

OMNIVORY CREATES CHAOS IN SIMPLE FOOD WEB MODELS

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Abstract. Omnivory, defined as feeding on more than one trophic level, was considered rare in nature because of its destabilizing effect. However, recent elaborate studies of natural food webs have shown that omnivory is ubiquitous. It is well known that a simple food chain model of three trophic levels can exhibit chaos if the functional responses are nonlinear. We investigate a three-species Lotka-Volterra model of omnivory in which a predator and a prey share the same resource (i.e., intraguild predation). We demonstrate that intraguild predation sometimes destabilizes food webs and induces chaos, even if the functional responses are linear. The route to chaos is the familiar period-doubling cascade. We compare our results to previous work and discuss the mechanism by which omnivory induces chaos.

Key words: *chaos; food web; intraguild predation; linear functional response; Lotka-Volterra model; omnivory; period-doubling cascade; stability.*

INTRODUCTION

Simple models of food webs sometimes exhibit very complex dynamics (Vance 1978, Gilpin 1979, Takeuchi and Adachi 1983, Vandermeer and Maruca 1998). Hastings and Powell (1991) found chaos in a food chain model of three trophic levels. In their model, the functional responses of the intermediate consumer and the top predator were assumed to be nonlinear and saturating (Holling 1959*a, b*). However, they considered a simple linear food chain and neglected omnivory, whereas numerous empirical studies have shown that omnivory is widespread in food webs (Polis et al. 1989, Winemiller 1990, Polis 1991, 1994, Diehl 1993, Coll and Guershon 2002, Denno and Fagan 2003, Arim and Marquet 2004). Hence there is a need for a comprehensive formal treatment of the population dynamics of omnivory (Diehl 1993).

Omnivory can be defined as feeding on more than one trophic level (Pimm and Lawton 1978, Pimm 1982). Intraguild predation is a simple kind of omnivory in which a predator and a prey share a common resource (Polis et al. 1989, Polis and Holt 1992). Simple three-species systems of intraguild predation can potentially produce complex population dynamics, since the populations interact indirectly through the

trophic cascade, exploitative competition, and apparent competition (Polis et al. 1989, Diehl 1993). On the one hand, McCann and Hastings (1997) incorporated nonlinear functional responses in a model of intraguild predation and showed that omnivory could work as a stabilizing agent. On the other hand, Holt and Polis (1997) found that intraguild predation could destabilize a positive equilibrium in a Lotka-Volterra model with linear functional responses, and Holt (1997) verified that the model could exhibit a limit cycle. Therefore, there exists a discrepancy between the dynamics of these two theoretical models, and finer examinations of these models are necessary to reveal whether omnivory is stabilizing or destabilizing.

In this article, we reinvestigate the three-species Lotka-Volterra model of intraguild predation studied by Holt and Polis (1997) and Holt (1997). The functional responses in this model are linear, and no constraints are imposed on the feeding rates, whereas the model in McCann and Hastings (1997) has nonlinear functional responses with a constraint on the consumption of the prey and resource by the predator. An increase in the rate of resource consumption results in a decrease in the rate of prey consumption and vice versa. We extend numerical analysis of our model into a range that has not been explored by Holt and Polis (1997) and Holt (1997) and demonstrate that intraguild predation sometimes destabilizes the model and induces chaos. In addition to the difference in functional response, our study is different from that of McCann and Hastings (1997) in the ranges of parameters. Since they

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determined the parameter values according to the energetically based arguments in Yodzis and Innes (1992), the feeding rates and efficiencies were confined within rather small ranges in their analysis. Here we explore a wider range of the resource consumption rate by the predator, and reveal that consumption of large amounts of the basal resource by the predator gives rise to chaos.

First, we introduce our model. Next, we investigate behaviors of solutions of the model. Finally, we compare our results to previous work and discuss the mechanism by which omnivory induces chaos.

MODEL

Let N_1 , N_2 , and N_3 denote the densities of a basal resource, an intermediate consumer (intraguild prey), and an omnivorous top predator (intraguild predator), respectively. We assume interactions of the Lotka-Volterra type between these populations. Our model can be described as

$$\begin{aligned}\frac{dN_1}{dt} &= (b_1 - a_{11}N_1 - a_{12}N_2 - a_{13}N_3)N_1 \\ \frac{dN_2}{dt} &= (-b_2 + a_{21}N_1 - a_{23}N_3)N_2 \\ \frac{dN_3}{dt} &= (-b_3 + a_{31}N_1 + a_{32}N_2)N_3\end{aligned}\quad (1)$$

where b_1 , b_2 , and b_3 are, respectively, the intrinsic growth rate of the resource, the mortality of the prey, and the mortality of the predator; a_{ij} denotes the coefficient of intraspecific competition in the resource; a_{ij} ($i < j$) is the rate of consumption; and a_{ij} ($i > j$) measures the contribution of the victim (resource or prey) to the growth of the consumer. The formulation is essentially the same as that in Holt and Polis (1997) and Holt (1997), although it does not explicitly include the conversion efficiencies.

For the later numerical analysis, we briefly summarize the stability analysis by Holt and Polis (1997). It is well known that the intraguild prey must be superior at exploiting the shared resource for persistence (Polis and Holt 1992, Holt and Polis 1997, Mylius et al. 2001, Revilla 2002). When a positive equilibrium exists and an index, $D = -a_{12}a_{23}a_{31} + a_{13}a_{21}a_{32} + a_{11}a_{23}a_{32}$, is negative, the equilibrium is unstable and there appear alternative stable states in which either the intraguild prey or the predator is extinct (Holt and Polis 1997). On the other hand, when a positive equilibrium exists and D is positive, stability of the equilibrium is not definite. If $a_{12}a_{23}a_{31}$ is large and $a_{13}a_{21}a_{32}$ is small, then the equilibrium is stable. However, if $a_{12}a_{23}a_{31} < a_{13}a_{21}a_{32}$, the equilibrium can be unstable

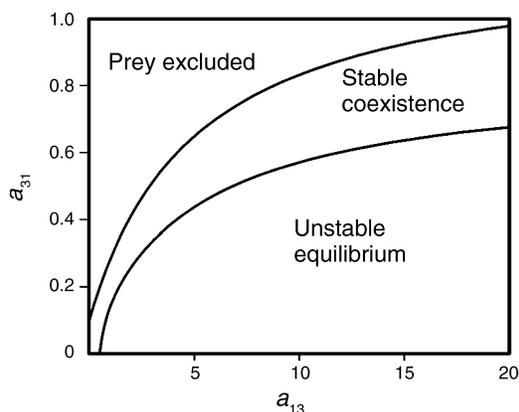


FIG. 1. Stability of the internal equilibrium in the parameter space of a_{13} and a_{31} , where a_{13} is the rate of resource consumption by the predator and a_{31} measures the contribution of the resource to the growth of the predator. The variables b_1 , b_2 , and b_3 are, respectively, the intrinsic growth rate of the resource, the mortality of the prey, and the mortality of the predator. The subscripts of a and b (1, 2, and 3, respectively) denote resource, consumer, and predator. Parameter values are $b_1 = 5$, $b_2 = 1$, $b_3 = 1.2$, $a_{11} = 0.4$, $a_{12} = 1$, $a_{21} = 1$, $a_{23} = 1$, and $a_{32} = 1$. See the *Results and Discussion* section for details.

(Holt and Polis 1997), and a limit cycle may appear (Holt 1997).

In the following, we numerically examine the model in a parameter range that has not been explored by Holt and Polis (1997) and Holt (1997).

RESULTS AND DISCUSSION

Now, we focus our attention on the consumption of the basal resource by the predator, since this feeding link differentiates our model from the linear food chain and has potential for destabilizing the system. When $a_{13} = a_{31} = 0$, the positive equilibrium is globally stable, if it exists (Harrison 1979). We fix the parameters other than a_{13} and a_{31} at arbitrary values as follows: $b_1 = 5$, $b_2 = 1$, $b_3 = 1.2$, $a_{11} = 0.4$, $a_{12} = 1$, $a_{21} = 1$, $a_{23} = 1$, and $a_{32} = 1$.

Fig. 1 shows stability of the positive equilibrium in which the prey and predator coexist, in the parameter space of a_{13} and a_{31} . Although the positive equilibrium in a simple linear chain is always globally stable, as a_{13} increases, the equilibrium becomes destabilized and there occurs a Hopf bifurcation (Guckenheimer and Holmes 1983). This destabilization may come from the delay of resource recovery due to the heavy exploitation by the predator. Then, we fix a_{31} at 0.1 and draw a bifurcation diagram using a_{13} as the bifurcation parameter. Fig. 2A illustrates predator density N_3 on the section on which N_2 is fixed at the equilibrium value. A point near $a_{13} = 5$ denotes that the orbit crosses the section only once and that it represents a limit cycle.

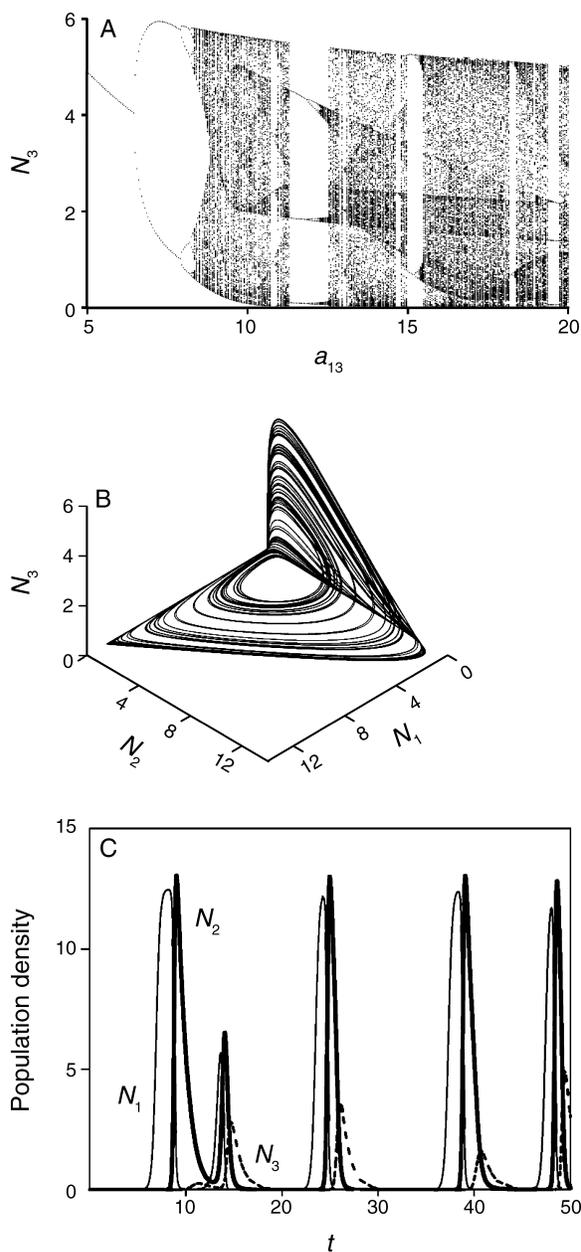


FIG. 2. (A) Bifurcation diagram, using the rate of resource utilization, a_{13} , as the bifurcation parameter. The vertical axis denotes predator density N_3 on the section where N_2 is at the equilibrium value. (B) An example of strange attractors in three-dimensional phase space. (C) An example of population fluctuations of the basal resource (N_1 , thin line), prey (N_2 , heavy line), and predator (N_3 , dashed line). The horizontal axis t denotes unitless time. Parameter values are $a_{31} = 0.1$; in (B) and (C), $a_{13} = 10$. Values of the other parameters are the same as in Fig. 1.

The panel in Fig. 2A demonstrates that chaotic dynamics appear via a period-doubling cascade (Guckenheimer and Holmes 1983).

An example of strange attractors and temporal population fluctuations is illustrated in Fig. 2B and C. Since the prey can efficiently exploit the resource, it rapidly increases when the resource is abundant. Hence, the resource declines. If the predator density is low at that time, the predator can increase only slightly even though the peak prey density is extremely high. In this case, there will be a second set of lower peaks of the resource and prey. The predator, which has grown during the first peaks of the resource and prey, can multiply into a large population. Conversely, when the predator density is high enough at the first prey and resource peaks, the predator rapidly multiplies into a higher peak than in the previous case. In this case, the second peaks of the resource and prey do not appear. Since the predator is omnivorous and the resource consumption rate, a_{13} , is very high, once the predator density has proliferated, the predator almost exhausts both the prey and resource and becomes nearly extinct. The basal resource and prey can recover with some delay, but the exact trajectory is very sensitive to their relative abundances, and we cannot anticipate which path it traces. This causes divergence of nearby trajectories and thus induces chaos.

We have found that intraguild predation can destabilize food webs and induce chaos, via a period-doubling cascade from a limit cycle, when the interactions between the populations are of the Lotka-Volterra type, or when the functional responses are linear. In our model, the condition $a_{12}a_{23}a_{31} < a_{13}a_{21}a_{32}$ or $a_{31}/a_{13} < (a_{21}/a_{12})(a_{32}/a_{23})$ is necessary for the Hopf bifurcation to occur. Accordingly, chaos requires that the predator should consume the basal resource at high rates (a_{13} large) while the efficiency of resource use by the predator (a_{31}/a_{13}) should be low. This parameter range has not been explored previously. Since McCann and Hastings (1997) determined the parameter values according to the energetically based arguments in Yodzis and Innes (1992), the predator's feeding rates and efficiencies do not differ significantly between the resource and prey. Although the energetic reasoning and allometric empiricism might be biologically more plausible, the resource-consumer thinking in Yodzis and Innes (1992) did not take omnivory into account. However, the quality of organisms as a resource changes with the trophic position (Denno and Fagan 2003). Because plant and animal diets differ greatly in their chemical composition, anatomy, and nutritional value, mixing them in the diet requires specific physiological and morphological adaptations (Coll and Guershon 2002). Thus if omnivores are less efficient in utilizing re-

sources in lower trophic levels, chaos may appear through the mechanism explained above.

McCann and Hastings (1997) found that the addition of omnivory to a simple food chain model stabilizes the food web. Since the functional responses in their model are nonlinear, even in the absence of omnivory, the interaction between the resource and prey and that between the prey and predator tend to be oscillatory, and chaotic dynamics are expected when the time scales of the two interactions differ significantly (Hastings and Powell 1991). The omnivorous predator can only increase the rate of consumption of either resource or prey at the cost of the diminished rate of consumption of the other. Furthermore, since their model includes a two-species type II functional response for the predator, increasing the rate of omnivory may play a role in decreasing the difference in time scale of the interactions and stabilizing the system.

In conclusion, our results suggest that an understanding of the stabilizing or destabilizing role of omnivory will require experimental studies that estimate the relative contributions of the different resources in the omnivore's diet. It will also be important to know in more detail how omnivores switch between basal resources and intraguild prey (Coll and Guershon 2002) and to incorporate these mechanisms into theoretical models. For further progress in understanding the implications of omnivory for the structure and dynamics of communities, empirical and theoretical studies of many more species assembled in various trophic combinations will be necessary (Diehl 1993, Lawler and Morin 1993, Morin and Lawler 1995).

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