h \leq 1$. For $h > 1$, the fixed point undergoes a supercritical (noncatastrophic) Hopf bifurcation when $\gamma(h) = d(h+1)h/(h-1)$, such that the trajectories converge to a unique stable limit cycle when the value of $\gamma(h)$ exceeds this threshold. With more than one predator, however, the system can have complex dynamics including multiple attractors and chaos ([Abrams et al., 2003](#)). Since coexistence at fixed points is not possible in this model, we shall focus on cycling populations.

Handling time evolves as new mutant predator strategies invade. Unlike [Kisdi and Liu \(2006\)](#), in this article we assume that mutations have only small phenotypic effects,

i.e., the mutant’s handling time is close to the resident predator’s (or one of the residents’) handling time. We also assume that mutations occur infrequently, so that the resident population has settled on its population dynamical attractor by the time the next mutant comes along. This latter assumption is standard in adaptive dynamics (see e.g. [Geritz et al., 1998](#)), but the results are robust with respect to more frequent mutations ([Meszena et al., 2005](#)).

Consider a system with a single resident predator strategy h , which has settled on the stable limit cycle of Eq. (3). The instantaneous per capita growth rate of a rare mutant predator with handling time h_{mut} is

$$\frac{1}{y_{\text{mut}}} \frac{dy_{\text{mut}}}{dt} = \gamma(h_{\text{mut}}) \frac{x(t; h, \gamma(h))}{1 + h_{\text{mut}} x(t; h, \gamma(h))} - d, \tag{4}$$

where $x(t; h, \gamma(h))$ is the density of the prey at time t as determined by the stable limit cycle of the resident population. The long-term invasion fitness of strategy h_{mut} , which determines whether the mutant eventually grows or declines in the resident population of h , is the time average of the instantaneous fitness,

$$s(h_{\text{mut}}, h) = \frac{\gamma(h_{\text{mut}})}{T(h)} \int_0^{T(h)} \frac{x(t; h, \gamma(h))}{1 + h_{\text{mut}} x(t; h, \gamma(h))} dt - d, \tag{5}$$

where $T(h)$ is the length of the limit cycle of the resident population of strategy h (cf. [Metz et al., 1992](#)).

The integrand in Eq. (5) with $h_{\text{mut}} = h$ will appear below repeatedly, hence we introduce the function

$$v(t; h, \gamma(h)) = \frac{x(t; h, \gamma(h))}{1 + h x(t; h, \gamma(h))} \tag{6}$$

for $t \in [0, T(h)]$, where $x(t; h, \gamma(h))$ is calculated along the stable limit cycle of Eq. (3) with a single predator. The limit cycle cannot be obtained analytically. We integrate Eq. (3) numerically using a simple predictor–corrector method, discard the transient during which the orbit converges to the limit cycle (convergence of the orbit being evaluated using a Poincare section), and integrate the system for a full cycle to obtain $x(t; h, \gamma(h))$ for $t \in [0, T(h)]$, where the system departs from the Poincare section at $t = 0$ and returns to the same point of the Poincare section at $t = T(h)$. Substituting into Eq. (6), we obtain $v(t; h, \gamma(h))$ numerically.

By repeated invasions of new mutants, handling time evolves in the direction of the fitness gradient $[\partial s(h_{\text{mut}}, h)/\partial h_{\text{mut}}]_{h_{\text{mut}}=h}$ ([Dieckmann and Law, 1996](#); [Geritz et al., 1998](#)). Directional evolution comes to a halt at evolutionarily singular strategies, where the fitness gradient vanishes. For the fitness function in Eq. (5), the condition for h^* to be a singular strategy is

$$\begin{aligned} \gamma'(h^*) &= \gamma(h^*) \frac{\int_0^{T(h^*)} v(t; h^*, \gamma(h^*))^2 dt}{\int_0^{T(h^*)} v(t; h^*, \gamma(h^*)) dt} \\ &= d \left(1 + \frac{\text{Var}(v(t; h^*, \gamma(h^*)))}{M(v(t; h^*, \gamma(h^*)))^2} \right), \end{aligned} \tag{7}$$

where Var and M stand for the variance and the mean value over time. The right-hand side depends on $x(t;h,\gamma(h))$, i.e., on the resident attractor via Eq. (6). To derive the last equality in Eq. (7), we used the condition that the resident's invasion fitness is necessarily zero, i.e.,

$$\frac{\gamma(h)}{T(h)} \int_0^{T(h)} v(t;h,\gamma(h)) dt = d \tag{8}$$

holds along the limit cycle.

3. Critical function analysis

Consider the particular slope of the trade-off function that makes a certain strategy singular. We shall refer to this as the critical slope. In our model, the critical slope at strategy $(h,\gamma(h))$ is the value of $\gamma'(h)$ given by Eq. (7).

A critical function $g(h)$ is a continuously differentiable function such that its slope is equal to the critical slope at all values of h and $g(h)$. Taking the critical slope from Eq. (7), a critical function is a solution of the ordinary differential equation

$$g'(h) = g(h) \frac{\int_0^{T(h)} v(t;h,g(h))^2 dt}{\int_0^{T(h)} v(t;h,g(h)) dt} \tag{9a}$$

There are infinitely many critical functions each corresponding to a different initial condition $g(0)$. As solutions of an ODE, critical functions cannot intersect one another and each solution is uniquely characterised by a single point. We shall denote the critical function that goes through a particular point (h_0,γ_0) by $g(h|h_0,\gamma_0)$. Our critical functions are the same as the A-boundaries of de Mazancourt and Dieckmann (2004), and are pieced together from the local invasion boundaries shown in Fig. 2 of Rueffler et al. (2004).

If the trade-off function $\gamma(h)$ coincides with a critical function $g(h)$, then every strategy h is singular. This is of course a highly degenerate situation. Given an arbitrary trade-off function, the singular strategies are the points where $\gamma'(h^*) = g'(h^*|h^*,\gamma(h^*))$ holds, i.e., where the trade-off function is tangential to a critical function.

Further, a singular strategy h^* is convergence stable if, in the neighbourhood of h^* , the fitness gradient $[\partial s(h_{mut},h)/\partial h_{mut}]_{h_{mut}=h}$ is positive for $h < h^*$ and negative for $h > h^*$. Using Eq. (5), this translates into the condition that $\gamma'(h)$ is greater than the right-hand side of Eq. (7) for $h < h^*$, but smaller than the right-hand side of Eq. (7) for $h > h^*$. In other words, the trade-off function must be more concave, or less convex, than the critical function $g(h|h^*,\gamma(h^*))$ in the vicinity of the singular point h^* for the singular point to be convergence stable (de Mazancourt and Dieckmann, 2004). The corresponding analytical condition for convergence stability is $[\partial^2 s/\partial h_{mut}^2 + \partial^2 s/\partial h \partial h_{mut}]_{h_{mut}=h=h^*} < 0$ (Eshel, 1983; Geritz et al., 1998).

Since the limit cycle of the predator–prey model cannot be calculated analytically, we had to integrate Eq. (3) numerically to obtain $x(t;h,g(h))$ and hence $v(t;h,g(h))$ defined in Eq. (6); and then solve Eq. (9a) by numerical integration to obtain the critical functions. The methods used to integrate the population dynamics (Eq. (3)) are described above (see at Eq. (6)). Eq. (9a) was easily solved using the simplest algorithm (Euler method with fixed stepsize $\Delta h = 0.05$) for various initial conditions. As discussed below, the critical functions are not analytic at the Hopf bifurcation line of the population dynamics, hence resolution very near to the Hopf bifurcation is limited.

The critical functions are shown in Fig. 1. Notice the following properties. Since Eq. (9a) can be rewritten in the form

$$g'(h) = d \left(1 + \frac{\text{Var}(v(t;h,g(h)))}{M(v(t;h,g(h)))^2} \right) \tag{9b}$$

analogously to Eq. (7), the critical functions are straight lines with slope d in the region where the predator–prey system attains a stable fixed point and thus the time variance of v is zero (light grey area in Fig. 1). Inside the region where the system has a stable limit cycle (clear area), the time variance is positive and hence the slope of the critical function is always greater than d . Since the right-hand side of Eq. (9a) is continuous, it follows that the critical functions must have a convex part near the Hopf

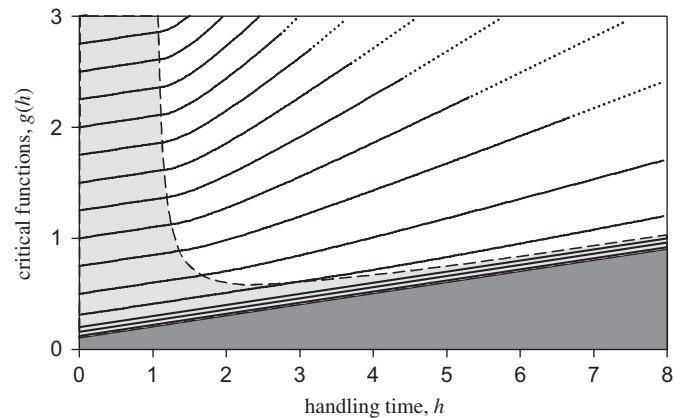


Fig. 1. Critical functions as obtained from numerical integration of Eq. (9a) are shown as continuous lines. Dotted lines are linear extrapolations of the critical functions; for these combinations of the handling time and the conversion factor, the limit cycle of the predator–prey system goes so near to extinction (population size less than 10^{-9}) that numerical integration becomes problematic and the model loses biological significance. The dashed line is the Hopf bifurcation line, below which the one predator–prey system with $\gamma = g$ attains a stable equilibrium (light grey area), whereas above the bifurcation line the system converges to a limit cycle (clear area). For large values of h , the Hopf bifurcation line converges to the straight line $\gamma = d(h+2)$. Predators with $\gamma \leq d(h+1)$ are not viable (dark grey area). In this figure, $d = 0.1$; qualitative properties remain the same for other values of d .

bifurcation line of the population dynamics. Moreover, because the size of the limit cycle grows at infinite speed at the Hopf bifurcation point (cf. Kuznetsov, 1995, p. 53), $\text{Var}(v(t;h,g(h)))$ in Eq. (9b) grows infinitely fast from zero and thus the second derivative $g''(h)$ goes to infinity as h approaches the bifurcation point from above. The numerical results in Fig. 1 indicate that for larger values of h , the critical functions become nearly linear; there are both slightly convex and slightly concave parts.

The critical functions give a quick visual way to identify evolutionarily singular strategies and their convergence stability once a trade-off function $\gamma(h)$ is given. Superimposing the graph of $\gamma(h)$ in Fig. 1, a critical function is tangential to $\gamma(h)$ at the singular points, and the relative curvatures show whether a certain singular point is convergence stable. Alternatively, we can construct a trade-off function such that there is e.g. a convergence stable singular strategy at a desired point. To do this, we choose the slope of the trade-off curve $\gamma(h)$ to be tangential to the critical function at the desired point, and the curvature of $\gamma(h)$ such that it is less convex than the critical function at this point (de Mazancourt and Dieckmann, 2004; see Fig. 2 below). In order to see whether such a singular strategy can be an evolutionary branching point, however, we must also investigate its evolutionary stability.

4. Evolutionary stability and evolutionary branching

A singular strategy h^* is locally evolutionarily stable if the invasion fitness $s(h_{\text{mut}}, h^*)$, as a function of the mutant strategy, attains a maximum at $h_{\text{mut}} = h^*$ (Maynard Smith, 1982). Substituting Eq. (7) for $\gamma'(h^*)$ into the second derivative of $s(h_{\text{mut}}, h^*)$, we obtain that

$$\partial^2 s(h_{\text{mut}}, h) / \partial h_{\text{mut}}^2 |_{h_{\text{mut}}=h=h^*} < 0 \text{ if and only if } \gamma''(h^*) < -2\gamma'(h^*) \left[\frac{\int_0^{T(h^*)} v(t; h^*, \gamma(h^*))^3 dt}{\int_0^{T(h^*)} v(t; h^*, \gamma(h^*)) dt} - \left(\frac{\int_0^{T(h^*)} v(t; h^*, \gamma(h^*))^2 dt}{\int_0^{T(h^*)} v(t; h^*, \gamma(h^*)) dt} \right)^2 \right] \tag{10}$$

i.e., if the trade-off function is sufficiently concave in the neighbourhood of h^* . The right-hand side of condition (10) corresponds to the convexity of the invasion boundary of Rueffler et al. (2004), called I-boundary by de Mazancourt and Dieckmann (2004).

Because in cycling populations $v(t; h^*, \gamma(h^*))$ can be obtained only numerically, this condition cannot be reduced to an explicit condition on the shape of the trade-off function $\gamma(h)$. However, the following analytical conditions can be given (see the Appendix for derivation):

- (1) *Necessary condition for evolutionary stability*—If h^* is evolutionarily stable then the trade-off function is concave at h^* , i.e., $\gamma''(h^*) < 0$. In cycling populations, the right-hand side of condition (10) is negative, whereas if the system attains a stable fixed point, then $v(t; h^*, \gamma(h^*))$ is constant in time and the bracketed expression is zero.
- (2) *Sufficient condition for evolutionary stability*— h^* is evolutionarily stable if

$$\gamma''(h^*) \leq -2\gamma'(h^*) \left(\frac{1}{1+h^*} - \frac{\gamma'(h^*)}{\gamma(h^*)} \right) \tag{11}$$

holds, i.e., if the trade-off function is sufficiently concave. If the trade-off function assumes the hyperbolic shape used by Kisdi and Liu (2006; see Eq. (1) above), then condition (11) is always satisfied with a

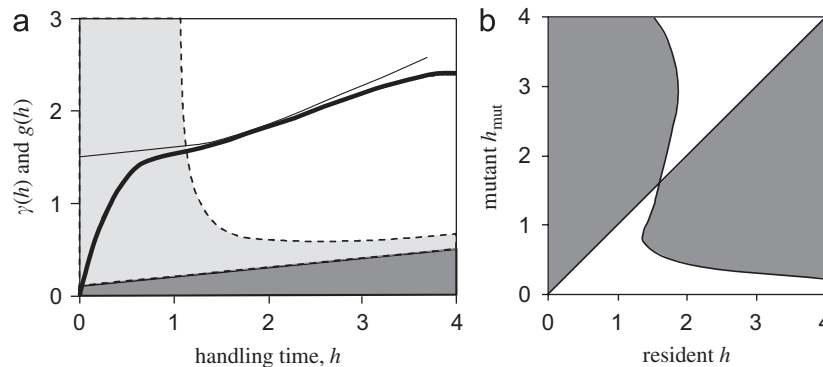


Fig. 2. Evolutionary branching in cycling populations. Panel (a) shows the trade-off function $\gamma(h)$ (thick curve) and the tangential critical function $g(h)$ (thin curve) with $d = 0.1$. Shading indicates the dynamical properties of the one predator–prey system as in Fig. 1 (clear: limit cycle, light grey: stable fixed point, dark grey: the predator is not viable). The trade-off function was chosen such that it would be tangential to the critical function at $(h, \gamma) = (1.6, 1.7)$, where the slope of the critical function is $g'(1.6) = 0.3172$ and its curvature is $g''(1.6) = 0.224$. The trade-off function was constructed using the *Interpolation* function of *Mathematica*[®] with the following points and derivatives: $(h, \gamma) = (0, 0)$; $(0.8, 1.5)$; $(1.6, 1.7)$ with slope $\gamma' = 0.3172$ and curvature $\gamma'' = 0.05$; $(4, 2.4)$ with slope 0; and $(5, 2.4)$ with slope 0. At $(h, \gamma) = (1.6, 1.7)$, the trade-off function thus has the same slope as the critical function and it is convex but less so than the critical function. The other points were chosen such that the trade-off satisfies the biological conditions (i)–(iii) described in Section 2. Given this trade-off, we expect an evolutionary branching point at $h^* = 1.6$. Panel (b) shows the pairwise invasibility plot obtained with the trade-off function in (a). Grey areas correspond to resident–mutant pairs where the mutant may invade, whereas in clear areas the mutant dies out. There is an evolutionary branching point at $h = 1.6$.

strict inequality. This extends the results of Kisdi and Liu (2006) such that all trade-off functions that are locally at least as concave as a hyperbolic function will always lead to a locally evolutionarily stable handling time.

For evolutionary branching, the singular strategy h^* must be convergence stable but not evolutionarily stable (Geritz et al., 1998). This constrains the convexity of the trade-off function on both sides. First, the trade-off must be less convex than the critical function [$\gamma''(h^*) < g''(h^*|h^*, \gamma(h^*))$]. As said above, the critical functions must be convex when h is just above the Hopf bifurcation of population dynamics. A nearly linear trade-off that is tangential to a critical function in this region thus satisfies the first condition. Second, the trade-off must be convex enough such that $\gamma''(h^*)$ exceeds the right-hand side of condition (10). In cycling populations, this threshold is negative, i.e., a nearly linear trade-off satisfies the second condition as well. Evolutionary branching is thus possible in cycling populations if, in the vicinity of the singular strategy, the trade-off function is not too convex or too concave. Locally linear trade-offs lead to evolutionary branching when the singular strategy h^* is just above the Hopf bifurcation, but often also elsewhere in the cyclic range of Fig. 1. Parts of the critical functions may however be slightly concave (not shown; examples include the critical function $g(h|0,30)$ for intermediate values of h with $d = 10$), in which case there is a small range of locally slightly concave trade-offs that lead to branching.

In Fig. 2, we construct an example for evolutionary branching. The trade-off curve $\gamma(h)$ in Fig. 2a is chosen such that it is tangential to the critical function $g(h|1.6,1.7)$ at the point $(h,\gamma) = (1.6,1.7)$. Further, $\gamma(h)$ is chosen to be slightly convex at this point such that the singular strategy is not evolutionarily stable, but less convex than the critical function such that the singular strategy is convergence stable. The corresponding pairwise invasibility plot in Fig. 2b indeed shows an evolutionary branching point at $h = 1.6$ (see Geritz et al. (1998) on how to read pairwise invasibility plots).

How likely is evolutionary branching in cycling populations? This can be measured by the difference between the minimum convexity necessary for lack of evolutionary stability and the maximum convexity compatible with convergence stability (de Mazancourt and Dieckmann, 2004). Although the right-hand side of condition (10) is always negative, numerical results show that it is rather near to zero: For $d = 0.02, 0.1, 1$ and 10 , the right-hand side of condition (10) is never more negative than -0.015γ . Trade-off functions that are easy to perceive as concave therefore do not allow for branching. As a first approximation, we can ignore the small range of concave trade-offs that can lead to branching and concentrate on convex trade-offs. For having a branching point, the trade-off must be less convex than the critical function. As Fig. 1 shows, the critical functions are nearly linear except near

the Hopf bifurcation line (this also holds for other values of d), which heavily constrains the shape of trade-offs that admit branching. Evolutionary branching is thus unlikely, except if the trade-off is locally convex and tangential to a critical function just over the Hopf bifurcation line. Fig. 3 shows the range of curvatures of the trade-off function that allows for branching, measured along two critical functions in Fig. 1.

If the population dynamics have a stable fixed point, two predators cannot coexist on a single prey, and therefore evolutionary branching is not possible. Indeed, in this case all convex trade-offs lead to convergence unstable singularities because the critical functions are linear ($\text{Var}(v(t;h,g(h))) = 0$ in Eq. (9b); cf. the linear segments of the critical functions in the light grey area in Fig. 1), whereas all concave trade-offs lead to evolutionarily stable strategies because the right-hand side of condition (10) is zero.

5. Evolutionarily stable coexistence

In this section, we extend the analysis to populations with two resident strategies, and investigate whether two predators with different handling times can, by small mutational steps, evolve evolutionarily stable trait values at which they continue to coexist. In other words, we are

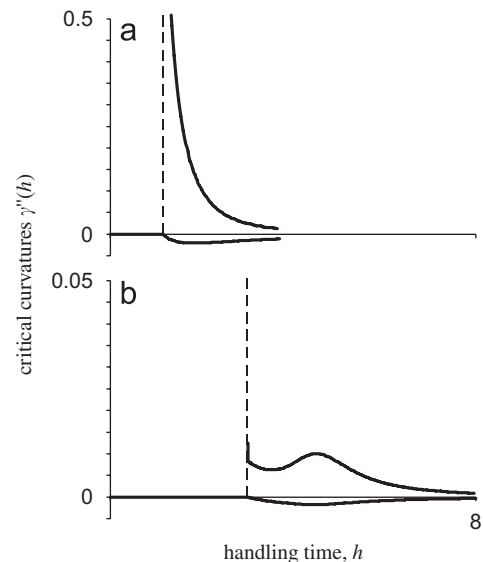


Fig. 3. The range of curvatures of the trade-off function such that an evolutionary singular strategy is a branching point, measured along the critical functions $g(h;0,1.5)$ in (a) and $g(h;0,0.3)$ in (b) with $d = 0.1$. The lower curve in each panel is the minimum convexity necessary for the lack of evolutionary stability (obtained from condition (10)). The upper curve is the curvature of the critical function; for convergence stability, the trade-off must be less convex than this. Evolutionary branching is thus possible if $\gamma''(h^*)$ is between the two curves. The dashed line shows the position of the Hopf bifurcation, to the left of which both curves are identically zero and branching is not possible. Notice the different vertical scales; branching is unlikely in (b). For other values of d , the local minimum seen in panel (b) may dip below the horizontal axis, i.e., the critical function may be slightly concave (not shown).

looking for conditions on the shape of the trade-off function $\gamma(h)$ such that the coalition of two handling strategies h_1^* and h_2^* is convergence stable as well as evolutionarily stable. Once again, we need to emphasise that we are concerned with the coexistence of predators with identical fitness functions, i.e., which share all their properties except for handling time.

The population dynamics of a single prey—two predators system are given by Eqs. (3) with $i = 1, 2$. Complicating matters, these systems may exhibit chaotic dynamics for some h_i and $\gamma(h_i)$ (although this does not appear to be common; Abrams et al., 2003). Chaos raises difficult problems concerning the computation and regularity of the invasion fitness function (Ferriere and Gatto, 1995). Here we shall assume that in the vicinity of the singular coalition h_1^* and h_2^* , all resident populations with two predator strategies have nonchaotic dynamics. This assumption can be checked numerically by calculating the Lyapunov exponents (see below).

The invasion fitness of a rare mutant strategy h_{mut} in the population of resident strategies h_1 and h_2 is given by

$$s(h_{mut}, h_1, h_2) = \frac{\gamma(h_{mut})}{T(h_1, h_2)} \int_0^{T(h_1, h_2)} \frac{x(t; h_1, \gamma(h_1), h_2, \gamma(h_2))}{1 + h_{mut}x(t; h_1, \gamma(h_1), h_2, \gamma(h_2))} dt - d \tag{12}$$

which is analogous to Eq. (5) except that prey density $x(t; h_1, \gamma(h_1), h_2, \gamma(h_2))$ is taken from the limit cycle of Eqs. (3) with two predators. A straightforward generalisation of Eq. (7) shows that the coexistence of h_1^* and h_2^* is singular, i.e., the fitness gradient vanishes at both h_1^* and h_2^* , if

$$\gamma'(h_i^*) = \gamma(h_i^*) \frac{\int_0^{T(h_1^*, h_2^*)} v_i(t)^2 dt}{\int_0^{T(h_1^*, h_2^*)} v_i(t) dt} \quad \text{for } i = 1, 2, \tag{13}$$

where $v_i(t)$ is shorthand for

$$v_i(t; h_1^*, \gamma(h_1^*), h_2^*, \gamma(h_2^*)) = \frac{x(t; h_1^*, \gamma(h_1^*), h_2^*, \gamma(h_2^*))}{1 + h_i^* x(t; h_1^*, \gamma(h_1^*), h_2^*, \gamma(h_2^*))} \tag{14}$$

(cf. Eq. (6)). Because the slope $\gamma'(h_1^*)$ now also depends on h_2^* and vice versa via $x(t; h_1^*, \gamma(h_1^*), h_2^*, \gamma(h_2^*))$, it is not possible to construct an entire critical function analogous to Eq. (9). Nevertheless, we can make the coexistence of an arbitrary pair of strategies h_1^* and h_2^* singular by choosing a trade-off function $\gamma(h)$ that has the slopes required by Eq. (13) locally at the points $h = h_1^*$ and $h = h_2^*$ (Kisdi, 2006).

The next step is to choose the convexity of $\gamma(h)$ such that the dimorphic singularity (h_1^*, h_2^*) is evolutionarily and convergence stable. Evolutionary stability can be evaluated separately for the constituent strategies h_1^* and h_2^* , and the dimorphic singularity is evolutionarily stable if and only if both strategies are (Geritz et al., 1998). Analogously to the monomorphic case, the condition for evolutionary

stability is

$$\gamma''(h_i^*) < -2\gamma(h_i^*) \left[\frac{\int_0^{T(h_1^*, h_2^*)} v_i(t)^3 dt}{\int_0^{T(h_1^*, h_2^*)} v_i(t) dt} - \left(\frac{\int_0^{T(h_1^*, h_2^*)} v_i(t)^2 dt}{\int_0^{T(h_1^*, h_2^*)} v_i(t) dt} \right)^2 \right] \quad \text{for } i = 1, 2. \tag{15}$$

The dimorphic singularity is thus evolutionarily stable if $\gamma''(h_i^*)$ is sufficiently negative for both $i = 1$ and 2 , i.e., if the trade-off function is sufficiently concave at h_1^* and also at h_2^* (see Rueffler et al., 2004).

Convergence stability of (h_1^*, h_2^*) is a more difficult problem, and in general it depends on the frequency and size of mutations in h_1 and in h_2 (Dieckmann and Law, 1996; Marrow et al., 1996; Matessi and Di Pasquale, 1996; Leimar, in press). Kisdi (2006), however, proved that (h_1^*, h_2^*) can be made convergence stable irrespectively of the distribution of mutations by choosing the trade-off function sufficiently concave both at h_1^* and at h_2^* . The proof is constructive in the sense that by numerical differentiation of the invasion fitness function, one can compute thresholds of $\gamma''(h_1^*)$ and $\gamma''(h_2^*)$ such that convergence stability of (h_1^*, h_2^*) is guaranteed for trade-off functions that are locally more concave than the threshold; however, we do not carry out this computation here.

We do, however, construct an example for evolutionarily and convergence stable coexistence in Fig. 4. Firstly, we choose two strategies, (h_1^*, γ_1^*) and (h_2^*, γ_2^*) , such that they coexist with one another and the system exhibits a stable limit cycle (not chaos). Secondly, using Eq. (13), we calculate the slope of the trade-off function at h_1^* and at h_2^* such that these two strategies form a dimorphic singularity. Thirdly, we make the trade-off function locally sufficiently concave by choosing negative values for $\gamma''(h_1^*)$ and $\gamma''(h_2^*)$; as seen above, this ensures both convergence and evolutionary stability of (h_1^*, h_2^*) . At this step, we have constructed $\gamma(h)$ in the neighbourhoods of h_1^* and of h_2^* up to second order. Finally, we connect these two pieces of the trade-off function in a smooth way (Fig. 4a). Biological motivation for the shape of this trade-off will be given in the Discussion.

Evaluating the invasion fitness function $s(h, h_1^*, h_2^*)$ confirms that the coexistence of h_1^* and at h_2^* is evolutionarily stable (Fig. 4b). Convergence to this singularity can be read from Fig. 4c. The fitness gradients of the coexisting strategies are such that the evolutionary trajectory is forced to (h_1^*, h_2^*) from its neighbourhood irrespectively of the frequency, size, and order of mutations (cf. Matessi and Di Pasquale, 1996).

We have chosen the singular strategies (h_1^*, γ_1^*) and (h_2^*, γ_2^*) such that they exhibit a limit cycle and not chaos. Using adaptive dynamics to judge convergence to this singularity, however, assumes that the fitness function is regular also when other strategy pairs are resident in the

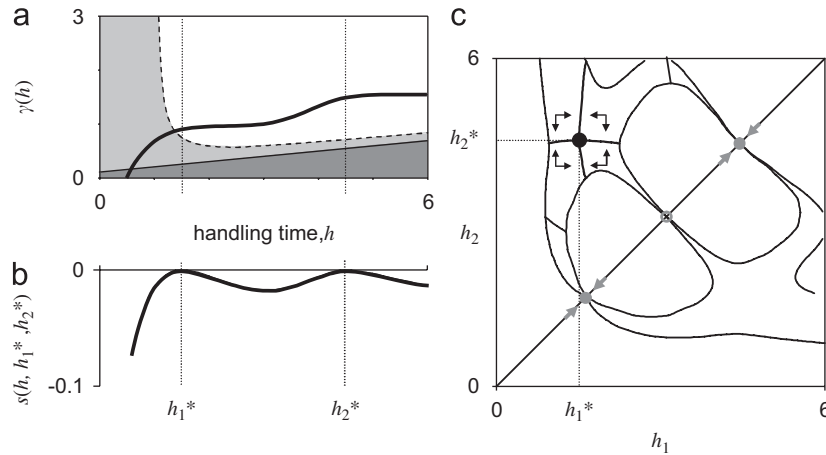


Fig. 4. Evolutionarily stable coexistence. (a) The shape of the trade-off curve. The trade-off is constructed such that for $d = 0.1$, the two strategies $(h_1^*, \gamma(h_1^*)) = (1.5, 0.9)$ and $(h_2^*, \gamma(h_2^*)) = (4.5, 1.5)$ form a dimorphic singularity. According to Eq. (13), the slope of the trade-off function at h_1^* and h_2^* must then be $\gamma'(h_1^*) = 0.2157$ and $\gamma'(h_2^*) = 0.1882$, respectively. The second derivatives were chosen to be $\gamma''(h_1^*) = -0.5$ and $\gamma''(h_2^*) = -1$. The trade-off function is an *Interpolation* function of *Mathematica* given the above points and derivatives, in addition to $(h, \gamma) = (0.5, 0)$ as starting point and $(h, \gamma) = (5, 1.55)$ with $\gamma' = 0$ as the point where full saturation is reached. See the Discussion for biological motivation of this trade-off function. Shading as in Fig. 2a. (b) Invasion fitness of a rare mutant h in the established dimorphic population of $(h_1^*, h_2^*) = (1.5, 4.5)$ with the trade-off in (a) and $d = 0.1$. No mutant has positive fitness, hence h_1^* and h_2^* form an evolutionarily stable coexistence. (c) Trait evolution plot for the trade-off in (a) and $d = 0.1$. Strategies h_1 and h_2 can coexist in the symmetrically shaped area. Because points mirrored on the main diagonal correspond to the trivial exchange of indices 1 and 2, we ignore the area below the main diagonal. Horizontal and vertical arrows show the direction of evolution of h_1 and of h_2 , respectively, and show that the coexistence of $(h_1^*, h_2^*) = (1.5, 4.5)$, marked with the black dot, is convergence stable. On the main diagonal, grey arrows indicate the direction of monomorphic evolution in a resident population of strategy $h = h_1 = h_2$. There are two monomorphic convergence stable ESSs (grey dots) separated by a convergence unstable singular strategy (grey circle). Note that the monomorphic convergence stable strategies are near to, but do not coincide with, h_1^* and h_2^* .

population. As a last step, therefore, we checked the population dynamics of the two predator—one prey system for strategy pairs (h_1, h_2) inside the area of coexistence in Fig. 4c, assuming the trade-off we constructed in Fig. 4a. We calculated the Lyapunov exponents of the attractor of Eqs. (3) using the continuous orthonormalisation procedure (Christiansen and Rugh, 1997) starting from a single initial point and for $t = 50,000$ after letting the transients die out. The results show that at least in a wide neighbourhood of (h_1^*, h_2^*) in Fig. 4, the population dynamics are not chaotic (data not shown). For strategy pairs far from the dimorphic singularity, two of the three Lyapunov exponents are close to zero, in which case it is hard to establish whether the dynamics are chaotic or not.

While (h_1^*, h_2^*) is a convergence and evolutionarily stable coexistence, this is not the only possible final state of evolution. In the example of Fig. 4, there are two alternative convergence and evolutionarily stable strategies of monomorphic populations. There is no evolutionary branching in this example, hence an initially monomorphic predator necessarily evolves to one of these monomorphic ESSs. The evolutionarily stable coexistence can be reached only if the predator is dimorphic at the onset or a sufficiently different predator strategy immigrates from outside the system.

It is much easier to construct an example for an evolutionarily stable coexistence than for evolutionary branching (see previous section). This is because here we do not have to navigate between the Scylla of convergence stability and the Charybdis of disruptive selection (lack of

evolutionary stability) as it is the case for branching (Fig. 3). Instead, both convergence stability and evolutionary stability will hold if the trade-off function is sufficiently concave at the two coexisting strategies. For this reason, evolutionarily stable coexistence of very similar predators (those which differ only in their handling time) may be more common than evolutionary branching.

6. Discussion

In this paper, we used a critical function analysis to investigate evolutionary branching and evolutionarily stable coexistence of cycling predators which share a common fitness function and differ only in their handling times and the associated efficiency of converting captured prey into offspring. This work is an extension of the model of Kisdı and Liu (2006): Here we analyse the same model but relax the assumption of a trade-off function given a priori between the evolving traits. Kisdı and Liu (2006) assumed a hyperbolic trade-off between handling time and conversion efficiency, and found no evolutionary branching and no evolutionarily stable coexistence. In contrast, the present critical function analysis shows that both evolutionary branching of handling time and evolutionarily stable coexistence of two different handling strategies are possible if the trade-off deviates from the hyperbolic shape. Our results confirm Kisdı and Liu (2006) in so far as we can exclude evolutionary branching also for trade-offs that are more concave than a hyperbolic function.

The method we call critical function analysis was introduced by de Mazancourt and Dieckmann (2004; see also Rueffler et al., 2004; Bowers et al., 2005). Although de Mazancourt and Dieckmann (2004) illustrated the method with only very simple examples, they, like we, could uncover a possible evolutionary scenario that was missed by previous studies (in their case, it was an evolutionary repellor). Our present results confirm the merits of the critical function analysis: It is straightforward to apply to considerably complex models (relying on numerical analysis when necessary); it can identify all possible evolutionary outcomes under various trade-offs; and it is helpful in estimating how likely these outcomes may be. Given that the choice of the trade-off function is often the least justified element of a model, performing a critical function analysis is highly preferable to assuming a trade-off function *ad hoc*.

Constructing the entire critical function is possible only for monomorphic populations (de Mazancourt and Dieckmann, 2004), but the method can be partially extended to analyse dimorphic populations as well (Kisdi, 2006; see also Rueffler et al., 2004). Here we used this extension to construct an example for an attracting, evolutionarily stable coexistence of two handling strategies in Fig. 4.

In the model we analysed (Eqs. (2)), we assumed that all predators have Holling type II functional responses. Reviewing empirical data on functional responses, Jeschke et al. (2004) found that the type II response is by far the most common in both invertebrate and vertebrate predators (although this does not necessarily imply that the widely used disc equation is the most adequate description, see Abrams, 1990). Models of nonequilibrium coexistence sometimes assume that one of the predators has a type I functional response (e.g. Armstrong and McGehee, 1980; Abrams and Holt, 2002; Abrams et al., 2003), but this type appears to be limited to filter feeders (Jeschke et al., 2004). Note that the Holling type I functional response is a limiting case of the type II response with zero handling time. A type I response could thus emerge by evolution; in our model, however, this does not happen (zero handling time is never viable).

The classic derivation of the Holling type II functional response assumes that handling predators are not searching for prey. For most predators, however, the longest part of handling is digestion, and digesting predators are able to forage. Nevertheless, Jeschke et al. (2002) showed that the functional response remains similar to the Holling type II response if the fraction of time spent by searching (“motivation”) is proportional to the hunger level of the predator, and hunger level saturates exponentially with starvation time. Moreover, Jeschke et al. (2002) recovered the exact Holling type II functional response with digestion time in place of handling time if the time needed for attack, killing, and consuming is negligible compared to the time needed for digestion. The same result was obtained as a limiting case of a much more sophisticated model by Metz and van Batenburg (1985). Note however that at high prey

densities, the functional response may deviate from the Holling type II function if predators catch prey also when they are too full to consume all (Metz et al., 1988).

Based on the model in Eqs. (2), we conclude that the handling time of cycling predators may undergo evolutionary branching (Fig. 2). Since handling time determines the shape of the Holling II functional response, evolutionary branching of handling time results in two predators such that their growth rates are different non-linear functions of prey density, and therefore they are able to coexist on a single prey when the population exhibits cycling dynamics (cf. Hsu et al., 1978a,b; Levins, 1979; Armstrong and McGehee, 1980; Abrams and Holt, 2002).

However, evolutionary branching does not appear to be very likely: For branching to occur, the convexity of the trade-off curve must fall in an interval that is rather narrow for most of the trait space (Fig. 3). Branching occurs easiest if the trade-off function is tangential to a critical function near to the Hopf bifurcation line in the clear area of Fig. 1, and it is convex at the point of tangency but less so than the critical function itself. Slightly concave trade-offs also yield branching but here the range is small. Further away from the Hopf bifurcation line the critical functions become nearly linear, and therefore branching is limited to a very narrow range of convexities.

Evolutionarily stable coexistence of different handling strategies is easier to obtain than evolutionary branching. Both evolutionary and convergence stability of a singular coexistence is ensured if the trade-off function is sufficiently concave in the neighbourhood of both constituent strategies. Trade-off functions that resemble a smoothed step function (like the one in Fig. 4a) are conducive to evolutionarily stable coexistence, because they can be strongly concave at the “steps” while retaining the slopes required by Eq. (13). Below we shall discuss this possibility further. It is however important to note that evolutionarily stable coexistence may occur with other trade-offs as well: For example, the two predator strategies that arise by evolutionary branching in Fig. 2 attain an evolutionarily stable coexistence (data not shown). Further, most coexisting predator species differ in their capture rates, death rates and other parameters, and this may or may not facilitate nonequilibrium coexistence. Our model shows that coexistence may be evolutionarily stable if the predators share the same fitness function. This is relevant to the early phase of coevolution of closely related predators; over time, other traits of the coexisting predators may slowly evolve and make the fitness functions different.

In case of step function-like trade-offs, typically there is no evolutionary branching point because the middle part of the trade-off is too convex, the “steps” are too concave, and the nearly linear parts are too steep or too flat compared to the critical functions. In such cases (e.g. in Fig. 4), an initially monomorphic population will evolve to an ESS. This ESS is however not globally stable. If a sufficiently different strategy invades, then the dimorphic

population can evolve to the evolutionarily stable coexistence. Evolutionary branching is thus not a necessary condition for an evolutionarily stable coexistence to exist (see the Appendix of Geritz et al., 1999).

Can real trade-offs look like a smoothed step function (similar to Fig. 4a)? This shape requires that the intake of nutrients (which will be converted into offspring) nearly saturates as the predator is handling the prey, but then additional handling makes a new source of nutrients available from the same prey body such that nutrient intake increases again, until this second source is also exhausted. If handling time is predominantly used for consumption, then this may be the case if the predator can open up and eat several body parts of the prey. For example, an insect predator may start with splitting the thorax and eating the flight muscles of its prey. As this body part is depleted, nutrient intake saturates; this is the first “step” of the trade-off function. Next, the predator can open the abdomen and consume its contents. Opening the second body part needs some handling time (which is the plateau between the two “steps”), but continued handling is rewarded by the second “step” of nutrient intake. If handling is mostly digesting, a similar step function-like trade-off can result if the prey body contains both easily digestible parts and parts that need long digestion. Intermediate digestion time does not yield more nutrients than the time sufficient to digest the easy parts, hence the plateau between the two “steps” of the trade-off.

In case of a step function-like trade-off, the evolutionarily stable coexistence consists of strategies that complete one or more “steps” (cf. Fig. 4). The evolutionarily stable population thus contains lazy predators that consume or digest only the first body part (thorax in the above example) and diligent predators that consume more (both the thorax and the abdomen). Lazy predators are at an advantage when prey is abundant, as they can find a new victim quickly and consume its most profitable body part instead of handling the first prey longer. In contrast, diligent predators are at an advantage when prey is scarce. As prey density oscillates along the limit cycle, each predator has favourable and unfavourable times.

Predators that are lazy in consumption leave potentially valuable nutrients behind in the carcass they have handled. Predators with short digesting time may also leave the hard-to-digest parts behind (instead of consuming and excreting them). If diligent predators come across these remains, their best strategy is to consume the leftovers. This may initiate the evolution of the diligent predator into a scavenger.

6.1. Coexistence versus evolutionary branching

The role of temporal variations in promoting diversification is very poorly explored. Most models that investigate evolutionary branching in nonequilibrium populations (Doebeli and Ruxton, 1997, Parvinen, 1999, 2002) or in

stochastic environments (Mathias et al., 2001; Mathias and Kisdi, 2002; Kisdi, 2002; Egas et al., 2004; Parvinen and Egas, 2004) also assume spatial heterogeneity in the environment and branching is largely driven by the spatial structure; the model of Abrams (2006) is similar, except that alternative resources substitute spatial heterogeneity. Note that even in these models, population cycles or stochastic environments could increase the level of diversity, i.e., more strategies could evolve than the number of habitats or resources (Kisdi, 2002; Egas et al., 2004; Abrams, 2006). Besides the present study, however, we are aware of only one model where nonequilibrium dynamics alone leads to the evolution of diversity: White et al. (2006) found evolutionary branching of fecundity in a population with discrete time, cycling dynamics, when fecundity is traded off with parental survival and the survival of juveniles exhibits overcompensating density dependence.

On the other hand, it is well understood that temporal variability can maintain coexistence without spatial structure or alternative resources, whether the variability stems from nonequilibrium population dynamics (Koch, 1974; McGehee and Armstrong, 1977; Hsu et al., 1978a,b; Levins, 1979; Armstrong and McGehee, 1980; Abrams and Holt, 2002; but see Abrams, 1999) or from periodic or stochastic environmental effects (Chesson, 1994; Abrams, 2004). Coexistence on an ecological time scale, however, does not necessarily imply that the system is also stable against new, potentially invading mutants, or that evolution leads to coexistence in the first place.

In fact, we need to distinguish four different questions about coexistence of several strategies: (i) whether two (or more) strategies can coexist on an ecological time scale; (ii) whether such coexistence can be evolutionarily stable and also attracting from nearby (polymorphic) starting points; (iii) whether an initially monomorphic population can become polymorphic via evolutionary branching; and (iv) whether the polymorphism emerging via branching is in the basin of attraction of an evolutionarily stable coexistence. Predators with different handling times can coexist on a single prey in cycling populations, but Kisdi and Liu (2006) found that such coexistence is not evolutionarily stable when both predators have the same hyperbolic trade-off given in Eq. (1). Similarly, in Ellner's (1985) model of the evolution of germination fraction and in the model of Olivieri et al. (1995) concerning the evolution of dispersal, different strategies can coexist in stochastic environments, but evolution eventually leads to the establishment of a monomorphic ESS. In these models, questions (ii)–(iv) are answered in the negative. Our Fig. 4 is an example where an evolutionarily stable coexistence exists but is not reachable from a monomorphic population (yes to (i)–(ii) but no to (iii)–(iv)); other such examples include e.g. by Meszéna et al. (1997), Geritz et al. (1999), Kisdi (1999) and Egas et al. (2004). Finally, Geritz et al. (1999), Kisdi (1999), Kisdi et al. (2001) and Dercole (2003) illustrate that evolutionary branching need not lead to an evolutionarily stable coexistence.

Following the standard nomenclature of adaptive dynamics, by “evolutionarily stable coexistence” we mean stability against invasion by mutants that differ in the focal trait (here handling time). Yet such coexistence is not necessarily stable against other traits evolving on a long-term evolutionary time-scale (Ito, in prep.). Hence a fifth question could be added to the above list, namely how robust is the coexistence with respect to further diversification of traits not explicitly investigated in the model (such as the capture rate, death rate, etc.). We however do not pursue this question here.

For models where two traits of the same strategy are linked by a trade-off (such as handling time and the conversion factor in our case), Bowers et al. (2005) have connected questions (i) and (iii) by proving the following statement: If two strategies in the vicinity of an evolutionarily singular strategy can coexist in a protected dimorphism, then evolutionary branching is also possible, provided that the convexity of the trade-off function at the singular strategy falls in a certain interval. Kisdi (2006) showed that a similar statement holds also for two coevolving strategies or species. In some models, however, the convexity of the trade-off is constrained either by assumption or by the nature of the problem. For example, the fractions of seeds entering dormancy and of germinating seeds must add up to one; hence the trade-off between these fractions is necessarily linear. Constrained trade-offs explain why some models exhibit the coexistence of similar strategies but no evolutionary branching.

If temporal variations due to nonequilibrium population dynamics or due to stochastic environments do indeed maintain coexistence in a wide range of ecological systems, then the above result of Bowers et al. (2005) suggests that they may also promote diversification in many other cases in addition to White et al. (2006) and the present study. In each particular system, however, it remains to be seen whether evolutionary branching is possible with biologically realistic trade-offs, and how wide is the range of parameters where branching occurs.

Acknowledgments

Our research is financially supported by the Academy Finland. Part of this work was done at the University of Turku (Finland).

Appendix

Here we prove separate necessary and sufficient conditions for a singular strategy h^* to be evolutionarily stable. $\gamma''(h^*) < 0$ is obviously necessary if the right-hand side of condition (10) is negative, i.e., if the bracketed expression in the right-hand side is positive. To see that it is indeed so, define $f_1(t) = v(t; h^*, \gamma(h^*))^{1/2}$ and $f_2(t) = v(t; h^*, \gamma(h^*))^{3/2}$. By

the Cauchy-Schwarz inequality, we have

$$\left[\int_0^T f_1(t) f_2(t) dt \right]^2 \leq \left[\int_0^T f_1(t)^2 dt \right] \left[\int_0^T f_2(t)^2 dt \right], \quad (\text{A.1})$$

i.e.,

$$\left[\int_0^T v(t; h^*, \gamma(h^*))^2 dt \right]^2 \leq \left[\int_0^T v(t; h^*, \gamma(h^*)) dt \right] \left[\int_0^T v(t; h^*, \gamma(h^*))^3 dt \right], \quad (\text{A.2})$$

where equality holds if and only if $f_2(t)/f_1(t) = v(t; h^*, \gamma(h^*))$ is constant, which is the case if and only if $x(t; h^*, \gamma(h^*))$ attains a stable fixed point. In cycling populations, condition (A.2) holds with a strict inequality, and this is equivalent to the bracketed term in condition (10) being positive.

To prove that condition (11) is sufficient for h^* to be evolutionarily stable, notice that $v(t; h, \gamma(h)) = x(t; h, \gamma(h))/(1 + hx(t; h, \gamma(h))) < 1/(1 + h)$ for every t , because $v(t; h, \gamma(h))$ increases with $x(t; h, \gamma(h))$, and $x(t; h, \gamma(h))$ is always less than 1, the carrying capacity of the prey, provided only that the predator is viable. Therefore

$$\int_0^T v(t; h^*, \gamma(h^*))^3 dt < \frac{1}{1 + h^*} \cdot \int_0^T v(t; h^*, \gamma(h^*))^2 dt,$$

and condition (10) is always fulfilled if

$$\gamma''(h^*) \leq -2\gamma(h^*) \left[\frac{1}{1 + h^*} \frac{\int_0^T v(t; h^*, \gamma(h^*))^2 dt}{\int_0^T v(t; h^*, \gamma(h^*)) dt} - \left(\frac{\int_0^T v(t; h^*, \gamma(h^*))^2 dt}{\int_0^T v(t; h^*, \gamma(h^*)) dt} \right)^2 \right]. \quad (\text{A.3})$$

Using Eq. (7), this can be re-written as

$$\gamma''(h^*) \leq -2\gamma(h^*) \left[\frac{1}{1 + h^*} \frac{\gamma'(h^*)}{\gamma(h^*)} - \left(\frac{\gamma'(h^*)}{\gamma(h^*)} \right)^2 \right], \quad (\text{A.4})$$

which is equivalent to condition (11).

References

- Abrams, P.A., 1990. The effects of adaptive behavior on the type-2 functional response. *Ecology* 71, 877–885.
- Abrams, P.A., 1999. Is predator-mediated coexistence possible in unstable systems? *Ecology* 80, 608–621.
- Abrams, P.A., 2000. The evolution of predator–prey interactions: theory and evidence. *Annu. Rev. Ecol. Syst.* 31, 79–105.
- Abrams, P.A., 2004. When does periodic variation in resource growth allow robust coexistence of competing consumer species? *Ecology* 85, 372–382.
- Abrams, P.A., 2006. Adaptive change in the resource-exploitation traits of a generalist consumer: the evolution and coexistence of generalists and specialists. *Evolution* 60, 427–439.
- Abrams, P.A., Holt, R.D., 2002. The impact of consumer-resource cycles on the coexistence of competing consumers. *Theor. Popul. Biol.* 62, 281–295.
- Abrams, P.A., Brassil, C.E., Holt, R.D., 2003. Dynamics and responses to mortality rates of competing predators undergoing predator–prey cycles. *Theor. Popul. Biol.* 64, 163–176.

- Armstrong, R.A., McGehee, R., 1980. Competitive exclusion. *Am. Nat.* 115, 151–170.
- Bowers, R.G., Hoyle, A., White, A., Boots, M., 2005. The geometric theory of adaptive evolution: trade-off and invasion plots. *J. Theor. Biol.* 233, 363–377.
- Chesson, P., 1994. Multispecies competition in variable environments. *Theor. Popul. Biol.* 45, 227–276.
- Christiansen, F.B., 1991. On conditions for evolutionary stability for a continuously varying character. *Am. Nat.* 138, 37–50.
- Christiansen, F., Rugh, H.H., 1997. Computing Lyapunov spectra with continuous Gram–Schmidt orthonormalization. *Nonlinearity* 10, 1063–1072.
- Dercole, F., 2003. Remarks on branching-extinction evolutionary cycles. *J. Math. Biol.* 47, 569–580.
- Dieckmann, U., Law, R., 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.* 34, 579–612.
- Doebeli, M., Ruxton, G.D., 1997. Evolution of dispersal rates in metapopulation models: branching and cyclic dynamics in phenotype space. *Evolution* 51, 1730–1741.
- Egas, M., Dieckmann, U., Sabelis, M.W., 2004. Evolution restricts the coexistence of specialists and generalists: the role of the trade-off structure. *Am. Nat.* 163, 518–531.
- Ellner, S., 1985. ESS germination strategies in randomly varying environments I. Logistic-type models. *Theor. Popul. Biol.* 28, 50–79.
- Eshel, I., 1983. Evolutionary and continuous stability. *J. Theor. Biol.* 103, 99–111.
- Ferriere, R., Gatto, M., 1995. Lyapunov exponents and the mathematics of invasion in oscillatory or chaotic populations. *Theor. Popul. Biol.* 48, 126–171.
- Geritz, S.A.H., Kisdi, E., Meszena, G., Metz, J.A.J., 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* 12, 35–57.
- Geritz, S.A.H., Van der Meijden, E., Metz, J.A.J., 1999. Evolutionary dynamics of seed size and seedling competitive ability. *Theor. Popul. Biol.* 55, 324–343.
- Hsu, S.B., Hubbell, S.P., Waltman, P., 1978a. Competing predators. *SIAM J. Appl. Math.* 35, 617–625.
- Hsu, S.B., Hubbell, S.P., Waltman, P., 1978b. A contribution to the theory of competing predators. *Ecol. Monogr.* 48, 337–349.
- Huisman, J.E.F., Weissing, F.J., 1999. Biodiversity of plankton by species oscillations and chaos. *Nature* 402, 407–410.
- Jeschke, J., Kopp, M., Tollrian, R., 2002. Predator functional responses: discriminating between handling and digesting prey. *Ecol. Monogr.* 72, 95–112.
- Jeschke, J., Kopp, M., Tollrian, R., 2004. Consumer–food systems: why type I functional responses are exclusive to filter feeders. *Biol. Rev.* 79, 337–349.
- Kisdi, E., 1999. Evolutionary branching under asymmetric competition. *J. Theor. Biol.* 197, 149–162.
- Kisdi, E., 2002. Dispersal: risk spreading versus local adaptation. *Am. Nat.* 159, 579–596.
- Kisdi, E., 2006. Trade-off geometries and the adaptive dynamics of two co-evolving species. *Evol. Ecol. Res.* 8, 959–973.
- Kisdi, E., Liu, S., 2006. Evolution of handling time can destroy the coexistence of cycling predators. *J. Evol. Biol.* 19, 49–58.
- Kisdi, E., Jacobs, F.J.A., Geritz, S.A.H., 2001. Red Queen evolution by cycles of evolutionary branching and extinction. *Selection* 2, 161–176.
- Koch, A.L., 1974. Competitive coexistence of two predators utilizing the same prey under constant environmental conditions. *J. Theor. Biol.* 44, 387–395.
- Kuznetsov, Y.A., 1995. *Elements of Applied Bifurcation Theory*. Springer, Berlin.
- Leimar, O. Multidimensional convergence stability and the canonical adaptive dynamics. In: Dieckmann, U., Metz, J.A.J. (Eds.), *Elements of Adaptive Dynamics*. Cambridge University Press, in press.
- Levins, R., 1979. Coexistence in a variable environment. *Am. Nat.* 114, 765–783.
- Liu, W., Xiao, D., Yi, Y., 2003. Relaxation oscillations in a class of predator–prey systems. *J. Differential Equations* 188, 306–331.
- Marrow, P., Dieckmann, U., Law, R., 1996. Evolutionary dynamics of predator–prey systems: an ecological perspective. *J. Math. Biol.* 34, 556–578.
- Matessi, C., Di Pasquale, C., 1996. Long-term evolution of multilocus traits. *J. Math. Biol.* 34, 613–653.
- Mathias, A., Kisdi, E., 2002. Adaptive diversification of germination strategies. *Proc. R. Soc. Lond. B* 269, 151–156.
- Mathias, A., Kisdi, E., Olivieri, I., 2001. Divergent evolution of dispersal in a heterogeneous and variable landscape. *Evolution* 55, 246–259.
- Maynard Smith, J., 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.
- de Mazancourt, C., Dieckmann, U., 2004. Trade-off geometries and frequency-dependent selection. *Am. Nat.* 164, 765–778.
- McGehee, R., Armstrong, R.A., 1977. Some mathematical problems concerning the ecological principle of competitive exclusion. *J. Differential Equations* 23, 30–52.
- Meszena, G., Czibula, I., Geritz, S.A.H., 1997. Adaptive dynamics in a 2-patch environment: a toy model for allopatric and parapatric speciation. *J. Biol. Syst.* 5, 265–284.
- Meszena, G., Gyllenberg, M., Jacobs, F.J.A., Metz, J.A.J., 2005. Link between population dynamics and dynamics of Darwinian evolution. *Phys. Rev. Lett.* 95, 078105.
- Metz, J.A.J., van Batenburg, F.H.D., 1985. Holling’s “hungry mantid” model for the invertebrate functional response considered as a Markov process. Part I. The full model and some of its limits. *J. Math. Biol.* 22, 209–238.
- Metz, J.A.J., Sabelis, M.W., Kuchlein, J.H., 1988. Sources of variation in predation rates at high prey densities: an analytic model and a mite example. *Exp. Appl. Acar.* 5, 187–205.
- Metz, J.A.J., Nisbet, R.M., Geritz, S.A.H., 1992. How should we define ‘fitness’ for general ecological scenarios? *Trends Ecol. Evol.* 7, 198–202.
- Metz, J.A.J., Geritz, S.A.H., Meszena, G., Jacobs, F.J.A., Van Heerwaarden, J.S., 1996. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In: van Strien, S.J., Verduyn Lunel, S.M. (Eds.), *Stochastic and Spatial Structures of Dynamical Systems*. North-Holland, Amsterdam, The Netherlands, pp. 183–231 Available online at <<http://www.iiasa.ac.at/cgi-bin/pubsrch?WP95099>>.
- Muratori, S., Rinaldi, S., 1989. Remarks on competitive coexistence. *SIAM J. Appl. Math.* 49, 1462–1472.
- Olivieri, I., Michalakis, Y., Gouyon, P.-H., 1995. Metapopulation genetics and the evolution of dispersal. *Am. Nat.* 146, 202–228.
- Parvinen, K., 1999. Evolution of migration in a metapopulation. *Bull. Math. Biol.* 61, 531–550.
- Parvinen, K., 2002. Evolutionary branching of dispersal strategies in structured metapopulations. *J. Math. Biol.* 45, 106–124.
- Parvinen, K., Egas, M., 2004. Dispersal and the evolution of specialisation in a two-habitat type metapopulation. *Theor. Popul. Biol.* 66, 233–248.
- Rueffler, C., Van Dooren, T.J.M., Metz, J.A.J., 2004. Adaptive walks on changing landscapes: Levins’ approach extended. *Theor. Popul. Biol.* 65, 165–178.
- White, A., Greenman, J.V., Benton, T.G., Boots, M., 2006. Evolutionary behaviour in ecological systems with trade-offs and non-equilibrium population dynamics. *Evol. Ecol. Res.* 8, 387–398.
- Wilson, W.G., Abrams, P.A., 2005. Coexistence of cycling, dispersing consumer species: Armstrong and McGehee in space. *Am. Nat.* 165, 193–205.