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Author(s): David M. Post, M. Elizabeth Connors and Debra S. Goldberg

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PREY PREFERENCE BY A TOP PREDATOR AND THE STABILITY OF LINKED FOOD CHAINS

DAVID M. POST,^{1,2,5} M. ELIZABETH CONNERS,³ AND DEBRA S. GOLDBERG⁴

¹Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853 USA

²Institute of Ecosystem Studies, Box AB, Millbrook, New York 12545 USA

³Biometrics Unit, Cornell University, Ithaca, New York 14853 USA

⁴Center for Applied Mathematics, Cornell University, Ithaca, New York 14853 USA

Abstract. Recent theoretical studies have shown the potential for chaotic dynamics in simple three-species food chains. Most of these studies have focused on linear food chains, although natural food chains are seldom isolated from the surrounding food web. There is a growing awareness that food web dynamics can be strongly influenced by the behavior and movement of predators, energy, and nutrients across ecosystem and subecosystem boundaries. Motivated by observations from lakes, where the pelagic food web is often linked to the littoral food web by mobile predators, we constructed a simple model to evaluate the dynamics of two food chains linked by a top predator with prey preference. Linking the two food chains had no qualitative effect on model dynamics, although it did increase the density of the top predator. Instead, the prey preference of the top predator changed the system dynamics. We found a range of prey preferences that could eliminate chaos, dampen oscillations, and even produce point stability in a previously oscillatory system. The strength of prey preference required to produce a point attractor in a previously chaotic system was positively related to the dimension of chaos (a measure of the complexity of chaos). Our results suggest that, although chaos is possible in food webs, common processes like prey preference reduce the potential for chaos.

Key words: chaos; food chain; food web; functional response; predation; prey preference.

INTRODUCTION

Simple mathematical models can produce surprisingly complex population dynamics (e.g., May 1974, 1976). Recently, much attention has focused on complex dynamics in three-species continuous-time food chain models (modeling three trophic levels; Hastings and Powell 1991, McCann and Yodzis 1994, Ruxton 1996, and others). These models have paralleled work on complex interactions in multilevel trophic food webs in terrestrial (Price et al. 1980, McLaren and Peterson 1994), marine (Paine 1980), and fresh water aquatic communities (Carpenter and Kitchell 1984, 1993, Power 1990). Previous models have addressed simple three-species food chains (Hastings and Powell 1991) and the effects of enrichment, prey refuges, and omnivory on three-species food chains (Abrams and Roth 1994, Ruxton 1996, McCann and Hastings 1997). No study has yet evaluated the dynamics of two three-species food chains linked by a top predator with prey preference. Prey preference is common in natural food webs and is likely to be important to food web dynamics.

Although many food web studies have focused on effectively linear food chains, even largely isolated

food chains are linked to surrounding food webs (Hairston and Hairston 1993, Polis and Strong 1996), and their dynamics may be strongly influenced by the flow of energy and nutrients across ecosystem and subecosystem boundaries. A good example is in lakes, where pelagic food webs (open water) are linked to littoral food webs (near shore) through predation and nutrient translocation by mobile predators (Schindler et al. 1996, Vanni 1996). While many aquatic food web studies have focused on pelagic food webs (e.g., Mills et al. 1987, Carpenter and Kitchell 1993), there is an acute awareness that littoral–pelagic coupling is critical to the food web dynamics of lakes (Lodge et al. 1988). The same is true for marine systems, where benthic–pelagic coupling is important to the flow of nutrients, propagules, and predators (Meyer et al. 1983, Boero et al. 1996); and terrestrial systems, where allochthonous inputs from marine systems can subsidize terrestrial food webs (Polis and Hurd 1996).

Here, we test the dynamics of two food chains linked by a mobile top predator with differing prey preferences. The model food web (Fig. 1) is motivated by observations from freshwater lakes, where the pelagic food web is often linked to the littoral food web by mobile predators (e.g., planktivorous and piscivorous fishes), but it is analogous to many other spatially linked food webs (see Polis et al. [1997] for a review). We first establish the dynamic behavior of an isolated food chain, then we test the effect of linking two iden-

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⁵ E-mail: dmp18@cornell.edu

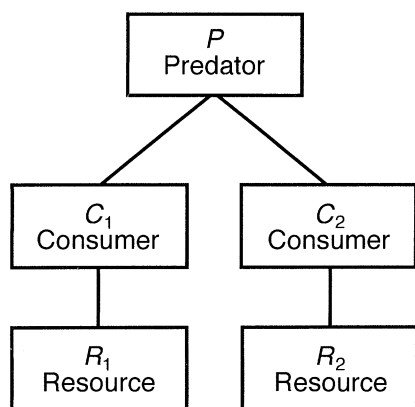


FIG. 1. A caricature of our model food web, where the top predator (P) feeds on two consumers (C_i), which, in turn, prey upon a resource (R_i).

tical food chains through a mobile top predator. Finally, we address the effect of different prey preferences on the dynamics of this food web. We are particularly interested in the hypothesis that prey preference may reduce the variability of a previously oscillatory system. We demonstrate that linking two food chains generally bounds the system away from zero and, for a range of prey preference values, can dampen oscillations and impart point stability.

MODEL

We constructed two food chains linked by a mobile top predator (Fig. 1). In this food web, a consumer (C_i) preys on a resource (R_i), and the mobile top predator (P) preys on both C_1 and C_2 . Our model is based on the three-species food chain of McCann and Yodzis (1994, 1995), which expanded the Hastings and Powell (1991) model by using the energetic arguments of Yodzis and Innes (1992). We further expanded the model by incorporating a prey preference function δ_i to link the two food chains through a top predator. The population dynamics of R_i , C_i , and P are described by the following system of coupled equations:

$$\frac{dR_i}{dt} = R_i(1 - R_i) - x_{C_i}y_{C_i}\frac{C_iR_i}{R_i + R_{0i}} \quad (1a)$$

$$\frac{dC_i}{dt} = x_{C_i}y_{C_i}\frac{C_iR_i}{R_i + R_{0i}} - \delta_i x_P y_P \frac{PC_i}{C_i + C_{0i}} - x_{C_i}C_i \quad (1b)$$

$$\frac{dP}{dt} = \delta_1 x_P y_P \frac{PC_1}{C_1 + C_{01}} + \delta_2 x_P y_P \frac{PC_2}{C_2 + C_{02}} - x_P P \quad (1c)$$

where R_{0i} and C_{0i} are half-saturation densities of the resource (R_i) and consumer (C_i), respectively; x_{C_i} and x_P are mass-specific metabolic rates, measured relative to the production-to-biomass ratio of the resource population; and y_{C_i} and y_P are measures of ingestion rate per unit metabolic rate of consumer species i and the predator (McCann and Yodzis 1994, 1995). When par-

ameterized this way, x_{C_i} and x_P scale the body size differences between the predator and consumer. Parameter values for x_{C_i} and x_P were chosen so that $P:C$ body mass ratio was within the range found in empirical data surveys (10^1 – 10^3 ; Peters 1983, Cohen et al. 1993). The parameters y_{C_i} and y_P constrain the metabolic type of the consumer and predator (endotherm, vertebrate ectotherm, and invertebrate ectotherm), where the maximum value of y is 1.6 for endotherms, 3.9 for vertebrate ectotherms, and 19.4 for invertebrate ectotherms (Yodzis and Innes 1992, McCann and Yodzis 1994). Parameter values for y_{C_i} and y_P were chosen to correspond to at least one of the plausible metabolic types. The model was designed to accommodate differences between the two food chains, although here we analyze the system with both food chains identically parameterized. We used a type II functional response for C_i preying on R_i , and P preying on C_i . This version of the model is nondimensional. The original dimensionalized model is presented in McCann and Yodzis (1995).

Prey selection was incorporated into the model as follows:

$$\delta_1 = \frac{\pi C_1}{\pi C_1 + (1 - \pi)C_2} \quad \text{and} \quad \delta_2 = \frac{(1 - \pi)C_2}{\pi C_1 + (1 - \pi)C_2} \quad (2)$$

where π is the preference ($0 \leq \pi \leq 1$) of P preying on C_1 . Note that $\delta_2 = 1 - \delta_1$. At $\pi = 1$, P preys only on C_1 , at $\pi = 0.5$, P preys on C_1 and C_2 in proportion to their biomass (i.e., no preference), and at $\pi = 0$, P preys only on C_2 . In essence, δ represents the proportion of time the predator spends feeding on each food chain. Prey switching (sensu Murdoch 1969) occurs such that, as the abundance of one prey declines, more of the predator's diet is derived from the other prey. This formulation of prey preference maintains the underlying type II functional response of the predator at $\pi = 1$ and $\pi = 0$, but allows prey switching at $0 < \pi < 1$. Switching can produce a sigmoidal (type-III-like) functional response. The sigmoidal functional response was originally derived ecologically from experiments that allowed switching between alternate prey (e.g., Holling 1965). Prey switching, and other learning behaviors, can be implicitly modeled using a sigmoidal functional response (e.g., Real 1977, Hassell 1978) and can stabilize model systems (Oaten and Murdoch 1975). We modeled switching explicitly to maintain the original model structure of Hastings and Powell (1991), and because it allowed prey preference to influence the shape of the functional response (Real 1977). We will discuss this point further in the *Discussion*. Our π is analogous to Chesson's α (Chesson 1983) and is similar to ω used to model omnivory and allochthonous inputs in simple food chains (McCann and Hastings 1997, Huxel and McCann 1998).

Because we are using two identical food chains, there

is an intrinsic symmetry to the dynamics of our model. The predator (P) dynamics are symmetric around $\pi = 0.5$, where there is no prey preference. The dynamics of R_1 and C_1 , at any value of π , are the same as those for R_2 and C_2 at $1 - \pi$. For $0 < \pi < 1$ (i.e., when all five species are linked), the type of dynamics displayed by the system (e.g., chaos, limit cycle, point stability) is the same for all five species. Thus, the type of dynamics displayed at $\pi = a$ is the same as at $\pi = 1 - a$. For simplicity, we will focus on the dynamics of the food chain preferred at $\pi = 1$ (i.e., R_1 , C_1 , P) and on preferences of $\pi \geq 0.5$.

RESULTS

Chaos

The parameters we chose to demonstrate chaotic dynamics in an isolated three-species food chain ($x_{C_1} = 0.15$, $x_P = 0.08$, $y_{C_1} = 2.3$, $y_P = 1.7$, $R_{0_1} = 0.25$, $C_{0_1} = 0.5$) were consistent with a number of biologically plausible food webs: vertebrate ectotherms as predator and consumer (body size ratio of 12:1), invertebrate ectotherms as predator and consumer (12:1), and a vertebrate ectotherm predator and an invertebrate ectotherm consumer (5500:1). Simply linking the food chains (moving from $\pi = 1$ to $\pi = 0.5$) generally shifted the attractor for P away from zero, but did not qualitatively change the system behavior (Fig. 2).

Varying π in the range 0–1 produced a variety of dynamics (Fig. 2). At moderate values of π , the system was bounded further away from zero, oscillations were dampened, chaos was eliminated ($0.59 \leq \pi \leq 0.77$), and the entire system moved into a region with a point attractor ($0.65 \leq \pi \leq 0.73$). On either side of the region with a point attractor, the model demonstrated the classic period-doubling route to chaos. While linking the system tended to bound the system further away from zero (by increasing the biomass of P), adding prey preference could dampen oscillations and even impart point stability on the food web. For π between 1 and 0.5, the food web was more stable than the three-species system or the linked system with no prey preference ($\pi = 0.5$).

We numerically simulated a number of parameter sets (>25) and initial conditions (>50) that produced complex dynamics. In all cases, linking the two food chains bounded the predator further away from zero and dampened oscillations, and for many we found prey preferences that produced point stability. The location and extent of the region with a point attractor were related to the correlation dimension of the unlinked three-species food chain (correlation dimension is a measure of the complexity of chaos; Grassberger and Procaccia 1983, Strogatz 1994). As the dimension of chaos increased, the range of π that produced a point attractor became smaller, until there was no longer a value of π that could produce point stability. At the same time, the values of π required to eliminate chaos

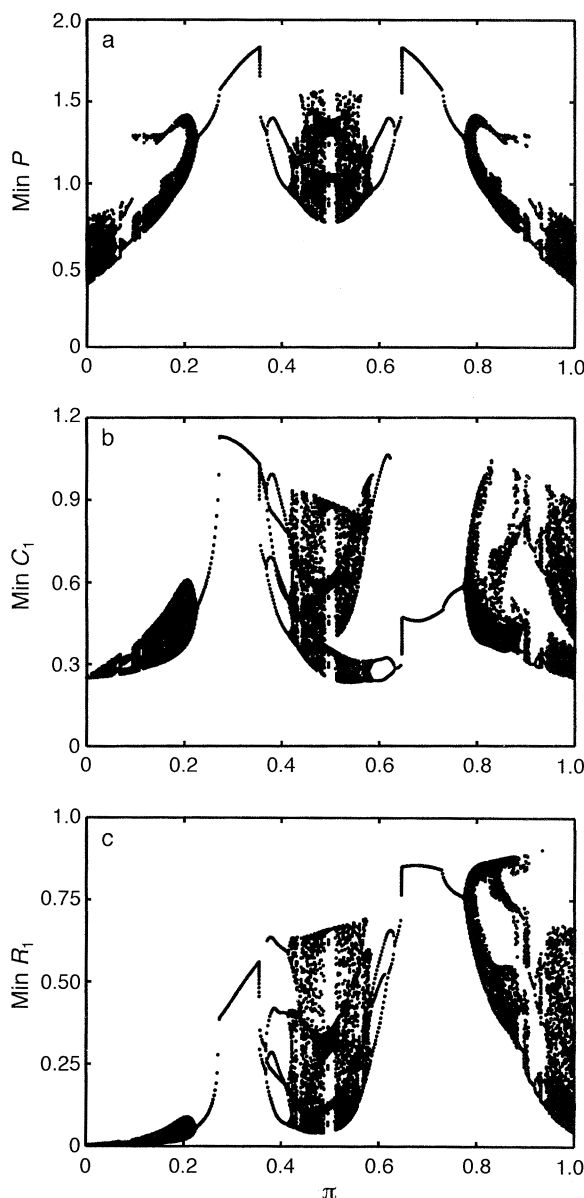


FIG. 2. Local minima across the range of $0 \leq \pi \leq 1$ for a model system that demonstrates chaotic dynamics as an isolated three-species food chain ($x_{C_1} = 0.15$, $x_P = 0.08$, $y_{C_1} = 2.3$, $y_P = 1.7$, $R_{0_1} = 0.25$, $C_{0_1} = 0.5$). The panels show results for (a) the top predator, (b) the preferred consumer, C_1 ; and (c) its resource, R_1 .

shifted to the extreme values of preference (e.g., closer to $\pi = 1$). Based on all of our simulations of chaotic food webs, we could produce point stability across the range $0.62 \leq \pi \leq 0.88$. Stronger prey preferences were required to dampen oscillations and eliminate chaos as the dimension of chaotic oscillation increased. As we increased the dimension of chaos, as long as the model system remained stable (none of the species populations went to zero), we always found a value of π that dampened the oscillations.

Limit cycles

The parameters we chose to demonstrate limit cycles in a three-species food chain ($x_{C_1} = 0.15$, $x_p = 0.08$, $y_{C_1} = 1.5$, $y_p = 1.5$, $R_{0_1} = 0.2$, $C_{0_1} = 0.5$) were consistent with the same set of biologically plausible food webs used in our chaos example. Our results for the limit cycle system were virtually identical to results for the chaotic system. Linking the limit cycle food chains bounded the predator biomass further away from zero, but did not appear to affect the consumer and resource biomass (Fig. 3). The changes were symmetric around $\pi = 0.5$ for the predator, but were noticeably asymmetric for the consumer and prey. The range of π over which the limit cycle system displayed a point attractor ($0.61 \leq \pi \leq 0.80$, for this parameter set) was broader than that for the chaotic system.

Point attractors

The parameters used to produce a system with a point attractor ($x_{C_1} = 0.4$, $x_p = 0.08$, $y_{C_1} = 1.5$, $y_p = 2$, $R_{0_1} = 0.2$, $C_{0_1} = 0.5$) were biologically consistent with vertebrate or invertebrate ectotherms as predator and consumer (body size ratio of 625:1). Other combinations of energetic types were not realistic for this parameter set. The most important result from the stable system was that the food web did not destabilize when linked or for any value of prey preference (Fig. 4). Consistent with our other results, linking the two food chains bounded the predator biomass further away from zero, but did not seem to strongly affect consumer and resource biomass.

DISCUSSION

Linking two simple food chains with a top predator consistently bounded the predator further away from zero, but it did not, by itself, increase stability. It was prey preference by the top predator that stabilized the previously oscillatory food chains.

Linking the two identical food chains can be interpreted as either adding species to the food web or as linking two spatially separate food chains that contain the same species. If we accept that the second food chain contains new species, then linking the food chains moved the model system from three to five species and increased the ratio of trophic links. The addition of more species alone (simply linking the system) did not qualitatively change the dynamics of this model food web. Rather, it was the behavioral aspect of prey preference that influenced stability. May (1973: 40) suggested a similar pattern for simple one- or two-species models, but did not elaborate on that point. This contrasts with early theoretical arguments (e.g., MacArthur 1955; but see Goodman [1975] for a discussion of problems related to the early theoretical arguments), and recent experimental results (e.g., Naeem and Li 1997) that suggest stability (constancy of fluctuations) should be positively related to the number of species in a food web.

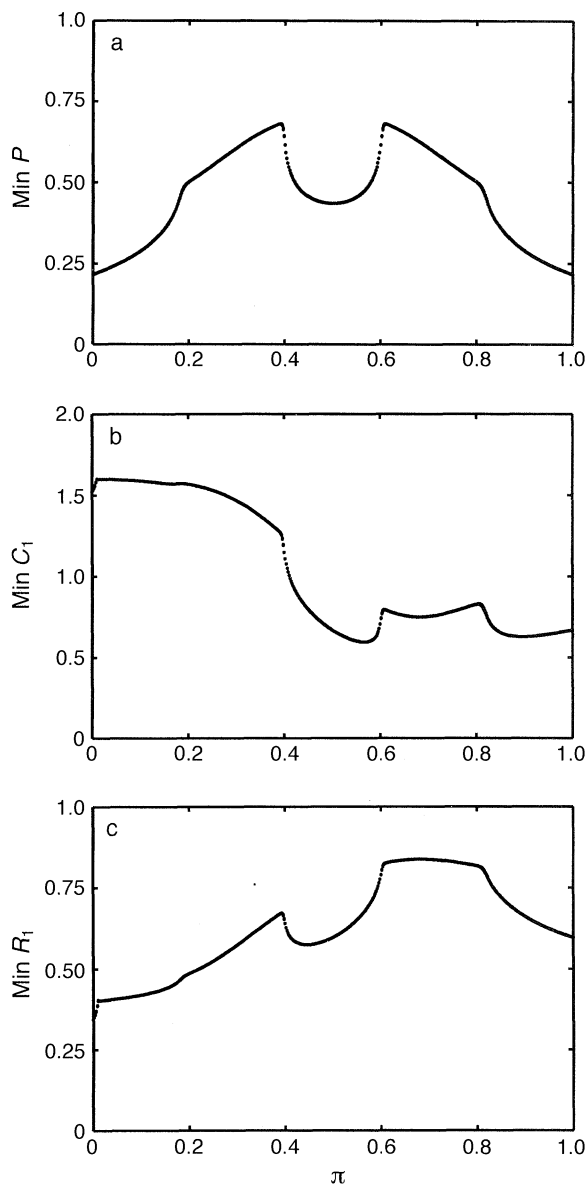


FIG. 3. Local minima across the range of $0 \leq \pi \leq 1$ for a model system that demonstrates stable limit cycles as an isolated three-species food chain ($x_{C_1} = 0.15$, $x_p = 0.08$, $y_{C_1} = 1.5$, $y_p = 1.5$, $R_{0_1} = 0.2$, $C_{0_1} = 0.5$). The panels show results for (a) the top predator; (b) the preferred consumer, C_1 ; and (c) its resource, R_1 .

Alternatively, if we interpret the linked food chains as spatially separate food chains that contain the same species, we have not increased the number of species, but rather compartmentalized a simple food chain. In this case, the preference would be for one compartment over the other. This could arise where the spatial arrangement of, or accessibility to, food chains makes feeding on one compartment energetically favorable, independent of prey availability. For example, many birds and amphibians feed in or over spatially distinct

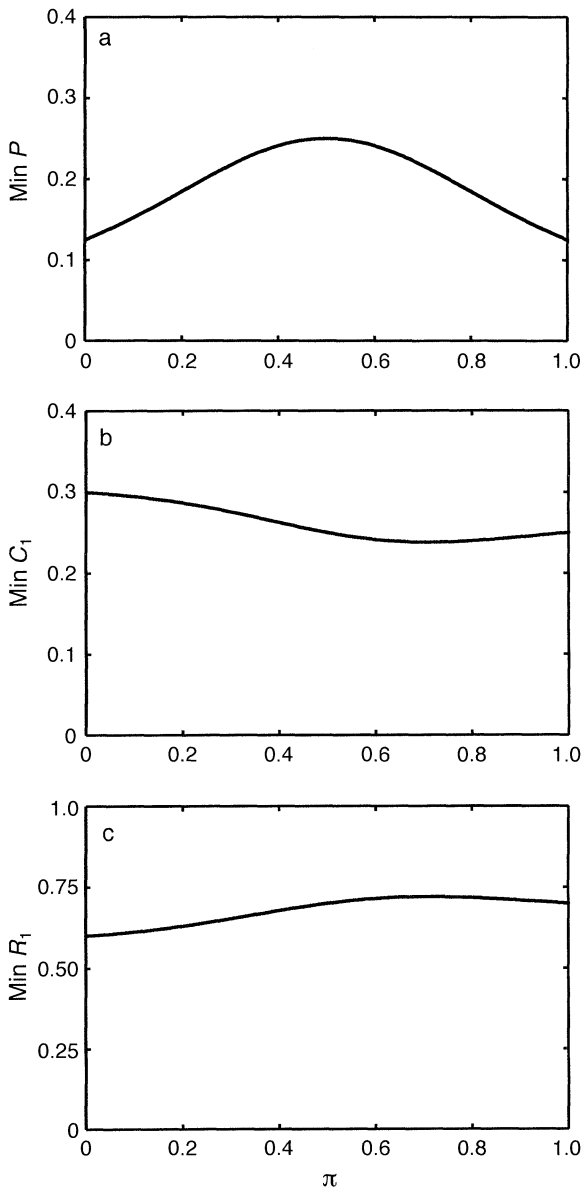


FIG. 4. Local minima across the range of $0 \leq \pi \leq 1$ for a model system that demonstrates point stability as an isolated three-species food chain ($x_{C_1} = 0.4$, $x_p = 0.08$, $y_{C_1} = 1.5$, $y_p = 2$, $R_0 = 0.2$, $C_0 = 0.5$). The panels show results for (a) the top predator; (b) the preferred consumer, C_1 ; and (c) its resource, R_1 .

aquatic habitat patches (e.g., McCarty 1997), and human predators often take fish from multiple lakes (Johnson and Carpenter 1994). Differences in preference (π) may arise from the proximity of the aquatic habitats to nesting and roosting sites, or, in the case of humans, the ease of access to fish-filled lakes. Again, in our model, it is not the linking of model compartments, but rather the intermediate prey preference that dampens oscillations.

Other studies have suggested that chaos develops in

food web models from the interaction of at least two incommensurate frequencies of oscillation (Hastings and Powell 1991, McCann and Yodzis 1994, 1995). Our results show that prey preference can eliminate chaos. This is similar to the results produced by McCann and Hastings (1997) for omnivory and by Huxel and McCann (1998) for allochthonous inputs. We suspect that our π , and ω used by McCann and Hastings (1997) and Huxel and McCann (1998), work like tuning parameters that eliminate chaos by causing the incommensurate frequencies to coalesce and collapse towards a stable limit cycle or a stable point attractor.

This raises the following question: what is prey preference tuning? Switching by the top predator changes the predator's functional response from type II to sigmoidal (like type III), and prey preference changes the shape of the sigmoidal functional response (e.g., Real 1977). Some, but not all, sigmoidal functional responses act to stabilize predator-prey dynamics and model food webs (Oaten and Murdoch 1975, and others). In our model, we think intermediate levels of prey preference (π) produce a stabilizing sigmoidal functional response. We stress that it is not just the switch from a type II to a sigmoidal functional response, but rather the specific range of sigmoidal functional responses that stabilizes our model system. This is supported by our observation that the values of π that produced point stability were positively correlated with the dimension of chaotic oscillations in the original unlinked three-species food chain. As the strength of chaos in the original unlinked $P-C-R$ system increased, stronger prey preference was required to dampen oscillations in the full $P-C_1-R_1$ system. In this and similar models, chaos is eliminated through a set of period-doubling reversals where the periodicity of the system is reduced from n to $n/2$, $n/4$, etc. (Fig. 2; McCann and Hastings 1997, McCann et al. 1998).

The prey preference values required to impart stability on this system are biologically plausible and likely to be commonly observed. Although prey preference is often hard to quantify, preference values in the $0.6 < \pi < 0.9$ range should be common in many systems. For example, largemouth bass are a common predator in lakes and reservoirs in North America. In small lakes and ponds, bass act as a link between benthic and pelagic food webs. Diets of largemouth bass suggest preference for small planktivorous fishes over benthic invertebrates (Keast 1975, Hodgson and Kitchell 1987, Olson 1996). Food webs of many small lakes and ponds with largemouth bass display dynamics similar to those of our model for $0.6 < \pi < 0.8$. Bass often significantly reduce the biomass of their preferred prey, relative to that of their alternative prey, and may dampen the oscillatory dynamics of the food web. This has produced some of the clearest and most persistent cases of top-down control of pelagic food webs (Carpenter and Kitchell 1993, Mittelbach et al. 1996, Post et al. 1997). Although we have discussed our model in the context

of a mobile top predator that links food chains in adjacent habitats, the model applies equally well to predators feeding on prey within a single habitat.

The original analysis of Hastings and Powell (1991) produced a wide range of chaotic dynamics for a three-species food chain. However, subsequent analyses demonstrated that chaos was biologically plausible over only a rather narrow range of parameters (McCann and Yodzis 1994, Ruxton 1996). Our results, and those of McCann and Hastings (1997) and McCann et al. (1998), suggest that, even within the biologically plausible range of chaos-generating parameters, ecologically common processes like allochthonous inputs, omnivory, and prey preferences can dampen population oscillations and eliminate chaos.

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