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Alternative Food, Switching Predators, and the Persistence of Predator-Prey Systems

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ABSTRACT: Sigmoid functional responses may arise from a variety of mechanisms, one of which is switching to alternative food sources. It has long been known that sigmoid (Holling's Type III) functional responses may stabilize an otherwise unstable equilibrium of prey and predators in Lotka-Volterra models. This poses the question of under what conditions such switching-mediated stability is likely to occur. A more complete understanding of the effect of predator switching would therefore require the analysis of one-predator/two-prey models, but these are difficult to analyze. We studied a model based on the simplifying assumption that the alternative food source has a fixed density. A well-known result from optimal foraging theory is that when prey density drops below a threshold density, optimally foraging predators will switch to alternative food, either by including the alternative food in their diet (in a fine-grained environment) or by moving to the alternative food source (in a coarse-grained environment). Analyzing the population dynamical consequences of such stepwise switches, we found that equilibria will not be stable at all. For suboptimal predators, a more gradual change will occur, resulting in stable equilibria for a limited range of alternative food types. This range is notably narrow in a fine-grained environment. Yet, even if switching to alternative food does not stabilize the equilibrium, it may prevent unbounded oscillations and thus promote persistence. These dynamics can well be understood from the occurrence of an abrupt (or at least steep) change in the prey isocline. Whereas local stability is favored only by specific types of alternative food, persistence of prey and predators is promoted by a much wider range of food types.

Keywords: predator-prey dynamics, alternative food, switching, optimal foraging, ideal free distribution, persistence.

Predators will switch to alternative food when the density of their preferred prey is low (Murdoch 1969). In population dynamical studies, switching is usually modeled as a sigmoid (Holling's Type III; Holling 1959) functional response. Because sigmoid functional responses can stabilize a predator-prey equilibrium in Lotka-Volterra models (Takahashi 1964; May 1974; Murdoch and Oaten 1975), it is argued that alternative food may play an important role in promoting the persistence of predator-prey systems.

Although it is often claimed that a sigmoid functional response may result from adaptive decisions, many optimal foraging models predict functional responses of other shapes (Holt 1983; Stephens and Krebs 1986; McNamara and Houston 1987). For example, Charnov's (1976) well-known model of optimal diets predicts a stepwise switch from a diet of profitable prey only to a mixed diet including alternative food (see also Werner and Hall 1974). The consequences of such stepwise switches for predator-prey (or host-parasitoid) population dynamics have been investigated by Gleeson and Wilson (1986), Colombo and Křivan (1993), Fryxell and Lundberg (1994, 1997), Křivan (1996, 1997*b*, 1998), Křivan and Sirot (1997), Sirot and Křivan (1997), Křivan and Sikder (1999), and Genkai-Kato and Yamamura (1999).

Fryxell and Lundberg (1994, 1997) have demonstrated, using numerical simulation studies of one-predator/two-prey models, that predators will switch to low-quality prey only when they have reduced the more profitable prey to low levels. At times when prey density is low, such a switch will diminish predation pressure on the profitable prey while at the same time buffering predator density. Together these two factors put an upper limit to the oscillations of the system composed of the predators and the profitable prey.

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Using control theory, Křivan (1996) confirmed these results by showing that if the unprofitable prey species is close to its carrying capacity (and therefore not strongly regulated by the predator), the stepwise switch may lead to reduced fluctuations in the three-species system. In addition, Křivan and Sikder (1999) showed that switching increases the range of parameters for which one-predator/two-prey systems are persistent; populations may fluctuate but no population goes extinct in the long run.

In this article, we will extend on these studies by focusing on the dynamics of the predator and the profitable prey. The main difference from previous studies is that we assume that the alternative food has no dynamics of its own, that is, alternative food is always available in constant amounts, unaffected by consumption. This simplification is justified for many arthropod predators because they can rely on plant-provided alternative food sources such as pollen or nectar, the availability of which is unlikely to be influenced by the predator's consumption (van Rijn and Sabelis 1993; van Rijn and Tanigoshi 1999; Eubanks and Denno 2000).

The advantage of this approach is that it reduces the dimension of the system from three to two, which allows the use of phase-plane analysis to study the consequences of the availability of alternative food. We will show that a nondynamic alternative leads to similar conclusions as are obtained from one-predator/two-prey models that we discussed above. Moreover, the simplification allows us to obtain analytical insight into how the properties of alternative food affect population dynamics in terms of stability of the equilibrium and persistence of predator and prey.

Usually, both top-down and bottom-up regulation (logistic density dependence in prey growth) are considered (e.g., Fryxell and Lundberg 1994, 1997; Křivan 1996). Bottom-up control (which has a strong stabilizing effect) may mask the effect of switching. Therefore, in this article, we do not consider bottom-up regulation; our food webs assume only top-down control.

A stepwise switch is predicted by optimal foraging theory assuming that predators are perfect and have complete information. In reality, the switch is likely to be more gradual (either because of imperfect switching or because there is genetic variation in the population). We will therefore investigate the consequences of both stepwise and more gradual switches.

The classical optimal foraging framework (see MacArthur and Pianka 1966; Stephens and Krebs 1986) assumes that prey and alternative food items are homogeneously mixed (fine-grained environments). Often, however, the alternative food and prey are spatially segregated. If this is the case, the decision for a predator becomes different: if it searches for alternative food, it will no longer encounter prey (and vice versa). Optimal foraging decisions in such coarse-grained environments lead to the "ideal free distribution" (Fretwell and Lucas 1970): the predators will distribute themselves in such a way that no individual is better off by changing its searching strategy. Křivan (1997*a*) has concluded that optimal foraging strategies of predators in a system with two spatially separated prey species may render the system persistent.

That switching of predators may contribute to persistence is not at all a new finding, but analytical results (and, hence, more precise predictions) are still hard to come by. Studying the more simple case where the alternative food is present in constant amounts allows us to analyze the link between optimal foraging and population dynamical consequences in more detail. Since it has long been known that stability of the population dynamical equilibrium gives only limited insight, we will analyze not only the conditions for stability but also those for long-term nonequilibrium persistence (bounded population fluctuations). This leads to specific hypotheses about which types of alternative food (in terms of availability, nutritional quality, and handling time) promote persistence and by which mechanism.

Fine-Grained Environments

Optimal Foraging and Switching

Consider a predator in an environment in which pointlike food items (prey and alternative food) differing in profitability (energy content divided by handling time) are randomly distributed. Let handling of a captured prey take T_N time units and handling of an alternative food item T_A time units. Then functional responses, that is, per capita consumption rates, with respect to prey and alternative food are given by

$$f_N(N, A) = \frac{N}{1 + T_N N + pT_A A},$$

$$f_A(N, A) = \frac{pA}{1 + T_N N + pT_A A}, \tag{1}$$

provided that a predator will consume an alternative food item upon encounter with probability p. This formulation implies that the densities of prey (N) and alternative food (A) are scaled with respect to search rate of the predators; this can be done without loss of generality.

Taking into account the nutritional value of prey (c_N) and alternative food (c_A), a predator's average food intake rate (which we will take to be proportional to its rate of reproduction) will equal

$$
\begin{aligned}
g(N, A) &= c_N f_N(N, A) + c_A f_A(N, A) \\
&= \frac{c_N N + p c_A A}{1 + T_N N + p T_A A}.
\end{aligned}
\tag{2}
$$

This expression is exactly of the same form as the "gain rate function" considered by Werner and Hall (1974) and Charnov (1976), which means that their conclusions apply directly to this model.

A well-known result in optimal foraging theory is that a predator maximizes its food intake rate by completely ignoring alternative food (i.e., $p = 0$) if

$$
\frac{c_A}{T_A} > \frac{c_N}{1 + T_N N}
\tag{3}
$$

(Stephens and Krebs 1986), that is, when the density of the prey is above the threshold density

$$
N_s = \frac{c_A}{c_N T_A - c_A T_N},
\tag{4}
$$

and consuming all food items it encounters ($p = 1$) otherwise. Note that the switch density depends only on the profitability of the alternative food (c_A/T_A); its density (A) is irrelevant. This classical result in optimal foraging theory is called the "zero-one rule" (Stephens and Krebs 1986) because alternative food is either always accepted or always ignored depending on the density of the more profitable prey type. Note that when the prey density is equal to N_s, the functional response $g(N, A)$ is independent of p. Therefore, if prey density is exactly N_s, optimal foraging theory does not provide us with a unique solution to the diet selection problem because all p in the interval $[0, 1]$ give the same predator fitness.

The functional response of optimally foraging predators with respect to prey is therefore given by

$$
f_N(N, A) = \begin{cases}
\dfrac{N}{1 + T_N N} & N > N_s \\[2ex]
\left[\dfrac{N}{1 + T_N N + T_A A}, \dfrac{N}{1 + T_N N}\right] & N = N_s \\[2ex]
\dfrac{N}{1 + T_N N + T_A A} & N < N_s
\end{cases},
\tag{5}
$$

while the functional response with respect to alternative food is given by

$$
f_A(N, A) = \begin{cases}
0 & N > N_s \\[2ex]
\left[0, \dfrac{A}{1 + T_N N + T_A A}\right] & N = N_s \\[2ex]
\dfrac{A}{1 + T_N N + T_A A} & N < N_s
\end{cases}.
\tag{6}
$$

The functional response to prey density is not uniquely determined at the threshold prey density N_s (fig. 1). The discontinuity in the functional response results from the predator's suddenly spending more time in consuming alternative food, which reduces the number of encounters with prey. The more time that is invested in consuming alternative food (which is proportional to $T_A A$), the greater the discontinuity in the functional response $f_N(N, A)$. It should be noted that the average food intake rate $g(N, A)$ contains no such discontinuity because at the threshold alternative food precisely compensates the drop in prey consumption.

Stepwise changes in functional response are rarely observed (Stephens 1985; McNamara and Houston 1987; Schoener 1987). Many explanations are conceivable for more gradual switching behavior, or "partial preferences." For example, predators need information on prey abundance, and contrary to the omniscience in predators obeying Charnov's (1976) assumptions, they will have to estimate prey density, with inherent effects of time lag and sampling error. We will model gradual switching behavior by assuming that the probability of a predator consuming an alternative food item is given by a sigmoid function:

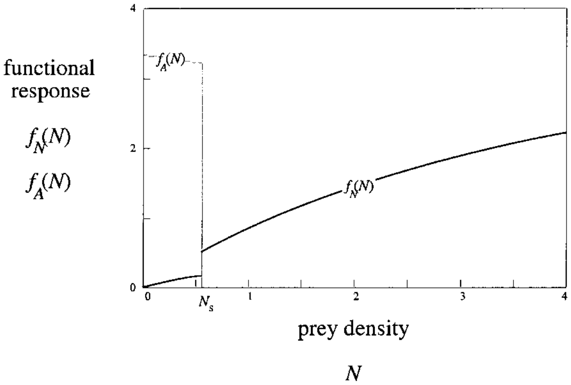

Figure 1: Functional response curve with switch for fine-grained environments predicted by optimal foraging theory. The dashed line represents alternative food consumption. Parameters: $c_N = 1.0$, $c_A = 0.1$, $T_N = T_A = 0.2$.

$$p(N) = \frac{N_s^m}{N^m + N_s^m}, \tag{7}$$

where $\sigma = m^{-1}$ determines the width of the predator's switching interval. The smaller the σ, the more closely $p(N)$ will approximate the optimum stepwise switch. A more gradual switching may also be the result of differences between individual predators, as this will lead to variation in optimal switching densities; then $p(N)$ would represent the cumulative probability function in which N_s is the median switching density.

Population Dynamics

To analyze the effect of various types of functional responses in a spatially homogeneous system, Murdoch and Oaten (1975) considered a simple Lotka-Volterra type of model,

$$\frac{dN}{dt} = rN - f_N(N)P,$$
$$\frac{dP}{dt} = P[c_N f_N(N) - \delta], \tag{8}$$

specifying the dynamics of prey (N) and predators (P), where $f_N(N)$ represents the functional response of the predators, that is, the per capita predation rate. Nutritional value of a prey (in terms of predator fitness) is given by c_N, and per capita mortality rate of the predators (or "starvation rate") is given by δ. In absence of predation, the prey population grows exponentially with a per capita rate r.

As prey items need to be handled and digested, a general aspect of functional responses is that they are likely to satiate when prey density is high. Such satiation is a destabilizing mechanism because the risk of predation now decreases with prey density (Holling 1959; May 1974; Murdoch and Oaten 1975). This poses the problem of which mechanisms counteract this inherent instability of predator-prey interactions.

If it is assumed that $f_N(N)$ has a sigmoid shape due to switching, equations (8) lack an important component. When a predator switches to another food source, it is still consuming something, and this will contribute to its reproduction. This food to offspring conversion does not show up in the equation describing the predator's population dynamics. Incorporating the contribution of alternative food to the per capita reproduction of the predators, $c_A f_A$, leads to

$$\frac{dN}{dt} = rN - f_N(N, A)P,$$
$$\frac{dP}{dt} = P[c_N f_N(N, A) + c_A f_A(N, A) - \delta]. \tag{9}$$

In general, the functional responses f_N and f_A will depend both on the densities of prey and alternative food densities. Since we assume that alternative food has no dynamics of its own, A can be treated as a parameter. For simplicity, we will therefore omit A from the arguments of the functions f_N and f_A. Before discussing the consequences of optimal foraging, we will first derive the conditions for local stability of the modified model (eqq. [9]) assuming arbitrary functional response curves.

Note that due to the fact that for $N = N_s$, the functional responses f_N and f_A are not uniquely given, and consequently, the right-hand side of system (9) is also nonunique. However, system (9) is still well defined because there exists a single trajectory starting from every initial point (Colombo and Křivan 1993; Křivan 1996).

Local Stability

Local stability analysis of system (9) (see appendix) reveals that there are two stability conditions. The first is the familiar condition

$$f_N'(\overline{N}) > \frac{f_N(\overline{N})}{\overline{N}} \tag{10}$$

(see also Murdoch and Oaten 1975). This implies that at equilibrium $\overline{N}$ an increase in prey density should be followed by a disproportionately large increase in the functional response (the functional response should increase supralinearly). This condition is met in, for example, the lower part of a classic sigmoid functional response. Therefore, equilibrium prey density should not be too high; otherwise, the functional response satiates (still increases with prey density but sublinearly), and the prey population will escape from predator control (Murdoch and Oaten 1975).

The second stability condition,

$$c_N f_N'(\overline{N}) + c_A f_A'(\overline{N}) > 0, \tag{11}$$

implies that the per capita growth rate of the predators should increase with prey density. As the second term will be negative (predators will consume less alternative food when prey density increases), the per capita growth rate will increase more slowly with prey density than in the absence of alternative food. In other words, reproduction of the predators is less tightly linked to prey density. The presence of alternative food therefore results in a weaker regulation of the predator population (see also Abrams 1987).

Note that there is an interaction between the two stability conditions: the presence of alternative food will lead to reduced equilibrium prey densities, a phenomenon called "apparent competition" (Holt 1977; see fig. 2). Alternative food may therefore push the equilibrium prey density into (but just as well out of) the interval where the functional response rises supralinearly (as in fig. 3).

Optimal Foraging and Population Stability

It is important to realize that the functional response predicted by optimal foraging theory (fig. 1) does not have a part with a supralinear increase (except in the special case in which the equilibrium density precisely coincides with the switching point, in which case the increase is infinite). As a consequence, such a functional response does not stabilize the equilibrium.

The stability analysis is based on the assumption that functional responses do not change abruptly. In other words, it is implicitly assumed that predators can only approximate the stepwise switch that maximizes food intake rate according to optimal foraging theory.

A more gradual switch (such as modeled in eq. [7]) may still lead to a functional response with a part that increases supralinearly (see fig. 3), but note that the range will be small unless switch precision is low. How, for a given switching precision, equilibrium density and the stable range depend on nutritional value of alternative food is shown in figure 4. For a stable equilibrium, alternative food should be sufficiently profitable but not too profitable. When precision increases (σ decreases), switches become steeper. However, at the same time, the stable range narrows, and therefore the region of stability in parameter space becomes smaller and eventually vanishes (fig. 5). (Similar graphs result when handling time of alternative food is varied instead of nutritional value.) The density of alternative food may have an effect on ecological stability only when predators are imprecise (or when there is variation in switching; fig. 6).

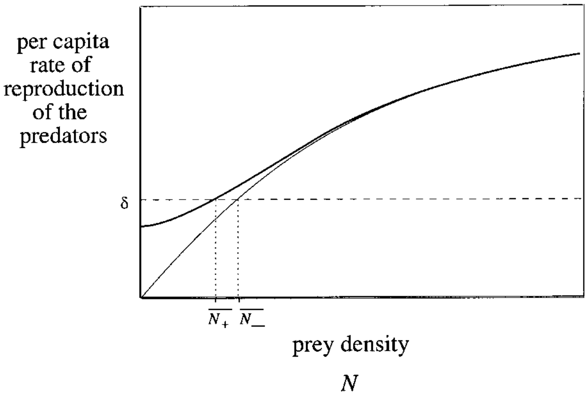

Figure 2: Reduction of equilibrium prey density as a consequence of the simultaneous presence of alternative food (apparent competition; Holt 1977). When there are no other factors affecting prey population growth, equilibrium density of the prey is determined entirely by the predator's numerical response. In absence of alternative food, equilibrium prey density equals $\bar{N}_-$ (where predator reproduction equals death rate), whereas in the presence of alternative food, it decreases to $\bar{N}_+$ (apparent competition). The predators are assumed to switch gradually.

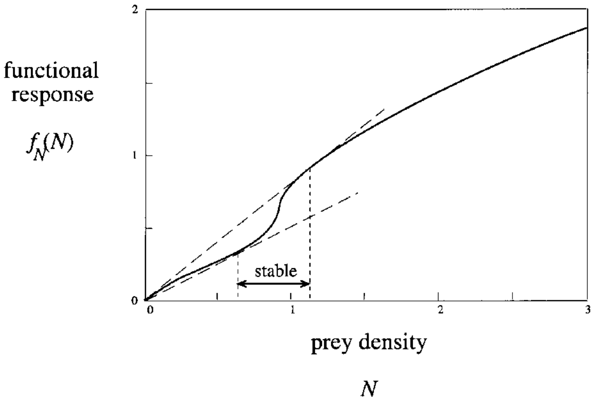

Figure 3: Graphical derivation of the range of stable equilibrium prey densities for gradually switching predators in a fine-grained environment. Within the indicated range, the slope of the functional response is larger than $f_N(N)/N$; outside, it is less.

Murdoch's work on switching predators (Murdoch 1969; Murdoch and Oaten 1975) spawned an extensive body of literature dealing with the so-called preference of predators for certain food types, that is, how the ratio of food types represented in the predator's diet differs from the ratio that it actually encounters. Theoretical work on the consequences of prey preference (see, e.g., Comins and Hassell 1976; Tansky 1978; Vance 1978; Hutson 1984; Matsuda 1985; Mukherjee and Roy 1998) usually assumes some kind of sigmoid preference curve, or a "switching function" that resembles superficially a sigmoid functional response. It should be kept in mind, however, that there is a fundamental difference between a sigmoid preference function and a sigmoid functional response. Sigmoid preference functions $p(N)$ do translate into a functional response with an accelerating part and may thus contribute to stability. However, they do not necessarily lead to a satiating functional response (which is an essential element causing a sigmoid shape). As a consequence, the effect of

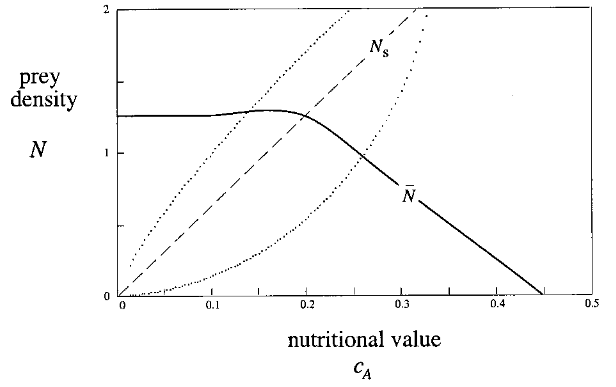

Figure 4: When the quality of the alternative food (c_A; in fine-grained environments) increases, both equilibrium prey density $\bar{N}$ (*solid line*) and switch prey density N_s (*dashed line*) change. The equilibrium is stable only when equilibrium density falls within the stable range around the switch prey density (indicated by *dotted lines*). (Numerical solution of equilibrium density and stable range for $r = 1.2$, $\delta = 1$, $c_N = 1$, $T_N = T_A = 0.2$, $A = 4$, $\sigma = 0.2$.)

a sigmoid preference function may be quite different from a sigmoid functional response.

Persistence

Stepwise switching of predators does not promote ecological stability, but that does not mean at all that predators and prey will eventually become extinct. Cycles will diverge away from the equilibrium, but eventually a limit cycle may be reached (Gleeson and Wilson 1986; Fryxell and Lundberg 1994). Křivan (1996) and Křivan and Sikder (1999) have analyzed such cycles for a one-predator/two-prey system. When one of the prey species is in fact alternative food with a constant density, the effect can be demonstrated straightforwardly using phase-plane analysis.

As per capita reproduction of the predators does not depend on predator density, the predator isocline runs parallel to the P-axis. The prey isocline is given by

$$rN = f_N(N)P \Leftrightarrow P = \frac{rN}{f_N(N)}. \tag{12}$$

Now switching of the predators has to be taken into account. For prey densities larger than the critical prey density ($N > N_s$), the isocline for stepwise switchers is given by

$$P = rN\frac{1 + T_N N}{N} = r(1 + T_N N), \tag{13}$$

whereas for low prey densities ($N < N_s$), it is given by

$$P = r(1 + T_N N + T_A A). \tag{14}$$

The predator's switching behavior thus introduces a discontinuity into the phase plane (at the line $N = N_s$) across which growth rate of the prey population suddenly changes. As a consequence, it causes a fault in the prey isocline, giving it a Z-like shape (fig. 7*A*). Above and below the Z, the growth changes in magnitude but not in sign. Across the fault (i.e., the vertical part of the Z), prey population growth rate changes sign. Near the fault, prey population growth is always in the direction of the discontinuity; therefore, trajectories will hit the fault, and as they can go neither left nor right, they have to move along the fault either up or down (except in the special case in which $\delta = c_A/T_A$ because then the whole fault consists of equilibria), depending on net growth of the predator population near the fault. We remark that when prey density reaches the fault and moves along it, partial preferences for the alternative food appear. Indeed, when a trajectory moves along the fault, prey density is constant and equal to N_s, which implies that $dN/dt = 0$ in equations (9). This allows us to compute the predator's partial preference for the alternative food type explicitly:

$$p = \frac{P}{ArT_A} - \frac{c_N}{A(c_N T_A - c_A T_N)}. \tag{15}$$

From the local stability analysis we know that an orbit starting near the equilibrium will diverge. However, at some instant, the orbit may hit the isocline fault. Then the orbit decreases vertically (assuming that the fault is to the left of the predator isocline) until it reaches the lower end and is released. If trajectories starting near the equi-

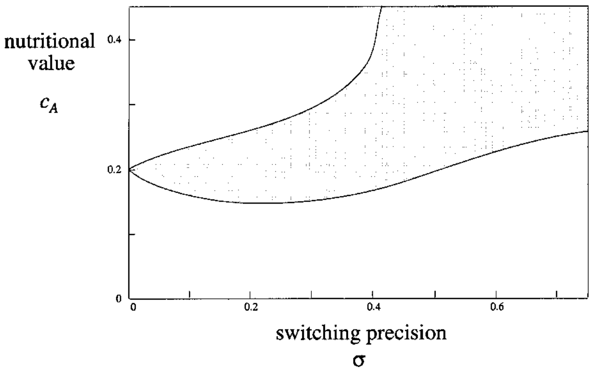

Figure 5: Stability domain as a function of nutritional value and switching precision of the predators in a fine-grained environment. (Numerical solution of the stability condition for $r = 1.2$, $\delta = 1$, $c_N = 1$, $T_N = T_A = 0.2$, $c_A = 0.1$, $A = 10$.)

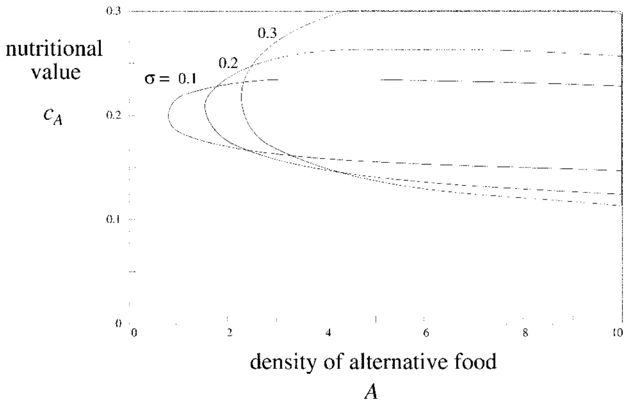

Figure 6: Stability domains as a function of nutritional value and density of the alternative food in a fine-grained environment for three values of the switching precision. Other parameters are $r = 1.2$, $\delta = 1$, $c_N = 1$, $T_N = T_A = 0.2$. Notice that if $c_A > \delta(A^{-1} + T_A) = A^{-1} + 0.2$, alternative food is no longer "alternative" because it then allows reproduction of the predators to exceed their death rate. This limit lies beyond the range of the graph.

librium are thus trapped, long-term behavior is determined by the trajectory that starts at the lower end of the fault. When this trajectory eventually returns to the discontinuity at some point in the isocline fault (which can occur in two ways; fig. 7*A*, 7*B*), it will be brought back to its starting point, and a limit cycle emerges. A parameter survey suggests that such limit cycles may occur in a large part of parameter space (fig. 8).

Thus, persistence may be promoted by alternative food of very marginal quality provided it is sufficiently abundant, even when it has no effect on ecological stability. In contrast to ecological stability, persistence depends strongly on the density of alternative food (cf. figs. 6, 8).

Coarse-Grained Environments

Optimal Foraging

The second important conceptual framework of optimal foraging theory is the patch-choice model (Stephens and Krebs 1986; Rosenzweig 1991). This model considers the distribution of consumers in a patchy environment, assuming that each consumer settles in the patch where its rate of energy intake (assuming this is proportional to fitness) is maximized.

We assume that food resources are distributed over two patches. The prey, whose density N is influenced by the predator population, occupy one patch (referred as the "prey patch"), while the alternative food, with constant density A, is found in the other patch (the "alternative patch"). Here we will consider the optimal decisions of "ideal and free" predators, that is, predators that have the ability to detect and the means to move to the most profitable patches (Fretwell and Lucas 1970). Thus, we will not discuss the important class of metapopulation models where movement is so slow that predator and prey in different patches may become dynamically uncoupled (Jansen 1995). We assume that predators can move very fast; this does not mean that they will distribute themselves evenly over the patches, as they are free to go to the more profitable patches. (See McPeek and Holt [1992], Fryxell and Lundberg [1993], and Holt and McPeek [1996] for a discussion of how natural selection may affect dispersal rates in true predator-prey metapopulations.)

When we denote the proportion of time that a predator will spend foraging in the alternative food patch by q (and, hence, proportion of time spent in the prey patch is $1 - q$), functional responses are given by

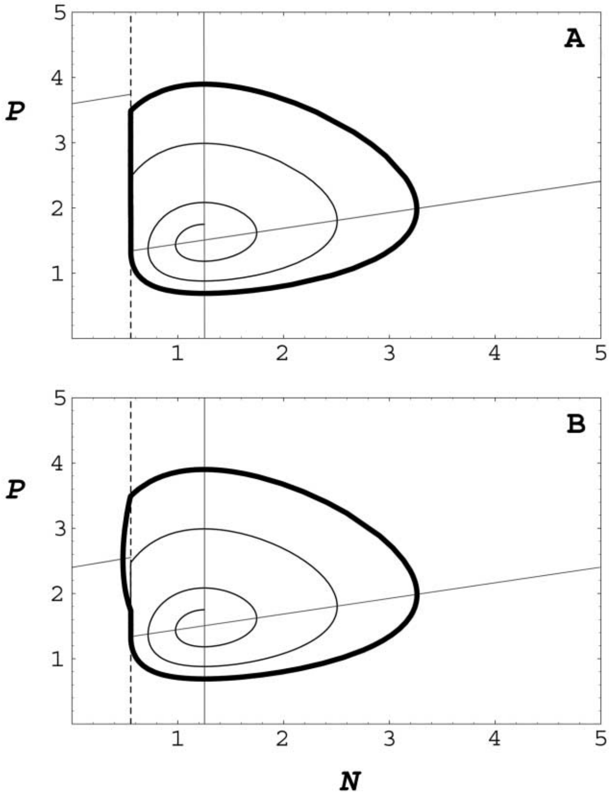

Figure 7: Phase plane with a discontinuous prey isocline as a result of diet expansion of the predator (fine-grained environments). A trajectory starting at the lower end of the isocline fault may hit the fault again either from the right (*A*) or from the left (*B*), leading to a limit cycle in both cases. Parameters: $r = 1.2$, $\delta = 1$, $c_N = 1$, $c_A = 0.1$, $T_N = T_A = 0.2$, and (*A*) $A = 10$ and (*B*) $A = 5$.

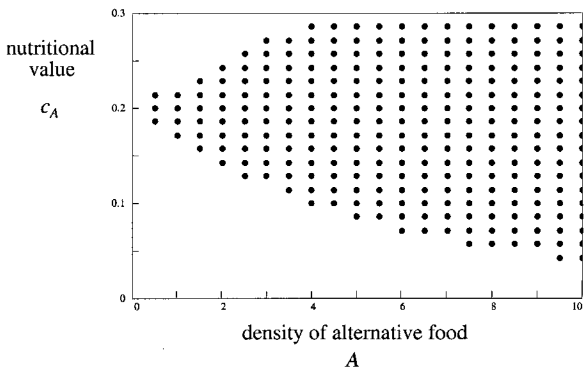

Figure 8: Entrapment of orbits (*filled circles*) for different combinations of nutritional value and abundance of the alternative food. The parameters are the same as in figure 6, except that $\sigma = 0$, which implies that the equilibrium is stable only if c_A equals exactly 0.2.

$$f_N(N, A) = \frac{(1-q)N}{1+T_N N},$$
$$f_A(N, A) = \frac{qA}{1+T_A A}. \tag{16}$$

As before, we assume that the densities of prey and alternative food are scaled with respect to predator search rate. Taking into account the nutritional value of prey (c_N) and alternative food (c_A), a predator's average food intake rate will equal

$$\begin{aligned} g(N, A) &= c_N f_N(N, A) + c_A f_A(N, A) \\ &= \frac{c_N(1-q)N}{1+T_N N} + \frac{c_A q A}{1+T_A A}. \end{aligned} \tag{17}$$

Note that this equation assumes that the encounter rate with food items is much higher than the frequency of transitions between sites. In a sufficiently coarse environment, transitions will occur relatively infrequently so that a predator in the prey patch will not encounter nor handle alternative food and vice versa. Thus, functional response in a given patch only depends on what is found locally. Were the predators to move often between the two patches, we would recover the equations for the fine-grained model. (Incidentally, here our model differs from that studied by Fryxell and Lundberg [1997], where their eq. [4.1] assumes essentially a fine-grained environment.)

Since the fitness of a predator is directly proportional to its per capita instantaneous growth rate $g(N, A)$, the optimal strategy is to forage exclusively in the prey patch ($q = 0$) if prey density is above the threshold density

$$N_s = \frac{c_A A}{c_N + A(c_N T_A - c_A T_N)}. \tag{18}$$

If prey density is below this threshold, the optimum strategy is to forage exclusively in the alternative food patch ($q = 1$).

The functional response of optimally foraging predators is therefore given by

$$f_N(N, A) = \begin{cases} \dfrac{N}{1+T_N N} & N > N_s \\ \dfrac{(1-q)N}{1+T_N N} & N = N_s\,, \\ 0 & N < N_s \end{cases} \tag{19}$$

while the functional response in alternative food patch is given by

$$f_A(N, A) = \begin{cases} 0 & N \geq N_s \\ \dfrac{qA}{1+T_A A} & N = N_s\,. \\ \dfrac{A}{1+T_A A} & N < N_s \end{cases} \tag{20}$$

Again, the functional responses both to prey and alternative food densities contain a discontinuity at the threshold prey density. This results from the fact that predators instantaneously move from one patch to the other when the prey density crosses the threshold N_s.

The change in foraging strategy q will be more gradual when predators need to sample the patches or when their assessment is imperfect. This can be modeled by

$$q(N) = \frac{N_s^m}{N^m + N_s^m}, \tag{21}$$

in which case a sigmoid functional response arises. Again, as $\sigma = m^{-1}$ increases, the above curves converge to the stepwise optimal switching function.

Population Dynamics, Persistence, and Stability

Population dynamics are again modeled by the Lotka–Volterra type model (9) with corresponding functional response given by equations (19) and (20). Now N denotes the prey density in the prey patch, and P is the overall predator density. Other parameters have the same meaning as those for the system of equations (9). For nonswitching predators foraging randomly (i.e., predators that spend a fixed proportion q [$0 < q < 1$] of their time in the alternative food patch), the corresponding population dynamics has one ecological equilibrium, which is unstable, and the system is nonpersistent.

For the gradual switching function, we can study the equilibrium stability as we did in the previous section. Again, the gradual switch modeled by equation (21) can stabilize the population equilibrium for exactly the same reasons as it does in a fine-grained environment (see appendix). Specifically, the first stability condition becomes

$$q'(N) < -[1 - q(N)]\frac{T_N}{1 + T_N N}. \tag{22}$$

This again implies that the predators switch sufficiently fast with respect to small changes in prey density (note that $q'(N)$ will be negative, as the predators will avoid the alternative patch when prey density increases).

Now we consider perfectly switching predators that follow the stepwise optimal patch choice. As for the case of fine-grained environment, flexible predator behavior leads to persistence via the emergence of a stable limit cycle. In the case of a coarse-grained environment, the limit cycle is globally stable because the prey isocline in the prey patch is L shaped and, thus, unbounded from above (see fig. 9).

Thus, the trajectory that starts at the lower point of the fault must necessarily hit the fault again, which leads to the emergence of a globally stable limit cycle. Starting with a sufficiently high initial prey density (i.e., to the right of the switching line $N = N_s$) all predators will choose the more profitable prey patch ($p = 0$). This results in unstable dynamics, and the trajectory will spiral away from the equilibrium. Eventually, it will reach the isocline fault ($N = N_s$), where both patches will be of equal quality, and some predators will move to the patch with alternative food. The trajectory then moves downward along the isocline fault for some time, the predators maintaining the ideal free distribution over the patches with prey and alternative food. When the trajectory reaches the lower point of the fault (see fig. 9), the prey population escapes from predator control, and the cycle starts anew. When predator-prey dynamics move along the fault, the density of the prey is kept constant by the predators, and the fraction of predators choosing the prey patch is given by

$$q = 1 - \frac{rc_N(1 + AT_A)}{P[c_N + A(c_N T_A - c_A T_N)]}. \tag{23}$$

Thus, as the trajectory moves down the fault, the ideal free distribution will change over time.

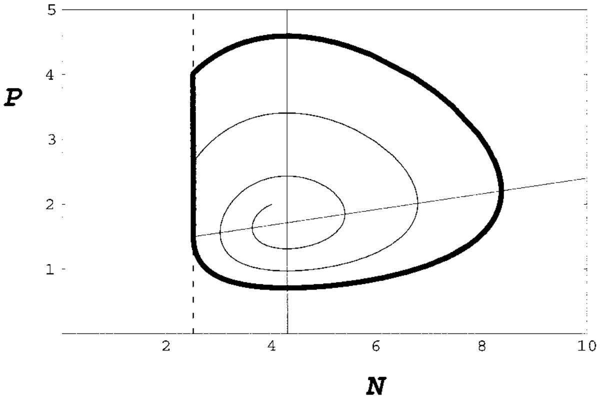

Figure 9: Phase plane with a discontinuous prey isocline due to patch switching by the predators (coarse-grained environments). The dashed line is the switching line. All trajectories do converge to the limit cycle denoted by the heavy line. Parameters: $r = 1.2$, $\delta = 3$ (mortality is the same in both patches), $c_N = 1$, $c_A = 0.25$, $T_N = 0.1$, $T_A = 0.1$, $A = 40$.

Discussion

That switching to alternative food sources may render predator-prey systems persistent is one of ecology's (few) common, and often unquestioned, truths. Because alternative food sources are likely to be ubiquitous, modelers therefore do not hesitate to incorporate S-shaped functional responses into their models, arguing that this represents a switch to alternative food sources when prey are scarce. However, this may easily lead to spurious conclusions. First of all, the contribution of the alternative food to the predator's numerical response should be taken into account. Second, one may wonder whether a given switching function is actually adaptive; sigmoid functional responses are demonstrably maladaptive in basic settings (Holt 1983). Third, it may be necessary to assess not only how the switch affects the equilibrium but also how it affects the global dynamics of the system. Even if alternative food does not stabilize the system, as seems likely for adaptive switches, it may still promote persistence. Finally, as this article suggests, alternative food sources that lead to stability may be different from those that promote persistence. We will now discuss these aspects in more detail.

Apparent Competition

The presence of alternative food may not only change the shape of the functional response, it may also increase equilibrium predator densities, which, in turn, will lead to a reduction in equilibrium prey density. This predator-mediated effect of alternative food on prey density, termed "apparent competition" by Holt (1977), may affect stability because it may shift equilibrium prey density either into or out of the range where the predators can regulate the prey population. In the extreme case, it may actually result in prey extinction (Holt et al. 1994; Bonsall and Hassell 1997).

The original studies of apparent competition assumed that populations are in equilibrium (Holt 1977). Our analysis suggests that this result only occurs under a rather narrow set of conditions. First, predators are expected to switch in a stepwise manner, whereas a stable equilibrium is more likely to result when predators are imprecise switchers (as this broadens the range over which the functional response curves upward). Second, the profitability of the alternative food should be within a certain range. If the profitability of the alternative food is too low, it will not be included in the predator's diet; if it is too high, the predator population will become unregulated.

Stability or Persistence?

Our analysis confirms the conclusions of earlier studies (Gleeson and Wilson 1986; Fryxell and Lundberg 1994, 1997; Křivan 1996) that whereas the conditions for stability of the equilibrium are rather narrow, parameter combinations that lead to stable limit cycles may be much broader. When under conditions of low prey density the predators switch to alternative food, predator population decrease is slowed down while, at the same time, predation pressure is relaxed, allowing the prey population to recover. In combination, these mechanisms may give rise to a limit cycle. This effect is not limited to stepwise switches, as limit cycles may also occur with more gradual switching (fig. 10).

It is important to stress that in fine-grained environments, persistence critically depends on the shape of the functional response in the low-prey-density range. Optimal foraging combined with gradual switching results in a functional response that might look quite similar to other sigmoid functions commonly used to represent switching, like

$$f(N) = \frac{N^2}{N^2 + H^2}, \tag{24}$$

but there is a crucial difference. The latter function has zero slope near $N = 0$, which implies that the prey isocline will approach the P-axis only as P goes to infinity: the predators will never be able to exterminate the prey, and persistence is guaranteed. In contrast, the functional response of an optimal forager is likely to have a positive slope near $N = 0$. The S-shaped isocline that results will intersect the P-axis (fig. 10); therefore, diverging oscillations near the axes are not precluded.

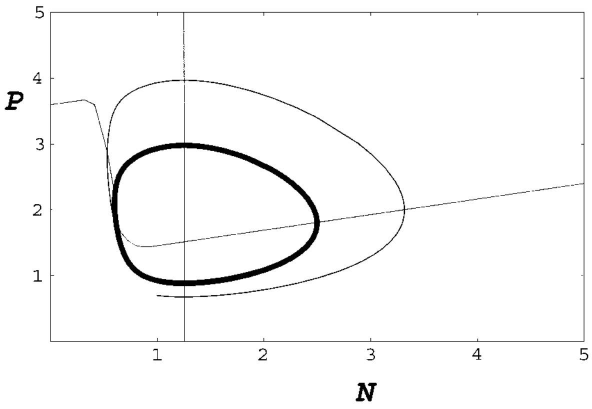

Figure 10: S-shaped prey isoclines and resulting limit cycle when predators switch gradually. Parameters: $r = 1.2$, $\delta = 1$, $c_N = 1$, $c_A = 0.1$, $T_N = T_A = 0.2$, $A = 10$, $\sigma = 0.1$.

Permanence (which means, loosely, that trajectories are bounded away from 0 [Hofbauer and Sigmund 1988]) will thus depend on the slope of the functional response at low prey densities, which is notoriously difficult to measure experimentally (van Lenteren and Bakker 1976; Hassell et al. 1977).

In coarse-grained environments, however, the functional response of (sub)optimal foragers will always start (at $N = 0$) with zero slope and will, therefore, come much closer to the classic sigmoid functional response of equation (24). The resulting N-isocline does not intersect the P-axis, and the system is always permanent (fig. 9).

We conclude that the importance of alternative food is not so much that it promotes stability but rather that it promotes persistence. Whether the alternative food occurs together with the prey (in fine-grained environments) or separately (in coarse-grained environments), its effect is always that the predator's switch to alternative food relieves predation pressure when prey density is low, thereby preventing unbounded oscillations.

It may not be so surprising that adding an intrinsically stable component (alternative food with fixed density) to an unstable system (the predator-prey interaction with satiating functional response) may help to render it persistent. However, persistence critically depends on how predator behavior couples the two subsystems. Persistence will not arise if the predators do not switch (neither in fine-grained nor in coarse-grained environments).

Our conclusions may also be of interest for the study of more complicated food webs than the one we considered. For example, Huxel and McCann (1998) have shown that a constant influx of alternative food sources ("allochthonous" inputs) may help to render persistent intrinsically unstable three-level food chains. Their model, however, did not include adaptive behavior (i.e., switching) of either the consumer or the top predator. It would be interesting to investigate how switching will affect the conditions for persistence of such longer food chains.

Perspectives for Biological Control

Insight in the effects of alternative food may help to devise strategies for biological control involving a supply of alternative food (van Rijn and Sabelis 1993; van Rijn et al. 2001). Classical optimal foraging theory suggests that the effect of alternative food can be predicted on the basis of its profitability alone. However, our analysis indicates that nutritional value, handling time, and abundance of alternative food should be considered separately. For example, sources of alternative food that have the same profitability but differ in handling time will have different population dynamical consequences.

Optimal strategies for biological control will depend on the desired population dynamical effect. If the aim is a reduced but stable prey density, one has to select alternative food according to precise specifications with respect to quantity and quality, whereas if the aim is to promote persistence, one may only need to supply low-quality alternative food in sufficient quantities. However, if the aim is neither stability nor persistence but eradication of the prey, one should add alternative food of higher quality: high enough for predator population maintenance (in absence of prey) but not so high that the predators will ignore the prey altogether.

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APPENDIX

Local Stability Analysis

The equilibrium of predator ($\overline{P}$) and prey ($\overline{N}$) follows from setting dN/dt and dP/dt of equations (9) equal to 0, which yields

$$r\overline{N} = f_N(\overline{N})\overline{P}[c_N f_N(\overline{N}) + c_A f_A(\overline{N})] = \delta. \qquad \text{(A1)}$$

Such an equilibrium will exist, for example, if

$$c_N f_N(0) + c_A f_A(0) < \delta \qquad \text{(A2)}$$

and if, for prey densities sufficiently large,

$$c_N f_N(N) + c_A f_A(N) > \delta. \qquad \text{(A3)}$$

Because we assume that $f_N(0) = 0$, the first of these conditions implies

$$c_A f_A(0) < \delta, \qquad \text{(A4)}$$

which means that predators cannot subsist on alternative food alone; the second condition simply means that the predator population will increase if there is sufficient prey.

The equilibrium is asymptotically stable if the determinant of the Jacobian,

$$\mathbf{J} = \begin{pmatrix} r - f_N'(\overline{N})\overline{P} & -f_N(\overline{N}) \\ \overline{P}[c_N f_N'(\overline{N}) + c_A f_A'(\overline{N})] & 0 \end{pmatrix}, \qquad \text{(A5)}$$

is positive and the trace is negative. (The prime denotes the derivative of a function with respect to its argument.)

The trace of $\mathbf{J}$ is

$$T = r - f_N'(\overline{N})\overline{P} = r\left(1 - \frac{f_N'(\overline{N})\overline{N}}{f_N(\overline{N})}\right), \qquad \text{(A6)}$$

which yields the first stability condition (10).

The condition on the determinant of $\mathbf{J}$ is

$$D = f_N(\overline{N})\overline{P}[c_N f_N'(\overline{N}) + c_A f_A'(\overline{N})] > 0, \qquad \text{(A7)}$$

which yields condition (11).

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