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Optimal Intraguild Foraging and Population Stability

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This article explores effects of adaptive intraguild predation on species coexistence and community structure in three species' food webs. Two Lotka–Volterra models that assume a trade-off between competition and predation strength are considered in detail. The first model does not explicitly model resource dynamics and is considered with both nonadaptive and adaptive intraguild predation; in the latter case predators choose their diet in order to maximize their instantaneous population growth rate. The second model includes resource population dynamics. Effects of adaptive intraguild predation on the community structure along a gradient in environment productivity are analyzed and compared with some experimental results of protist food webs. Conditions under which intraguild predation is adaptive are discussed for both models. It is proved that if intraguild predators are perfect optimizers then intraguild predation should decrease with increasing environmental productivity and adaptive intraguild predation is a stabilizing factor provided environmental productivity is high enough. © 2000 Academic Press

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INTRODUCTION

It has become clear that omnivory, defined as feeding or parasitizing more than one trophic level (Pimm and Lawton, 1977; Pimm and Lawton, 1978; Pimm 1991) is common in food webs (Polis *et al.*, 1989; Polis, 1991; Diehl, 1993; Dawah *et al.*, 1995; Sukhdeo and Bansemir, 1996; Winemiller, 1996; Fagan, 1997; Holt and Polis, 1997; Agrawal *et al.*, 1999). Intraguild predation is a special case of omnivory where predation occurs among members of the same guild that exploit the same class of resources (Polis, 1988; Polis *et al.*, 1989; Polis and Holt, 1992; Holt and Polis, 1997). Theoretical studies show that intraguild predation can destabilize population dynamics because the intraguild prey have difficulty persisting in a food web where they both compete for

food with and are eaten by the intraguild predators (Holt and Polis, 1997; McCann and Hastings, 1997). Contrary to these theoretical observations, intraguild predation in some natural and laboratory food webs neither shortens species coexistence nor increases population fluctuations (Morin and Lawler, 1995; Morin and Lawler, 1996; Fagan, 1997; Holyoak and Sachdev, 1998; Morin, 1999). Lawler and Morin (1993) and Morin and Lawler (1996) compared several protist microcosms with and without intraguild predation and showed that omnivores reached greater abundances than other nonomnivorous predators and sometimes exhibited smaller fluctuations in population densities.

To examine this contradiction, Polis *et al.* (1989), Polis and Holt (1992), and Holt and Polis (1997) searched for mechanisms which may explain coexistence

in Lotka–Volterra type systems with intraguild predation. Polis *et al.* (1989) conducted an isocline analysis for an intraguild predation model which did not consider resource dynamics. They showed that if the two species coexist without intraguild predation then adding intraguild predation can lead to exclusion of the intraguild prey from their system. Holt and Polis (1997) considered a tri-trophic mechanistic model which includes resource dynamics. Using Tilman's R^* rule (Tilman, 1990) they showed that intraguild predators and intraguild prey can coexist only if the intraguild predators are inferior to the intraguild prey at exploiting a common resource. If the intraguild predator is a superior competitor for the shared resource then even without the intraguild predation, the intraguild prey will be outcompeted and excluded. Holt and Polis (1997) argued that if intraguild predators follow optimal foraging theory rules, coexistence may be achieved by dropping the intraguild prey from the predator's diet when the resource is abundant. This would allow the intraguild prey population to recover, which again could be included in the intraguild predator's diet.

The aim of the present article is to further explore the effects of intraguild predation on coexistence in tri-trophic food webs, especially when intraguild predation is adaptive. I will consider two basic population dynamical models inspired by some recent studies of protist food webs (Lawler and Morin, 1993; Morin and Lawler, 1995; Morin and Lawler, 1996; Holyoak and Sachdev, 1998; Morin, 1999). Some species of protists are cannibalistic and, when feeding on their own guild, undergo a shift in morphology where they typically rearrange their mouthparts so that they can ingest other protist cells (these are called giants, cannibals, or macrostomes). The transformed cannibal morphs cannot then consume bacteria (the common resource) without dividing when they then either transform back to bacteria eating cells or remain as cannibals (Giese, 1973; M. Holyoak, personal communication). Models in this article reflect, but are not limited to, such a situation. The first model is based on a competition Lotka–Volterra type model. Analysis of this model reveals the effects of intraguild predation on stability and species coexistence. I study separately two cases: (i) intraguild predation is nonadaptive (extending the analysis of Polis *et al.*, 1989), and (ii) intraguild predation is adaptive because predators choose their diet in order to maximize their instantaneous per capita population growth rate. I then analyze a more mechanistic model for competition which includes explicit resource population dynamics. This model was studied numerically by Holt and Polis (1997) but only for a fixed strength of intraguild predation. I therefore conduct a more general analysis that focuses on the effects of adaptive intraguild predation on stability.

My main objectives are (1) to study the effects of adaptive intraguild predation on the community structure and on population stability along a gradient in environment productivity, (2) to study the strength of adaptive predation along a gradient in environmental productivity, and (3) to compare my analysis with the experimental results obtained by Lawler and Morin (1993) and Morin (1999).

THE LOTKA–VOLTERRA MODEL

Let x and y be two species competing for a common resource R (Fig. 1). Besides competing with species x, individuals of species y may also feed on them. In what follows, u denotes the strength of predation relative to the strength of competition. This parameter can be interpreted either on an individual level, as the proportion of prey in the diet of an average predator, or on the population level, as a proportion of predators that feed on prey. Values of u greater than zero but smaller than one produce an omnivorous link between species y and the common resource. This sort of omnivory has been called intraguild predation and individuals of species y are called intraguild predators and individuals of species x are intraguild prey (Polis, 1988; Polis *et al.*, 1989; Polis and Holt, 1992; Holt and Polis, 1997).

In this section I do not consider resource dynamics explicitly; population dynamics of species x and y are described by the Lotka–Volterra equations combining competition for a common resource with predation

$$x' = r_1 x \left(1 - \frac{x}{K_1} - \alpha \frac{(1-u)\,y}{K_1}\right) - \lambda u x y$$
$$y' = r_2(1-u)\,y \left(1 - \frac{(1-u)\,y}{K_2} - \beta \frac{x}{K_2}\right) + u y (e \lambda x - m). \tag{1}$$

Model (1) assumes a trade-off between predation and competition, which means that increased predation on species x reduces competition for the common resource and vice versa. Such a trade-off is motivated by some species of protists which are cannibalistic and which, when feeding on their own guild, undergo a shift in morphology which allows them to ingest other protist cells. Then u is the proportion of cannibals (also called giants or macrostomes) in species y. A similar system with intraguild predation but without the trade-off between predation and competition was analyzed by Polis *et al.* (1989).
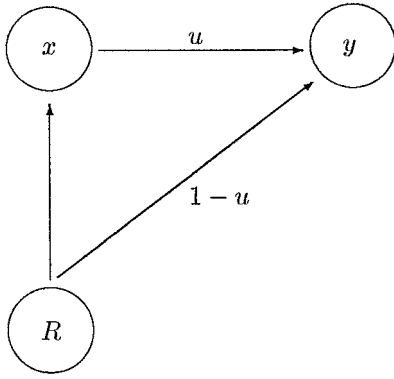
FIG. 1. A tri-trophic chain with intraguild predation. For zero predation strength ($u = 0$) the two populations x and y compete for the common resource R only. When predation strength equals one, the food web topology is described by a linear tri-trophic food chain with top predators y feeding on intermediate prey species x.

Model (1) comprises three different food web topologies. With a zero predation strength (1) describes a competitive system, for predation strength equal to one it describes a tri-trophic linear food chain, and for an intermediate predation strength it describes an intraguild predation system. As I assume that predation strength is adaptive I have to analyse all three food web topologies.

When the predation strength is zero ($u = 0$), system (1) becomes a competitive Lotka–Volterra system

$$x' = r_1 x \left(1 - \frac{x}{K_1} - \alpha \frac{y}{K_1} \right)$$
$$y' = r_2 y \left(1 - \frac{y}{K_2} - \beta \frac{x}{K_2} \right) \tag{2}$$

which for $\alpha < K_1/K_2$ and $\beta < K_2/K_1$, has one stable interior equilibrium,

$$E^{(2)} = \left(\frac{K_1 - \alpha K_2}{1 - \alpha\beta}, \frac{K_2 - \beta K_1}{1 - \alpha\beta} \right).$$

For $u = 1$, system (1) becomes a predator–prey linear food chain,

$$x' = r_1 x \left(1 - \frac{x}{K_1} \right) - \lambda xy$$
$$y' = (e\lambda x - m) y, \tag{3}$$

which has the following stable interior equilibrium:

$$E^{(3)} = \left(\frac{m}{e\lambda}, \frac{(eK_1\lambda - m) r_1}{eK_1\lambda^2} \right).$$

I remark that in contrary to the strictly competitive system (2) prey cannot be excluded from the equilibrium $E^{(3)}$ for any parameter values (provided all parameters are positive). Thus, while for the competitive system the density of the potential prey species x at the interior equilibrium is positive only for $\alpha < K_1/K_2$, no such condition is necessary to guarantee positivity of the equilibrial prey density in the predator–prey system. This suggests that for a low predation strength, model (1) is expected to behave similarly to the competitive system (2), while for high predation strengths its behavior is expected to be more related to the predator–prey system (3).

Nonadaptive Intraguild Predation

For a fixed strength of intraguild predation ($0 < u < 1$) model (1) has one interior equilibrium $E^{(1)}$; see Appendix A. In what follows I will consider two cases with respect to u.

If intraguild predation is weak, i.e.,

$$u < \frac{r_2}{r_2 + m},$$

then the interior equilibrium $E^{(1)}$ is positive and locally stable if the following conditions are met (see Appendix A):

$$\alpha < \tilde{\alpha}(u) = \frac{K_1 r_2 (1 - u)}{K_2 (r_2(1-u) - mu)} - \frac{K_1 \lambda u}{r_1 (1-u)}$$
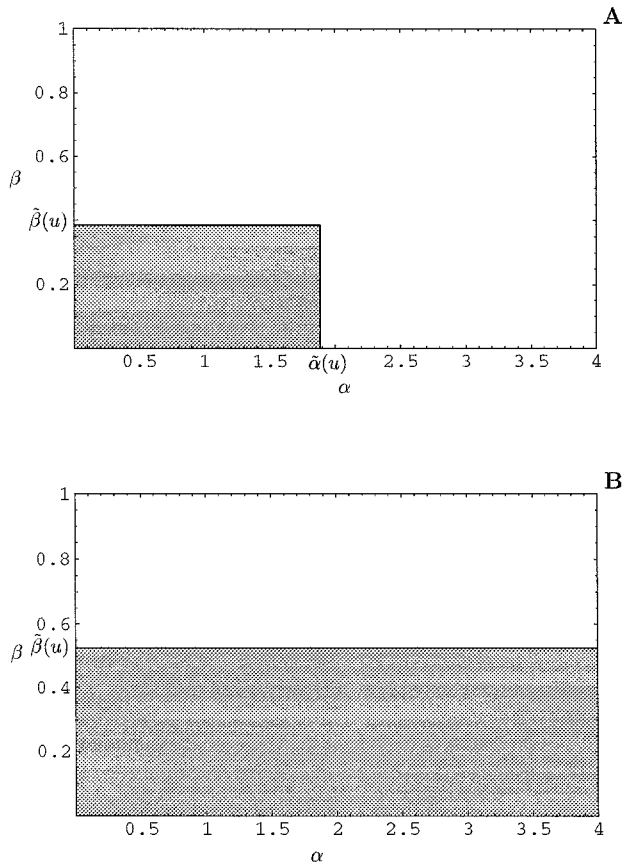
and

$$\beta < \tilde{\beta}(u) = \frac{K_2}{K_1} \left(1 + \frac{u(eK_1\lambda - m)}{r_2(1-u)} \right).$$

Condition $\alpha < \tilde{\alpha}(u)$ implies positivity of the equilibrial intraguild prey density and $\beta < \tilde{\beta}(u)$ implies positivity of the equilibrial intraguild predator density, respectively. Thus, in the (α, β) state space the region of parameters that leads to stability is a rectangle (Fig. 2A) as in the case of the strictly competitive model (2).

If intraguild predation is strong, by which I mean that the per capita loss rate of the intraguild predators (mu) exceeds that maximum gain in the competition part ($r_2(1-u)$), i. e.,

$$\frac{r_2}{r_2 + m} < u < 1,$$

then equilibrium $E^{(1)}$ is positive and stable if $\beta < \tilde{\beta}(u)$ as in the case of the strictly predator–prey system (see

because besides strong competition for resources there is an additional mortality due to intraguild predation which can drive intraguild prey to extinction. As the strength of intraguild predation increases further, competition decreases leading to intraguild prey coexistence despite increased predation. I conclude that for $K_2 > mr_1/(\lambda r_2)$ low levels of intraguild predation make the conditions for intraguild prey persistence $(\alpha < \tilde{\alpha}(u))$ either more stringent than the strictly competitive system or impossible to satisfy. In contrast, higher values of intraguild predation promote survival of the intraguild prey at the interior equilibrium as the condition $\alpha < \tilde{\alpha}(u)$ becomes less stringent for u converging to $r_2/(r_2 + m)$. For a high strength of intraguild predation $(u > r_2/(r_2 + m))$ intraguild prey always survive in the system.

If the predator carrying capacity is low $(K_2 < mr_1/(\lambda r_2))$ then a switch from exploiting a common resource to devouring the intraguild prey itself facilitates survival of the intraguild prey, and low levels of intraguild predation do not necessarily make the condition for prey persistence more stringent.

Next I consider how intraguild predation influences persistence of intraguild predators. If predators survive at equilibrium $E^{(3)}$, i.e., when $K_1 > m/(e\lambda)$, then $\tilde{\beta}(u)$ is an increasing function of u (Fig. 3D) and $\tilde{\beta}(u) \geqslant K_2/K_1$ for all values of u. In this case intraguild predation enhances coexistence of intraguild predators in the system because it reduces competition for the common resource and intraguild predators get more food by feeding on the intraguild prey. On the contrary, if the carrying capacity K_1 is low, so that predators do not survive indefinitely by feeding on prey only $(K_1 < m/(e\lambda))$, then intraguild predation makes the condition for predator survival in the system very stringent (Fig. 3E).

I want to relate these results to those observed by Morin (1999) and Lawler and Morin (1993). Morin (1999) experimented with two freshwater protists, *Colpidium striatum* (intraguild prey) and *Blepharisma americanum* (intraguild predator), at two different bacterial lever (common resource). He showed that while *Blepharisma* density increased with increased bacterial density, *Colpidium* did not increase in density in response to increased environmental productivity. Therefore, increasing productivity in his experiments increased K_2 but it had no effect on K_1. He showed that, at the lower level of environmental productivity, *Colpidium* excluded *Blepharisma* in three of four replicates. At higher levels of productivity both species coexisted. Such a pattern is consistent with my model with a low strength of intraguild predation $(u < r_2/(r_2 + m))$. Under these conditions $\tilde{\alpha}(u)$ is a decreasing function of K_2 while $\tilde{\beta}(u)$ is increasing. For low K_2 intraguild predators (*Blepharisma*) are

FIG. 2. Values of competitive coefficients α and β that lead to a stable interior equilibrium of model (1) (shaded area). In (A) the predation strength satisfies $u < r_2/(r_2 + m)$, $(u = 0.2)$ while in (B) $u > r_2/(r_2 + m)$, $(u = 0.8)$. Parameters are: $\lambda = 0.1$, $e = 0.1$, $K_1 = 40$, $K_2 = 15$, $r_1 = 1$, $r_2 = 1$, $m = 0.3$.

Fig. 2B and Appendix A). As predators cannot exclude the prey population in the predator–prey model (3) it is not surprising that intraguild predators cannot exclude the intraguild prey when intraguild predation is strong.
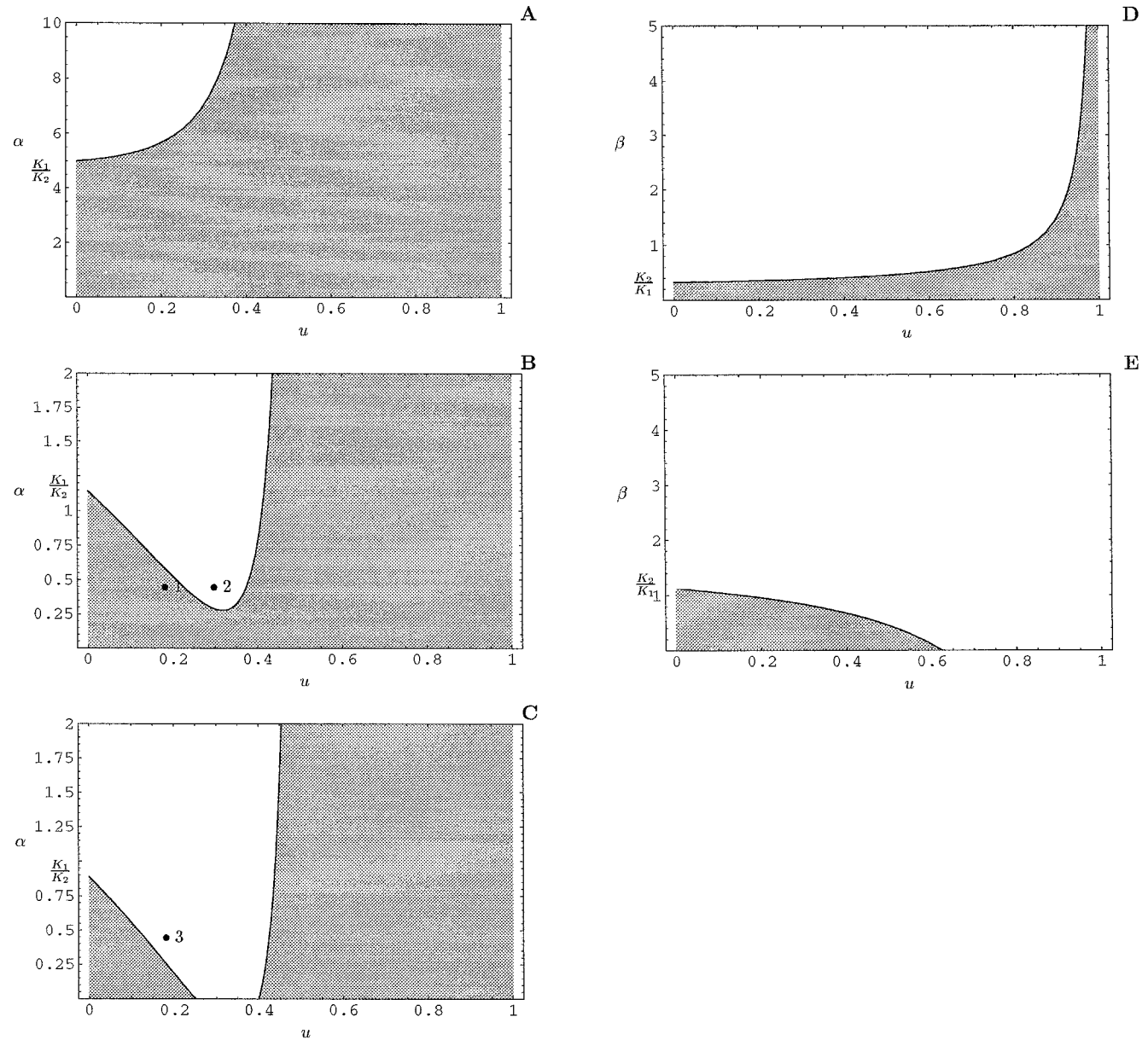
I now consider how intraguild predation influences coexistence of intraguild prey and intraguild predators. For a low intraguild predator carrying capacity (i.e., $K_2 < mr_1/(\lambda r_2)$) function $\tilde{\alpha}(u)$ increases with u (Fig. 3A). For intermediate predator carrying capacity $(mr_1/(\lambda r_2) < K_2 < 4mr_1/(\lambda r_2))$ function $\tilde{\alpha}(u)$ is positive and decreases for low levels of intraguild predation, while for u approaching $r_2/(r_2 + m)$ it tends to infinity (Fig. 3B). For high values of $K_2 > 4mr_1/(\lambda r_2)$, $\tilde{\alpha}$ is negative for some values of intraguild parameter u (Fig. 3C). This can be interpreted as follows. When the intraguild predator carrying capacity is high $(K_2 > mr_1/(\lambda r_2))$ then as intraguild predation increases from zero it becomes more difficult for the intraguild prey to survive in the system

FIG. 3. Values of competition coefficients α and β that lead to species coexistence for model (1) with nonadaptive intraguild predation for various predation strengths (shaded area). (A) assumes a low intraguild predator carrying capacity $K_2 < mr_1/(\lambda r_2)$, ($K_2 = 0.8$), (B) assumes an intermediate intraguild predator carrying capacity $mr_1/(\lambda r_2) < K_2 < 4mr_1/(\lambda r_2)$, ($K_2 = 3.5$), and (C) assumes a high intraguild predator carrying capacity $K_2 > 4mr_1/(\lambda r_2)$, ($K_2 = 4.5$). If species y can survive by feeding on species x only, (i. e., $eK_1\lambda > m$) then intraguild predation enhances coexistence of intraguild predators in the system (Fig. 3D), ($K_1 = 14$). Otherwise, intraguild predators are prone to extinction (Fig. 3E), ($K_1 = 4$). For points 1, 2, and 3 see the explanation given in the text. Other parameters are $K_1 = 4$, $K_2 = 4.5$, $\lambda = 1$, $e = 0.1$, $r_1 = 1$, $r_2 = 1$, $m = 1$.

outcompeted by their prey because $\tilde{\beta}(u)$ is too small to satisfy the inequality $\beta < \tilde{\beta}(u)$. As K_2 increases the two conditions for interior equilibrium stability ($\alpha < \tilde{\alpha}(u)$, $\beta < \tilde{\beta}(u)$) are satisfied and both species coexist (for the intraguild prey species this is graphically illustrated by point 1 at Fig. 3B). For still higher values of K_2, the

intraguild prey species is outcompeted by predators (see point 3 in Fig. 3C) because $\tilde{\alpha}(u)$ is too small. Contrary to Morin (1999), Lawler and Morin (1993) observed that intraguild predators sometimes excluded its prey. In the framework of my model this could be explained by a higher strength of intraguild predation in their system

which may lead to exclusion of prey (see point 2 in Fig. 3B) for the same nutrient level for which coexistence is possible for a lower strength of intraguild predation (see point 1 in Fig. 3B). Alternatively, differences between Morin (1999) and Lawler and Morin (1993) could also be caused by some other factors such as variation in composition and densities of the common resource (bacteria) which cause changes in parameters of the system without influencing the predation strength u (Polis *et al.*, 1989; Holt and Polis, 1997).

Adaptive Predation

Next I assume that the predation strength is adaptive and that intraguild predation arises as competition for resources becomes more severe. I measure animal fitness by the per capita population growth rate and I compute the evolutionary stable strategy (ESS) for optimal predation strength. I consider a mutant of species y that plays a strategy u^* in a residential population of individuals playing a strategy u. Then fitness of the mutant will be

$$F(u^*, u) = (1 - u^*) F_1 + u^* F_2, \qquad (4)$$

where

$$F_1 = r_2 \left(1 - \frac{(1 - u) y}{K_2} - \beta \frac{x}{K_2} \right)$$

is the fitness of an individual which feeds on the common resource only and

$$F_2 = e\lambda x - m$$

is the fitness of an individual which feeds on species x only. Maximization of F gives the ESS under which no individual can unilaterally increase its fitness by changing its strategy. This gives

$$u(x, y) = \begin{cases} 0 & \text{if } y < y_1(x) \\ 1 - \dfrac{(r_2 + m) K_2}{r_2 y} + \dfrac{\beta r_2 + e\lambda K_2}{r_2 y} x \\ & \text{if } y_1(x) < y \quad \text{and} \quad x < x_1 \\ 1 & \text{if } x > x_1, \end{cases} \qquad (5)$$

where

$$y_1(x) = \frac{1}{r_2} ((r_2 + m) K_2 - (\beta r_2 + e\lambda K_2) x)$$

and

$$x_1 = \frac{(r_2 + m) K_2}{\beta r_2 + e\lambda K_2};$$

see Fig. 4.

Lines $y = y_1(x)$ and $x = x_1$ split the phase plane in three regions (Fig. 5). In the left region ($y < y_1(x)$ which automatically implies that $x < x_1$) population dynamics are described by the competitive system, in the central region they are described by the intraguild system, and in the right region ($x > x_1$) they are described by the predator–prey system. In the central region the predation strength u increases with increasing densities of species x and y (Fig. 4). Therefore, if densities of both species are low ($y < y_1(x)$) there will be no intraguild predation and population dynamics are described by the competitive Lotka–Volterra system (2). A straightforward calculation shows that the corresponding interior equilibrium $E^{(2)}$ ($\alpha < K_1/K_2$ and $\beta < K_2/K_1$) belongs to the left region of the state space provided that

$$\frac{e\lambda K_1 - m(1 - \alpha\beta)}{e\lambda\alpha} < K_2.$$

For high prey densities ($x > x_1$) competition is severe and it pays predators to feed only on species x. Population dynamics are then described by the predator–prey system (3). A straightforward calculation shows that the corresponding equilibrium $E^{(3)}$, if positive, belongs to the right region of the state space when

$$K_2 < \frac{m\beta}{e\lambda}.$$

This condition, together with positivity of $E^{(3)}$, implies that $\beta > K_2/K_1$, which excludes existence of a stable interior equilibrium $E^{(2)}$ for the strictly competitive system.

For intermediate population densities (satisfying $x < x_1$ and $y_1(x) < y$) intraguild predation is the evolutionarily stable strategy. Population dynamics are given by

$$x' = x \left(\frac{K_1 r_1 r_2 + K_2 (m + r_2)(K_1 \lambda - \alpha r_1)}{K_1 r_2} \right.$$

$$\left. - \frac{(e K_2 \lambda + r_2 \beta)(K_1 \lambda - \alpha r_1) + r_1 r_2}{K_1 r_2} x - \lambda y \right) \quad (6)$$

$$y' = (e\lambda x - m) u$$
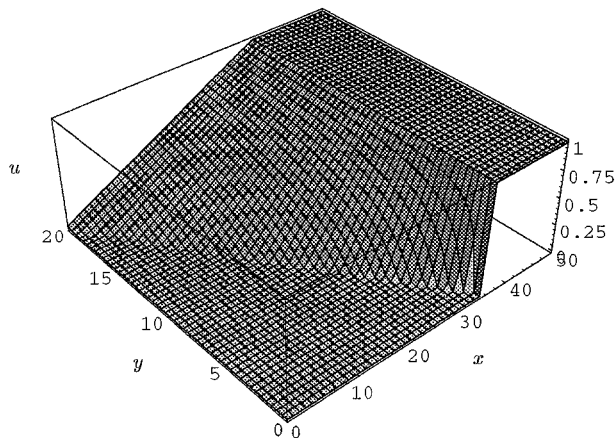
FIG. 4. Dependence of predation strength $u(x, y)$ given by (5) on population densities. Parameters are $\lambda = 0.1$, $e = 0.1$, $K_1 = 40$, $K_2 = 15$, $r_1 = 1$, $r_2 = 1$, $\alpha = 0.3$, $\beta = 0.4$, $m = 0.3$.
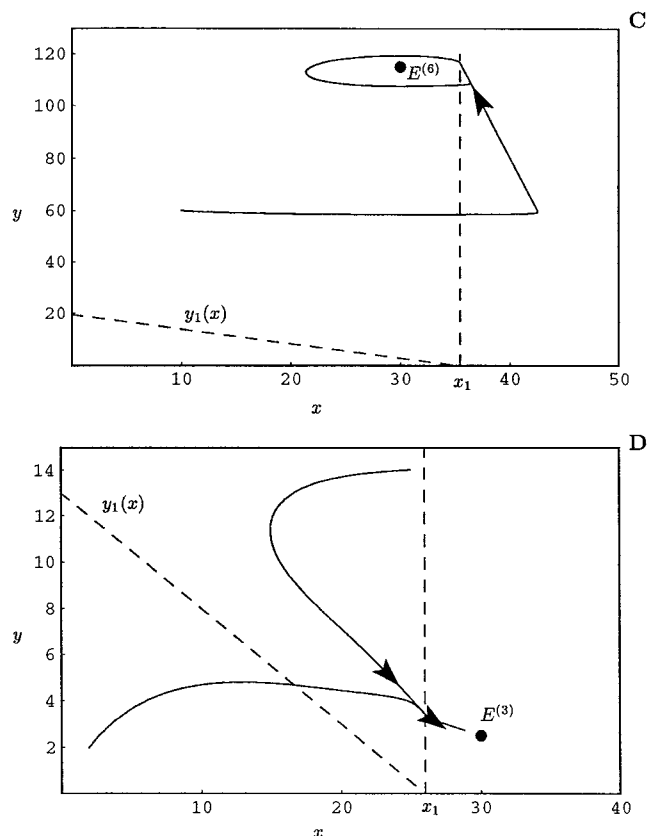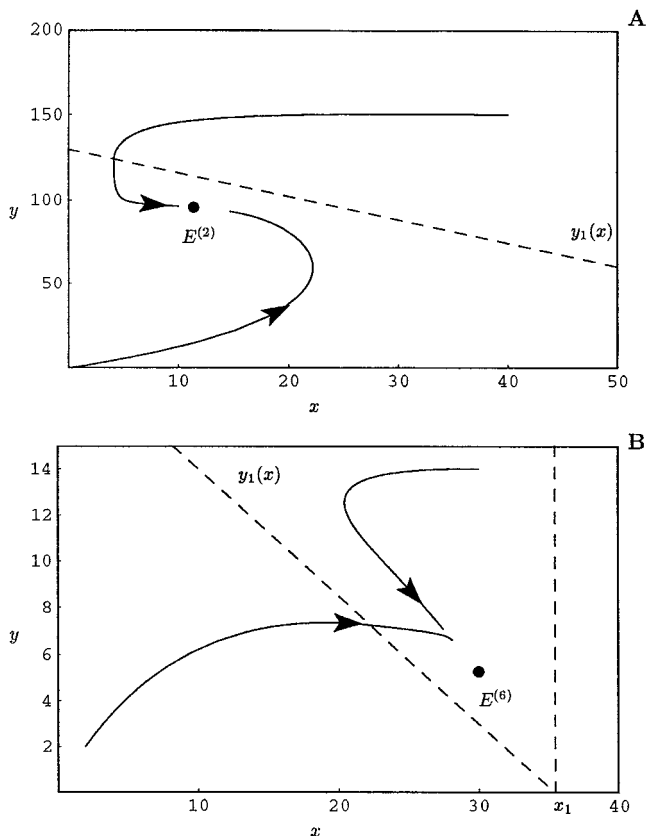
with interior equilibrium

$$E^{(6)}$$

$$= \left(\frac{m}{e\lambda}, \frac{e\lambda(K_1(K_2\lambda + r_1) - \alpha K_2 r_1) - m(\beta K_1\lambda + r_1 - \alpha\beta r_1)}{eK_1\lambda^2} \right).$$

This equilibrium belongs to the central region of the state space (which automatically implies positivity) if

$$\frac{m\beta}{e\lambda} < K_2 < \frac{e\lambda K_1 - m(1 - \alpha\beta)}{e\lambda\alpha}, \qquad (7)$$

and the strength of intraguild predation at this equilibrium is

$$u^{(6)} = \frac{r_1(e(K_1 - \alpha K_2)\lambda - (1 - \alpha\beta)m)}{K_1\lambda(e\lambda K_2 - m\beta) + e\lambda r_1(K_1 - \alpha K_2) - mr_1(1 - \alpha\beta)}.$$

FIG. 5. Population dynamics for model (1) with adaptive predation strength and high prey carrying capacity ($K_1 > m/(e\lambda)$). In (A) the carrying capacity of species y is high ($K_2 = 100$) and both populations coexist at the competitive equilibrium $E^{(2)}$ without any intraguild predation. Lowering the carrying capacity ($K_2 = 15$) leads to a positive strength of intraguild predation at $E^{(6)}$. In (B) this equilibrium is locally stable and in (C) ($K_1 = 50$, $r_1 = 40$, $r_2 = 1$, $\alpha = 2$) it is unstable and a limit cycle emerges. For yet a lower carrying capacity ($K_2 = 10$) the strength of predation at $E^{(3)}$ equals one, which means that the food web structure is described by a tri-trophic linear food chain. Other parameters are $\lambda = 0.1$, $e = 0.1$, $K_1 = 40$, $r_1 = 1$, $r_2 = 1$, $\alpha = 0.3$, $\beta = 0.4$, $m = 0.3$.

Equilibrium $E^{(6)}$ is locally stable provided the x-isocline has a negative slope, i.e., when $(eK_2\lambda + r_2\beta)(K_1\lambda - \alpha r_1) + r_1 r_2 > 0$ which holds for small values of the competition coefficient α.

Following Morin's experiment I study the dependence of population dynamics on the carrying capacity of species y, K_2. I will assume that the two populations coexist when the strength of predation is zero, i.e., $\alpha < K_1/K_2$ and $\beta < K_2/K_1$. There are two distinct cases which I consider separately.

First, I assume that the carrying capacity of species x is high, i.e.,

$$K_1 > \frac{m}{e\lambda},$$

which implies positivity of $E^{(3)}$ and the following inequality:

$$\frac{K_1}{\alpha} > \frac{K_1 e\lambda - m(1-\alpha\beta)}{e\alpha\lambda} > K_1\beta > \frac{m}{e\lambda}\beta. \qquad (8)$$

From the above analysis it follows that model (1) with adaptive predation strength has in principle three interior equilibria $E^{(2)}$, $E^{(3)}$, and $E^{(6)}$. I will show that for each K_2 value only one of these equilibria is feasible. The following qualitative cases are possible:

(a)   If $K_1/\alpha > K_2 > (K_1 e\lambda - m(1-\alpha\beta))/(e\lambda\alpha)$ then the competitive equilibrium ($E^{(2)}$) is positive and it belongs to the left region of the phase space (Fig. 5A). At this equilibrium the topology of our food web is described by the strictly competitive system. Inequality (7) implies that equilibrium $E^{(6)}$ of the intraguild system does not belong to the central region of the phase space and equilibrium $E^{(3)}$ of the strictly predator–prey system does not belong to the right region of the phase space due to (8), respectively.

(b)   If $(K_1 e\lambda - m(1-\alpha\beta))/(e\lambda\alpha) > K_2 > (m\beta)/(e\lambda)$ then equilibrium $E^{(6)}$ of the intraguild system belongs to the central region of the phase space and the predation strength at this equilibrium is positive (Fig. 5B). Equilibrium $E^{(2)}$ of the competitive system does not belong to the left region of the phase space and equilibrium $E^{(3)}$ of the predator–prey system does not belong to the right region of the phase space, respectively. If the equilibrium $E^{(6)}$ is unstable then numerical simulations suggest that a limit cycle centered at this equilibrium appears (Fig. 5C). Thus, for an intermediate carrying capacity K_2 our food web topology at the equilibrium $E^{(6)}$ is described by an intraguild predation system.
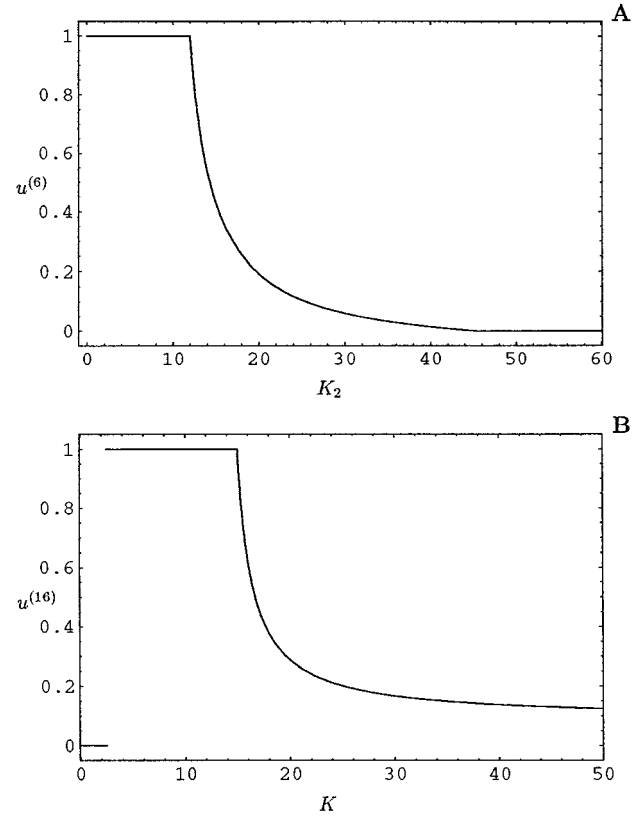
FIG. 6. Dependence of predation strength on (A) predator carrying capacity ($\lambda = 0.1$, $e = 0.1$, $K_1 = 40$, $r_1 = 1$, $r_2 = 1$, $\alpha = 0.3$, $\beta = 0.4$, $m = 0.3$) for the Lotka–Volterra model (5) and (B) on the resource carrying capacity $\lambda = \lambda_1 = \lambda_2 = 0.1$, $e_{12} = e_{23} = e_{13} = 0.1$, $r = 1$, $m_2 = 0.02$, $m_3 = 0.06$ for the model with resource dynamics (9).

(c)   If $(m\beta)/(e\lambda) > K_2$ then equilibrium $E^{(3)}$ of the predator–prey system belongs to the right region of the phase space and individuals of species y feed exclusively on individuals of species x at this equilibrium (Fig. 5C). The other two equilibria do not belong to the appropriate regions of the state space; see (8). At this equilibrium the food web topology is a linear chain.

Figure 6A shows the equilibrial predation strength of the adaptive model (1) as a function of the carrying capacity K_2. As K_2 increases, the strength of intraguild predation decreases.

Second, I assume that the carrying capacity of species x is low, i.e.,

$$K_1 < \frac{m}{e\lambda},$$

which implies that equilibrium $E^{(3)}$ is not positive and

$$\frac{m\beta}{e\lambda} > K_1\beta > \frac{K_1 e\lambda - m(1 - \alpha\beta)}{e\alpha\lambda}.$$

It follows that $E^{(6)}$ cannot belong to the central region of the state space. Thus, the only feasible interior equilibrium is $E^{(2)}$ at which no intraguild predation occurs and the two populations are competing for the common resource.

THE MECHANISTIC MODEL

In the previous section competition between the two species was modeled by a Lotka–Volterra system which does not explicitly consider the common resource dynamics. Here I consider resource dynamics and the model is based on the mechanistic description of competition and predation

$$R' = R\left(r\left(1 - \frac{R}{K}\right) - \lambda x - (1 - u)\,\lambda_1 y\right)$$

$$x' = x(e_{12}\lambda R - u\lambda_2 y - m_2) \qquad (9)$$

$$y' = y((1 - u)\,\lambda_1 e_{13} R + u\lambda_2 e_{23} x - m_3).$$

The parameter u has the same meaning as in the case of the two-dimensional model. Parameter λ is the search rate of x individuals and λ_1 and λ_2 are the search rates of y individuals for the common resource and for species x, respectively, and e_{ij} is a factor which describes how the ith $(i = 1, 2)$ food type is converted to new offspring of the jth $(j = 2, 3)$ consumer. For a fixed positive predation strength u, system (9) was numerically studied by Holt and Polis (1997). While the strictly competitive system $(u = 0)$ does not have any interior equilibrium, intraguild predation leads to the emergence of an interior equilibrium which may be either stable or unstable (Holt and Polis, 1997).

As in the previous section I study the effects of the strength of adaptive predation on species stability and coexistence. First I determine the evolutionarily optimal predation strength. I consider a mutant individual of species y that plays a strategy u^* in a residential population of individuals playing a strategy u. Then the fitness of this mutant is given by (4), where

$$F_1 = \lambda_1 e_{13} R - m_3$$

is the fitness of an individual which feeds on the common resource only and

$$F_2 = \lambda_2 e_{23} x - m_3$$

is the fitness of an individual which feeds only on species x. Maximization of F gives:

(a) if the common resource is abundant compared to abundance of species x $(\lambda_1 e_{13} R > \lambda_2 e_{23} x)$ then the optimal strategy of y individuals is to feed on the common resource only $(u = 0)$,

(b) if the common resource is less abundant compared to abundance of species x $(\lambda_1 e_{13} R < \lambda_2 e_{23} x)$ then the optimal strategy of y individuals is to feed exclusively on species x $(u = 1)$,

(c) if $\lambda_1 e_{13} R = \lambda_2 e_{23} x$ then the optimal strategy of y individuals is not uniquely specified.

In species density space I denote the region where the optimal strategy is to feed on the common resource only as G^0 (case (a)) and the region where predators feed on species x exclusively as G^1 (case (b)). The region in which optimal strategy is not uniquely determined (case (c)) separates G^0 from G^1 and it is denoted as M (Fig. 7). In G^0 population dynamics are given by a strictly competitive system:

$$R' = R\left(r\left(1 - \frac{R}{K}\right) - \lambda x - \lambda_1 y\right)$$

$$x' = x(e_{12}\lambda R - m_2) \qquad (10)$$

$$y' = y(\lambda_1 e_{13} R - m_3).$$

This system has no interior equilibrium and the weaker competitor will always be excluded from the system following Tilman's (1990) R^* rule. First, I assume that individuals of species y are weaker competitors, i.e.,

$$\frac{m_2}{e_{12}\lambda} < \frac{m_3}{e_{13}\lambda_1}. \qquad (11)$$

Then all trajectories (assuming $K > m_2/(e_{12}\lambda)$) of (10) converge to

$$E_1^{(10)} = \left(\frac{m_2}{e_{12}\lambda}, \frac{r(e_{12}K\lambda - m_2)}{e_{12}K\lambda^2}, 0 \right).$$

The equilibrium $E_1^{(10)}$ is in G^0 if

$$\frac{e_{23}K\lambda_2 r}{e_{13}K\lambda\lambda_1 + e_{23}\lambda_2 r} < \frac{m_2}{e_{12}\lambda}. \tag{12}$$

In the region G^1 the food web topology is described by a tri-trophic linear food chain:

$$R' = R\left(r\left(1 - \frac{R}{K}\right) - \lambda x \right)$$
$$x' = x(e_{12}\lambda R - \lambda_2 y - m_2) \tag{13}$$
$$y' = y(\lambda_2 e_{23} x - m_3).$$

This system has one interior equilibrium,

$$E^{(13)} = \left(K\left(1 - \frac{\lambda m_3}{e_{23}\lambda_2 r}\right), \frac{m_3}{e_{23}\lambda_2}, \right.$$
$$\left. \frac{e_{23}\lambda_2 r(e_{12}K\lambda - m_2) - m_3\lambda^2 e_{12}K}{e_{23}\lambda_2^2 r} \right).$$

Equilibrium $E^{(13)}$ is positive if

$$0 < m_3 < \frac{e_{23}\lambda_2 r(e_{12}K\lambda - m_2)}{\lambda^2 e_{12}K} \tag{14}$$

and it is globally asymptotically stable in G^1 (which means that all trajectories which stay in G^1 converge to this equilibrium; Hofbauer and Sigmund, 1984, p. 64). Equilibrium $E^{(13)}$ belongs to G^1 provided

$$\frac{e_{23}K\lambda_2 r}{e_{13}K\lambda\lambda_1 + e_{23}\lambda_2 r} < \frac{m_3}{e_{13}\lambda_1}.$$

The boundary equilibrium $E_1^{(10)}$ of system (10) is also a boundary equilibrium of system (13).

Next I analyze population dynamics in the plane $\lambda_1 e_{13} R = \lambda_2 e_{23} x$ where both pure strategies give the same fitness. There exists an equilibrium of system (9) driven by the optimal intraguild predation strategy which is in the plane M; see Appendix B. If

$$\frac{m_2}{e_{12}\lambda} < \frac{m_3}{e_{13}\lambda_1} < \frac{e_{23}K\lambda_2 r}{e_{13}K\lambda\lambda_1 + e_{23}\lambda_2 r} \tag{15}$$

then, locally around this equilibrium, all trajectories of system (9) are driven to the plane M and when they reach this plane, population dynamics are described by the following differential-algebraic system of equations:

$$R = \frac{\lambda_2 e_{23}}{\lambda_1 e_{13}} x$$

$$x' = x\left(\frac{(\lambda_2 r - \lambda_1 m_2)}{\lambda_1 + \lambda_2} \right.$$
$$\left. - \frac{\lambda_2((e_{13} - e_{12}e_{23})K\lambda\lambda_1 + e_{23}\lambda_2 r)x}{e_{13}K\lambda\lambda_1(\lambda_1 + \lambda_2)} - \frac{\lambda_1\lambda_2 y}{\lambda_1 + \lambda_2} \right)$$

$$y' = y(\lambda_1 e_{13} R - m_3); \tag{16}$$

see Appendix B. The interior equilibrium is

$$E^{(16)} = \left(\frac{m_3}{\lambda_1 e_{13}}, \frac{m_3}{e_{23}\lambda_2}, \frac{m_3\lambda e_{12} - e_{13}\lambda_1 m_2}{e_{13}\lambda_1\lambda_2} + \frac{r}{\lambda_1} \right.$$
$$\left. - \frac{m_3(K\lambda\lambda_1 e_{13} + e_{23}\lambda_2 r)}{e_{13}e_{23}K\lambda_1^2\lambda_2} \right)$$

Equilibrium $E^{(16)}$ is positive due to (15) and it is stable in the switching plane M if the x-isocline has a negative slope. This holds, e.g., when $e_{12}e_{23} < e_{13}$ which I will assume. Under these conditions equilibrium $E^{(16)}$ is locally stable (Fig. 7A) and the strength of intraguild predation at $E^{(16)}$ is

$$u^{(16)} =$$

$$\frac{e_{23}K\lambda_1(e_{13}\lambda_1 m_2 - e_{12}\lambda m_3)}{e_{23}m_3(\lambda_2 r - e_{12}K\lambda\lambda_1) + e_{13}K\lambda_1(e_{23}\lambda_1 m_2 + \lambda m_3 - e_{23}\lambda_2 r)}.$$

Finally I study the topology of the food web which is described by (9) and population stability as a function of the common resource carrying capacity K. In principle the adaptive system (9) has two interior equilibria $E^{(16)}$ and $E^{(13)}$. As I assume that individuals of species x are superior competitors (see (11)) and that $E_1^{(10)}$ exists (i.e., $K > m_2/(e_{12}\lambda)$) there are the following possibilities with respect to decreasing common resource carrying capacity K:

(a) If $m_3/(e_{13}\lambda_1) < (e_{23}K\lambda_2 r)/(e_{13}K\lambda\lambda_1 + e_{23}\lambda_2 r)$ then the only feasible, locally stable interior equilibrium is $E^{(16)}$ (Fig. 7A). At this equilibrium the food web topology is an intraguild predation system and the strength of intraguild predation is $u = u^{(16)}$.

(b) If $m_2/(e_{12}\lambda) < (e_{23}K\lambda_2 r)/(e_{13}K\lambda\lambda_1 + e_{23}\lambda_2 r) < m_3/(e_{13}\lambda_1) < (e_{23}\lambda_2 r(e_{12}K\lambda - m_2))/(\lambda^2 e_{12}Ke_{13}\lambda_1)$ then $E^{(13)}$ is feasible, locally stable and at this equilibrium individuals of species y feed on species x only ($u = 1$; Fig. 7B). At this

A

C

B

D
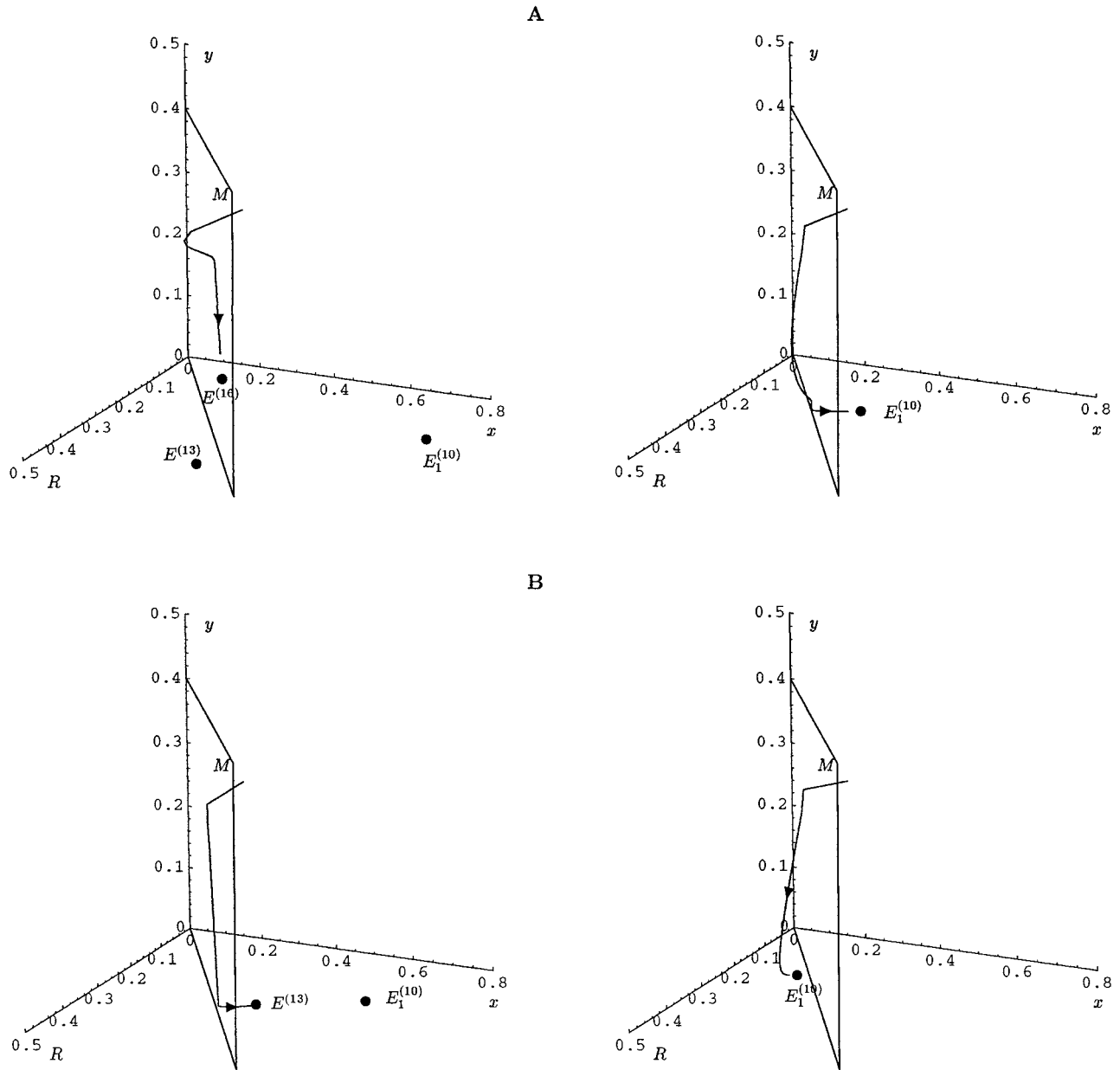
FIG. 7. Population dynamics for system (9) with adaptive predation strength when individuals of species x are superior competitors to individuals of species y. The figures describe qualitative effects for decreasing values of the resource carrying capacity. In (A) ($K = 0.8$) equilibrium $E^{(16)}$ is locally stable and the strength of intraguild predation, is positive at this equilibrium. In (B) ($K = 0.5$) equilibrium $E^{(13)}$ is locally stable and at this equilibrium the food web topology is a linear tri-trophic food chain. For yet lower values of the resource carrying capacity (C) ($K = 0.3$) the environmental productivity is not sufficient to support top predators at positive densities, and only prey survive at the equilibrium $E_1^{(10)}$. For very low environmental productivity (D) ($K = 0.2$) the strength of predation at equilibrium $E_1^{(10)}$ is zero and the competitively weaker species y is outcompeted from the system by species x. Other parameters are $\lambda_1 = 1$, $\lambda_2 = 1$, $\lambda = 1$, $e_{12} = 0.1$, $e_{13} = 0.1$, $e_{23} = 0.1$, $r = 1$, $m_2 = 0.02$, $m_3 = 0.04$.

equilibrium the food web topology is a tri-trophic linear food chain.

(c) If $m_2/(e_{12}\lambda) < (e_{23}K\lambda_2 r)/(e_{13}K\lambda\lambda_1 + e_{23}\lambda_2 r) < (e_{23}\lambda_2 r(e_{12}K\lambda - m_2))/(\lambda^2 e_{12}Ke_{13}\lambda_1) < m_3/(e_{13}\lambda_1)$ then neither $E^{(13)}$ nor $E^{(16)}$ exist and the only feasible equi-

librium is $E_1^{(10)}$ at which predators go extinct (Fig. 7C). The food web topology at this equilibrium is a tri-trophic linear food chain as in case (b); because $E_1^{(10)}$ belongs to G^1.

(d) If $(e_{23}K\lambda_2 r)/(e_{13}K\lambda\lambda_1 + e_{23}\lambda_2 r) < m_2/(e_{12}\lambda)$ then the only feasible equilibrium is $E_1^{(10)}$ (Fig. 7D).

The food web topology at this equilibrium is a strictly competitive system because $E_1^{(10)}$ belongs to G^0.

In Fig. 6B I plot the equilibrial optimal predation strength as a function of the environmental productivity K. For low values of K (case (d)) species y does not survive at the equilibrium $E_1^{(10)}$, which belongs to G^0 and the predation strength is therefore $u = 0$. When K increases (case (c)) the equilibrium $E_1^{(10)}$ moves to G^1 and the strength of predation discontinuously switches to $u = 1$. Yet, the environmental productivity is too low to maintain population y at a positive density. For still larger values of K (case (b)) the environmental productivity is high enough to support top predators in the tri-trophic linear food chain at a positive density. As the environmental productivity increases further (case (a)) intraguild predation appears at the locally stable equilibrium $E^{(16)}$ and the predation strength decreases with an increasing environmental productivity K.

This pattern is consistent with Morin's (1999) observations. Assume that in his experiments species x individuals are more efficient competitors. Then for a low environ-mental productivity K, only species x survives at the equilibrium (cases (c) and (d)). As the environmental productivity increases (cases (a) and (b)), both species coexist. However, because Morin does not provide data on the proportion of macrostomes in his system (which reflects the predation strength u) I cannot verify that the strength of intraguild predation follows my observations along a gradient in environmental productivity. If u is inflexible then Morin's data may better be explained by models in Polis *et al.* (1989) and Holt and Polis (1997).

If predators are superior competitors, i.e.,

$$\frac{m_2}{e_{12}\lambda} > \frac{m_3}{e_{13}\lambda_1},$$

then interior equilibrium $E^{(16)}$ is never attractive and there are two alternative equilibria

$$E_2^{(10)} = \left(\frac{m_3}{e_{13}\lambda_1}, 0, \frac{r(e_{13}K\lambda_1 - m_3)}{e_{12}K\lambda_1^2} \right)$$
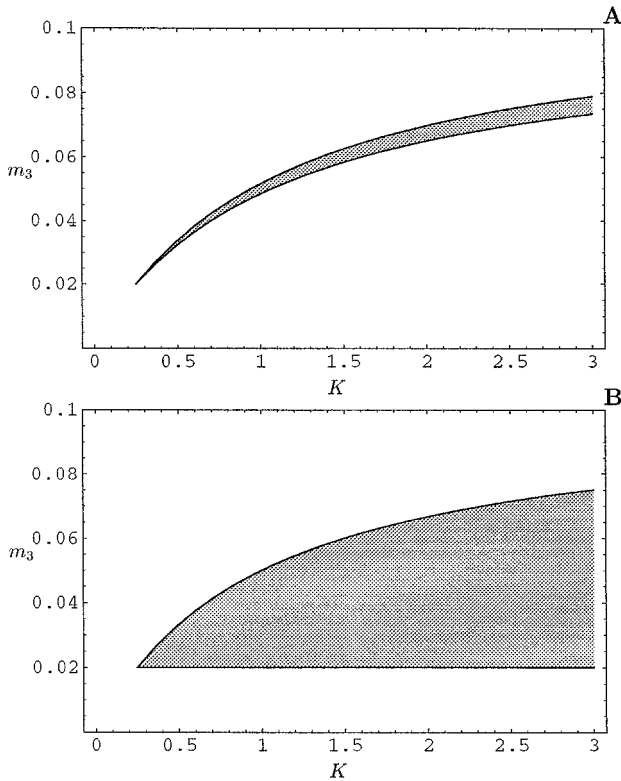
and $E^{(13)}$ at which no intraguild predation occurs.

Comparison of Stability for Adaptive and Nonadaptive Intraguild Predation

A direct calculation shows that for a fixed strength of intraguild predation $u = u^{(16)}$ the interior equilibrium of system (9) with nonadaptive intraguild predators coincides with $E^{(16)}$. Thus the stability of $E^{(16)}$ as the equilibrium of the nonadaptive system (9) can be compared with its stability as an equilibrium of the adaptive system. Condition (15) implies the local stability of $E^{(16)}$ as the equilibrium of the adaptive system while conditions for local stability of $E^{(16)}$ as the equilibrium of the nonadaptive system are given in Appendix C (see also Holt and Polis, 1997). It is shown there that conditions ensuring local stability of $E^{(16)}$ as the equilibrium of the nonadaptive system are more restrictive than are those for the adaptive system. The set of parameters for which local stability holds for the nonadaptive system is shown in Fig. 8A while for the adaptive system it is shown in Fig. 8B. We see that adaptive intraguild predation enlarges the set of parameters for which the interior equilibrium is locally stable.

FIG. 8. The range of parameters in (K, m_3) state space that leads to local stability of equilibrium $E^{(16)}$ for nonadaptive intraguild predation (A) and for adaptive intraguild predation (B). Parameters are $\lambda_1 = 1$, $\lambda_2 = 1$, $\lambda = 1$, $e_{12} = 0.1$, $e_{13} = 0.1$, $e_{23} = 0.1$, $r = 1$, $m_2 = 0.02$.

DISCUSSION

In this article I extended the isocline analysis of Polis *et al.* (1989) to include a trade-off between predation and

competition. Such a trade-off is well documented for some protist species which normally feed on bacteria but the presence of a potential prey species induces development of large-mouthed macrostomes (Giese, 1973). I analyzed the effect of the strength of intraguild predation on stability and I proved that, when environmental productivity is not too low, a low strength of intraguild predation is destabilizing because it makes it difficult or impossible for intraguild prey to persist in the system. Conversely, a high strength of intraguild predation promotes intraguild prey persistence relative to the competitive system in which predation strength is zero (Figs. 3B and 3C). If the predator can survive by feeding on its prey alone then intraguild predation increases persistence of the intraguild predators relative to the strictly competitive system (Fig. 3D). Otherwise, intraguild predation makes survival of intraguild predators more difficult (Fig. 3E). Holt and Polis (1997) suggested that species coexistence in systems with intraguild predation may be caused by an adaptive change in the strength of intraguild predation. Computing the ESS I proved that there is a threshold in the potential intraguild prey density below which intraguild predation is not an ESS when the intraguild predator density is low. Under these conditions the resulting food web is of a strictly competitive type. This means that when densities of the two competing species are low then intraguild predation is not selected. As the density of either the potential intraguild predator or the potential intraguild prey increases, intraguild predation occurs. For high intraguild prey densities the predation strength is 1 and the food web is a linear food chain. I then studied the dependence of population dynamics with adaptive predation strength on the potential intraguild predator carrying capacity. If the carrying capacity of the intraguild predator is high then the food web topology is strictly a competitive system in which either both populations coexist at a competitive equilibrium (Fig. 5A) or the potential intraguild predator competitively excludes the other species. As the carrying capacity of the potential intraguild predator decreases the food web topology changes from the competitive system to an intraguild predation system. The corresponding equilibrium can be either locally stable (Fig. 5B) or unstable (Fig. 5C). As the carrying capacity of the intraguild predator decreases further, predation strength increases to one and the food web becomes a linear food chain. At the corresponding equilibrium predators feed on their prey only (Fig. 5D). My model predicts that as the carrying capacity (which is proportional to the environmental productivity) for the intraguild predator increases, the adaptive strength of predation decreases (Fig. 6A).

Second, I considered a more mechanistic model in which resource dynamics are influenced by consumption. For nonadaptive intraguild predation this model was studied by Holt and Polis (1997). They proved that a necessary criterion for coexistence is that the intraguild prey is a superior competitor to the intraguild predator. I proved that under the same conditions adaptive intraguild predation can be a stabilizing factor which leads to emergence of a locally stable population equilibrium with a positive strength of intraguild predation if environmental productivity is high enough. If intraguild prey are inferior competitors relative to intraguild predators then such an equilibrium cannot arise. Local stability analysis of the system as a function of the resource carrying capacity resembles the Lotka–Volterra competition model. For low resource carrying capacities the two species are competing for the common resource and the better competitor displaces the other species (Fig. 7D). As the resource carrying capacity increases, topology of the food web changes from a strictly competitive system to a strictly tri-trophic linear food chain. At the corresponding equilibrium the predation strength is one and either resource productivity is not high enough to support a positive equilibrial density of predators (Fig. 7C) or all species coexist at the corresponding equilibrium. For still higher resource carrying capacities a new equilibrium appears (Fig. 7A). At this equilibrium, predation strength is between zero and one and intraguild predation arises. Dependence of the strength of predation at the corresponding equilibrium on environmental productivity is similar to the case of the Lotka–Volterra model discussed previously (Fig. 6B). I conclude that in both models with adaptive intraguild predators, intraguild predation should decrease with increasing environmental productivity.

It was shown that optimal foraging enhanced species coexistence through the emergence of a limit cycle for systems where nonomnivorous predators feed optimally on two prey types (Gleeson and Wilson, 1986; Křivan, 1996; Křivan and Sikder, 1999; Boukal and Křivan, 1999; van Baalen *et al.*, submitted). The mechanism that leads to coexistence in the present article is different because stability was achieved through the appearance of a new equilibrium rather than a limit cycle (although numerical simulations suggest that for the two dimensional model a limit cycle can also exist). In the model with resource dynamics, adaptive intraguild predation leads to the emergence of a locally stable equilibrium point at which both pure strategies (i.e., feeding on resource only or feeding on prey only) give the same fitness. A similar mechanism was observed in Sirot and Křivan (1997). This new equilibrium for the adaptive

system is also an equilibrium for the nonadaptive system when predation strength equals $u^{(16)}$.

These theoretical results can be related to the experimental studies of Morin (1999). He found in laboratory experiments with bacteria and two freshwater protists, *Colpidium striatum* (the intraguild prey) and *Blepharisma americanum* (the intraguild predator), that the intraguild prey excluded the intraguild predator when bacterial production was low, while both species coexisted at higher levels of bacterial production. Assuming that protists adaptively adjust their intraguild predation strength to other species' densities, this prediction is consistent with models discussed in this article. It would be interesting to compare the strength of intraguild predation observed in experiments with those predicted here. Experimental design with protists seems to be particularly suitable for such experiments.

APPENDIX A

Positivity and Stability of $E^{(1)}$

System (1) can be rewritten as a Lotka–Volterra competitive system

$$x' = r_1 x \left(1 - \frac{x}{K_1} - \frac{r_1 \alpha(1-u) + \lambda u K_1}{r_1 K_1} y \right)$$

$$y' = r_2 y \left(1 - u - \frac{mu}{r_2} - \frac{(1-u)^2 y}{K_2} \right.$$

$$\left. - \frac{\beta r_2(1-u) - K_2 e \lambda u}{r_2 K_2} x \right).$$

I define

$$A(u) = \frac{r_1 \alpha(1-u) + \lambda u K_1}{r_1 K_1},$$

$$B(u) = 1 - u - \frac{mu}{r_2},$$

$$C(u) = \frac{(1-u)^2}{K_2},$$

$$D(u) = \frac{\beta r_2(1-u) - K_2 e \lambda u}{r_2 K_2}.$$

The interior equilibrium of (1) is given by

$$E^{(1)} = (x^{(1)}, y^{(1)})$$

$$= \left(\frac{K_1(C(u) - A(u) B(u))}{C(u) - K_1 A(u) D(u)}, \frac{B(u) - K_1 D(u)}{C(u) - K_1 A(u) D(u)} \right).$$

The trace of Jacobian of (1) evaluated at the interior equilibrium $E^{(1)}$ is

$$\frac{r_1}{K_1} x^{(1)} + r_2 C(u) y^{(1)} > 0$$

and the determinant is

$$r_1 r_2 x^{(1)} y^{(1)} \left(\frac{C(u)}{K_1} - A(u) D(u) \right).$$

Using the Routh–Hurwitz criterion I find that the real parts of eigenvalues are negative if the determinant of Jacobian is positive, which holds if

$$\beta < \phi(\alpha) = \frac{r_1(1-u)}{K_1 \lambda u + \alpha r_1(1-u)} + \frac{e K_2 \lambda u}{r_2(1-u)}.$$

Now I consider the question of positivity of the interior equilibrium. As I am interested only in the case in which the interior equilibrium is stable, I will assume that $C(u) - K_1 A(u) D(u) > 0$. Under this condition $x^{(1)} > 0$ if either $u > r_2/(r_2 + m)$ because in this case $B(u)$ is negative, or $u < r_2/(r_2 + m)$ and

$$\alpha < \tilde{\alpha}(u) = \frac{K_1 r_2(1-u)}{K_2(r_2(1-u) - mu)} - \frac{K_1 \lambda u}{r_1(1-u)}. \quad (17)$$

Similarly, $y^{(1)} > 0$ if

$$\beta < \tilde{\beta} = \frac{K_2}{K_1} \left(1 + \frac{u(e K_1 \lambda - m)}{r_2(1-u)} \right). \quad (18)$$

Because $\phi(\tilde{\alpha}) = \tilde{\beta}$ and $\phi(\alpha)$ is a decreasing function it follows that for $u < r_2/(r_2 + m)$ and for α and β which satisfy (17) and (18) stability condition, $\beta < \phi(\alpha)$ is met.

For a high strength of intraguild predation $u > r_2/(r_2 + m)$, $x^{(1)}$ is always positive, equilibrial predator density is positive if $\beta < \tilde{\beta}(u)$, and the condition for equilibrium stability $\beta < \phi(\alpha)$ is automatically satisfied because

$$\tilde{\beta}(u) \leqslant \lim_{\alpha \to \infty} \phi(\alpha) < \phi(\alpha)$$

for every $u > 0$.

APPENDIX B

Population Dynamics of (9) in M

Let f^0 denote the right hand side of the strictly competitive system (10) and f^1 of the strictly predatory system (13). Let $n = (\lambda_1 e_{13}, -\lambda_2 e_{23}, 0)$ be a perpendicular vector to the switching plane M. Then in M I obtain ($\langle \cdot, \cdot \rangle$ denotes the scalar product)

$$\langle n, f^0 \rangle < 0$$

if $y > y^0(x)$ and

$$\langle n, f^1 \rangle > 0$$

if $y > y^1(x)$ where

$$y^0(x) = \frac{e_{13} K \lambda_1 (m_2 + r) - x((e_{12} K \lambda + r) e_{23} \lambda_2 + \lambda e_{13} K \lambda_1)}{e_{13} K \lambda_1^2}$$

and

$$y^1(x)$$
$$= \frac{-e_{13} K \lambda_1 (m_2 + r) + x((e_{12} K \lambda + r) e_{23} \lambda_2 + \lambda e_{13} K \lambda_1)}{e_{13} K \lambda_1 \lambda_2}.$$

The region of M defined by $y^0(x) < y$, $y^1(x) < y$ is called the sliding domain because trajectories of (9) which enter it move in M unless they cross either $y^0(x)$ or $y^1(x)$ and leave M. Moreover, nearby trajectories are driven both from G^0 and G^1 to the sliding domain. This implies that for every trajectory in the sliding domain

$$\lambda_1 e_{13} R'(t) = \lambda_2 e_{23} x'(t),$$

which allows us to compute explicitly the strength of intraguild predation u,

$$u(x, y) = -\frac{m_2 + r}{(\lambda_1 + \lambda_2) y}$$
$$+ \frac{e_{13} K \lambda \lambda_1 + e_{23} \lambda_2 (e_{12} K \lambda + r)}{e_{13} K \lambda_1 (\lambda_1 + \lambda_2) y} x + \frac{\lambda_1}{\lambda_1 + \lambda_2}.$$

Existence and uniqueness of solutions of (9) driven by the optimal predation strength follow from Filippov (1988) (see also Colombo and Křivan, 1993). Population dynamics in the sliding domain are given by system (16) which has one interior equilibrium $E^{(16)}$. I remark that condition (15) implies that $E^{(16)}$ belongs to the sliding domain.

APPENDIX C

Local Stability of the Interior Equilibrium of (9)

Conditions for local stability of $E^{(16)}$ for the nonadaptive system with $u = u^{(16)}$ can be derived by using the Routh–Hurwitz criterion (Holt and Polis, 1997). These conditions are

$$a_0 > 0, a_1 > 0, a_2 > 0, a_1 a_2 > a_0,$$

where

$$a_0 = \lambda_2 u^{(16)} R^{(16)} x^{(16)} y^{(16)}$$
$$\times \left((1 - u^{(16)}) \lambda \lambda_1 (e_{12} e_{23} - e_{13}) + \frac{u^{(16)} \lambda_2 e_{23}}{K} \right),$$

$$a_1 = (1 - u^{(16)})^2 \lambda_1^2 e_{13} R^{(16)} y^{(16)}$$
$$+ (u^{(16)})^2 \lambda_2^2 e_{23} x^{(16)} y^{(16)} + \lambda e_{12} \lambda R^{(16)} x^{(16)},$$

and

$$a_2 = \frac{R^{(16)} r}{K}.$$

Therefore conditions $a_0 > 0$, $a_1 > 0$, and $a_2 > 0$ are satisfied. Consider the case in which condition (15), which ensures local stability of $E^{(16)}$ as the equilibrium of the adaptive system, holds. Then a_0 is positive (I assume that $e_{13} - e_{12} e_{23} > 0$) if

$$\frac{e_{23} \lambda_1 \lambda_2 r (K \lambda (e_{13} - e_{12} e_{23}) + m_2 e_{23}))}{e_{13} \lambda_1 \lambda (K \lambda \lambda_1 (e_{13} - e_{12} e_{23}) + e_{23} \lambda_2 r)}$$
$$< \frac{m_3}{e_{13} \lambda_1} < \frac{e_{23} K \lambda_2 r}{e_{13} K \lambda \lambda_1 + e_{23} \lambda_2 r}.$$

Thus we see that the condition for positivity of a_0 is more restrictive than is condition (16). The conditions under which $a_1 a_2 > a_0$ are more complicated and I do not list them here.

I conclude that conditions ensuring local stability of $E^{(16)}$ as the equilibrium of the nonadaptive system are more restrictive than are those for the adaptive system.

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