Re-evaluating the omnivory–stability relationship in food webs

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SUMMARY

Under equilibrium conditions, previous theory has shown that the presence of omnivory destabilizes food webs. Correspondingly, omnivory ought to be rare in real food webs. Although early food-web data appeared to verify this, recently many ecologists have found omnivory to be ubiquitous in food-web data gathered at a high taxonomic resolution. In this paper, we reinvestigate the role of omnivory in food webs using a non-equilibrium perspective. We find that the addition of omnivory to a simple food-chain model (thus a simple food web) locally stabilizes the food web in a very complete way. First, non-equilibrium dynamics (e.g. chaos) tend to be eliminated or bounded further away from zero, via period-doubling reversals invoked by the omnivorous trophic link. Second, food chains without interior attractors tend to gain a stable interior attractor with moderate amounts of omnivory.

1. INTRODUCTION

It has been put forth, using Lotka–Volterra models, that the presence of omnivory destabilizes food webs (Pimm & Lawton 1978; Pimm 1982). More precisely, loss of stability here refers to the finding that omnivory makes *interior point attractors* (i.e. stable equilibria with all species present) statistically rare. Accordingly, theorists predicted that omnivory ought to be rare in food webs. Early food-web data—data compiled with low taxonomic resolution—appeared to verify this hypothesis.

Recently, Polis (1991) has revived this issue by showing that data from the Coachella Valley desert food web are replete with omnivory. Perhaps not surprisingly, many researchers have made the same observations for a range of communities (see Diehl 1993, or Winemiller 1996, for review); suggesting that omnivory may be the rule in food webs not the exception. Polis and others (e.g. Polis *et al.* 1989; Polis 1991, 1994; Polis & Strong 1996; Winemiller 1996) have argued cogently that the early food webs are simply not detailed enough—they lack taxonomic resolution.

Here we re-evaluate some long-standing theoretical views on the role of omnivory, complexity and stability in food webs (May 1973; Pimm & Lawton 1978; Pimm 1982). Our investigation expands on previous studies by considering both equilibrium and non-equilibrium dynamics in a simple three-species food web. For reasons described below, we take as a natural starting point the well-studied three-species food-

chain model first put forth by Rosenzweig (1973):

$$\left. \begin{aligned} \frac{dR}{dt} &= F_R = R \left(1 - \frac{R}{K} \right) - x_C y_C \frac{CR}{R + R_0}, \\ \frac{dC}{dt} &= F_C = -x_C C \left(1 - y_C \frac{R}{R + R_0} \right) \\ &\quad - x_P y_P \frac{PC}{C + C_0}, \\ \frac{dP}{dt} &= F_P = -x_P \left(1 - y_P \frac{C}{C + C_0} \right), \end{aligned} \right\} \quad (1)$$

where R is resource density, C is consumer density, and P is top predator density. The parameters correspond to a paper by Yodzis & Innes (1992), where K is the resource carrying capacity, R_0 and C_0 are the half saturation density of the resource, R , and consumer, C , respectively, x_i is the mass-specific metabolic rate of species i , measured relative to the production-to-biomass ratio of the resource population, and y_i is a measure of ingestion rate per unit metabolic rate of species i .

System (1) is an appropriate starting point for several reasons. First, it contains more biological detail in the functional and numerical responses than the Lotka–Volterra models previously used. This makes the model more nonlinear, which can be very important when considering non-equilibrium behaviour.

Second, the dynamics of the system (1) are well known (Hastings & Powell 1991; Klebanoff & Hastings 1994; McCann & Yodzis 1995), so previous food-chain results can be easily contrasted with an extended system which includes omnivory.

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With the addition of omnivory, the three-species food chain of system (1) becomes the following simple three-species food-web model:

$$\left. \begin{aligned} \frac{dR}{dt} &= F_R = R \left(1 - \frac{R}{K} \right) - x_C y_C \frac{CR}{R + R_0} \\ &\quad - \omega x_P y_{PR} \frac{PR}{R_{02} + (1 - \omega)C + \omega R}, \\ \frac{dC}{dt} &= F_C = -x_C C \left(1 - y_C \frac{R}{R + R_0} \right) \\ &\quad - (1 - \omega) x_P y_{PC} \frac{PC}{\omega R + (1 - \omega)C + C_0}, \\ \frac{dP}{dt} &= F_P = -x_P P \\ &\quad + (1 - \omega) x_P y_{PC} \frac{CP}{\omega R + (1 - \omega)C + C_0} \\ &\quad + \omega x_P y_{PR} \frac{PR}{\omega R + (1 - \omega)C + R_{02}}, \end{aligned} \right\} \quad (2)$$

where the type II functional response of system (1) is modified to include a two-species type II functional response for the top predator, P , such that parameter ω controls the top predators preference for either resource, R , or consumer, C ; accordingly, R_{02} is the new half saturation density of the resource, R , now being consumed by the top predator, P , and the parameter, y_P , is split into two ingestion rates per unit metabolic rate, y_{Pj} , where j defines the ingestion rate for P on prey item j . Note that the parameter ω can be thought of as the strength of omnivory.

To clarify the meaning of the omnivory parameter, ω , it is useful to consider a few examples. When $\omega = 0.00$, system (2) is equivalent to the three-species food-chain model of system (1). Increasing ω beyond 0.00 creates an omnivorous link in system (2) between the top predator, P , and the resource, R , changing the system to a simple three-species food web. This omnivorous link gains strength as ω increases; at $\omega = 0.5$, the top predator, P , is a pure generalist— P consumes both populations (C and R) exactly according to their proportion in the community. Increasing ω still further pushes system (2) into a form of intraguild predation (i.e. the top predator is now more a competitor than a predator), until finally, at $\omega = 1.0$, system (2) becomes a purely consumptive competition model with two consumers feeding on one resource. As we are only concerned with questions of omnivory in this paper, we consider values of ω less than or equal to 0.50.

Interestingly, Yodzis & Innes (1992) related this class of consumer–resource models to energetic arguments based on patterns in the data for body size and metabolic type. In doing this, they established a link between data and theory; a link that allows us to choose parameter sets that can be deemed biologically plausible. For example, all x_i parameters we use were chosen such that the $P:C$ body mass ratios fall between the typical range (10^1 – 10^3) found in data surveys (Peters 1983; Cohen *et al.* 1993). The y_i values were also chosen to be consistent with at

least one of the metabolic types (endotherms, invertebrate ectotherms and invertebrates) delineated in Yodzis & Innes (1992).

In the next four sections, we draw from four biologically plausible parameter sets that correspond to the following set of representative dynamical outcomes of system (1) (or, equivalently, system (2) at $\omega = 0.0$): chaos, transient chaos, limit cycles and stable solutions. We make three additional assumptions. First, we assume that the predator, P , is less efficient in consuming R than it is in consuming C ($y_{PR} < y_{PC}$). Secondly, we assume that the predator, P , is less efficient in consuming the resource, R , than is the intermediate consumer, C ($y_{PR} < y_C$). Third, we assume that the top predator has a half saturation density on the resource, R , that is equivalent to the consumer, C ($R_{02} = C_0$). The final assumption is arbitrarily set to simplify the analysis. We return to these assumptions in the discussion.

2. CHAOS

Figure 1a–c depicts the local minima attained on solutions to system (2) across a range of the omnivory parameter, ω , for P , C and R , respectively. The parameters ($x_C = 0.40$, $x_P = 0.08$, $y_C = 2.009$, $y_{PR} = 2.00$, $y_{PC} = 5.00$, $R_0 = 0.16129$, $R_{02} = 0.50$, $C_0 = 0.50$) are consistent with an invertebrate predator–invertebrate consumer–invertebrate resource food chain experiencing chaotic dynamics (McCann & Yodzis 1994a). There are two interesting points. First, increasing the strength of omnivory invokes a period-doubling reversal—omnivory has killed the chaos for $\omega > 0.15$. Second, omnivory raises the floor of the attractor in all three cases (i.e. the minima attained by P , C and R tend to increase with increasing ω). Since it is reasonable to assume that a system becomes less vulnerable to demographic stochasticity as its minimum densities move further from zero, then omnivory has enhanced the persistence of the simple three-species food web.

3. TRANSIENT CHAOS

Transient chaos is a relatively new dynamic in the ecological literature; yet, it may be very important (Hastings & Higgins 1994; Hastings 1996). In a crude sense, it can be characterized by two primary phases: (i) a very long bounded phase that behaves chaotically; and (ii) a relatively quick, precipitous drop to an attractor. Although the system eventually reaches an attractor, the transient phase cannot be ignored as it occurs on time scales far greater than those experienced in most ecological interactions. Interestingly, such dynamics have begun to be uncovered more frequently as models become more coupled and increase in dimension (Engbert & Drepper 1994; Hastings & Higgins 1994; McCann & Yodzis 1994b; Hastings 1996).

Figure 2a–c depicts the local minima attained on solutions to system (2) as ω is varied, for P , C and R , respectively. The parameters ($x_C = 0.40$,

Figure 1. For a range of values of the parameter, ω , a set of local minima are taken from solutions to system (2) discussed in the text for: (a) the top predator, P ; (b) the intermediate consumer, C ; and (c) the resource, R . All other parameters are held constant at $x_C = 0.40$, $x_P = 0.08$, $y_C = 2.009$, $y_{PR} = 2.00$, $y_{PC} = 5.00$, $R_0 = 0.161\,29$, $R_{02} = 0.50$, $C_0 = 0.50$. These parameters are taken from the chaotic solutions to system (1) found in Hastings & Powell (1991) and later modified by McCann & Yodzis (1994a).

$x_P = 0.08$, $y_C = 2.009$, $y_{PR} = 2.00$, $y_{PC} = 2.876$, $R_0 = 0.161\,29$, $R_{02} = 0.50$, $C_0 = 0.50$) are consistent with a number of food-chain possibilities: an invertebrate predator–invertebrate consumer–invertebrate resource food chain; a vertebrate ectotherm predator–vertebrate ectotherm consumer–vertebrate ectotherm resource food chain; or a vertebrate ecto-

Figure 2. For a range of values of the parameter, ω , a set of local minima are taken from solutions to system (2) discussed in the text for: (a) the top predator, P ; (b) the intermediate consumer, C ; and (c) the resource, R . All other parameters are held constant at $x_C = 0.40$, $x_P = 0.08$, $y_C = 2.009$, $y_{PR} = 2.00$, $y_{PC} = 2.876$, $R_0 = 0.161\,29$, $R_{02} = 0.50$, $C_0 = 0.50$. These parameters are taken from transient chaotic solutions found in McCann & Yodzis (1994b).

therm predator–invertebrate consumer–invertebrate resource food chain. All experience transient chaotic dynamics in which the second phase of the dynamic is characterized by an abrupt loss in the top predator population (McCann & Yodzis 1994b).

Quite a bit of dynamic behaviour occurs throughout ω in figure 2. First at $\omega = 0.11$, the system expe-

riences a cyclic fold in which the interior goes from no positive solution to a limit-cycle solution. At this point, another limit cycle is present (although not visible in figure 2) from $\omega = 0.11$ to $\omega = 0.50$. This limit cycle is unstable (a saddle cycle) and acts as a separatrix between two basins of attraction (the second attractor is a limit cycle on the C – R plane). Both basins exist from $\omega = 0.11$ to $\omega = 0.50$, but only the interior basin is shown in figure 2*a–c*.

Several points arise from the dynamics implicit in figure 2*a–c*. Increasing omnivory, ω , makes system (2) go from a system without an interior solution to one with an interior solution (note though that the system now has two basins of attractions). In addition, as ω increases still further, the interior attractor goes from a limit cycle to a point attractor. As noted before, omnivory again tends to bound the minima further away from zero densities. Omnivory stabilizes the system in this case in a very complete way: *omnivory creates an attracting interior solution, stabilizes it locally and makes the solutions more bounded away from zero (i.e. more persistent)*.

4. LIMIT CYCLES

Figure 3*a–c* is analogous to the previous figures except that the parameters ($x_C = 0.40$, $x_P = 0.15$, $y_C = 2.009$, $y_{PR} = 2.00$, $y_{PC} = 5.0$, $R_0 = 0.33$, $R_{02} = 0.50$, $C_0 = 0.50$) were changed to give limit-cycle solutions to system (1) (McCann & Yodzis 1995). Again, these parameters are consistent with a number of food-chain possibilities: an invertebrate predator–invertebrate consumer–invertebrate resource food chain; a vertebrate ectotherm predator–vertebrate ectotherm consumer–vertebrate ectotherm resource food chain; or a vertebrate ectotherm predator–invertebrate consumer–invertebrate resource food chain.

In general, figure 3 is consistent with the results from figures 1 and 2—that omnivory tends to stabilize food webs and enhance persistence. However, it does show that very strong omnivory can, in fact, cause the opposite effect. For example, in figure 3*b*, the intermediate consumer density (C) is driven towards zero for very high values of ω ($\omega \geq 0.47$).

5. POINT ATTRACTORS

Figure 4*a–c* depicts the values of the point attractor attained on solutions to system (2) across a range of the omnivory parameter, ω , for P , C and R , respectively. The parameters ($x_C = 0.40$, $x_P = 0.01$, $y_C = 2.009$, $y_{PR} = 2.00$, $y_{PC} = 5.0$, $R_0 = 0.50$, $R_{02} = 0.90$, $C_0 = 0.90$) are consistent with a number of food-chain possibilities: an invertebrate predator–invertebrate consumer–invertebrate resource food chain; a vertebrate ectotherm predator–vertebrate ectotherm consumer–vertebrate ectotherm resource food chain; or a vertebrate ectotherm predator–invertebrate consumer–invertebrate resource food chain (Yodzis & Innes 1992). The pa-

Figure 3. For a range of values of the parameter, ω , a set of local minima are taken from solutions to system (2) discussed in the text for: (a) the top predator, P ; (b) the intermediate consumer, C ; and (c) the resource, R . All other parameters are held constant at $x_C = 0.40$, $x_P = 0.08$, $y_C = 2.009$, $y_{PR} = 2.00$, $y_{PC} = 2.876$, $R_0 = 0.16129$, $R_{02} = 0.90$, $C_0 = 0.90$. These parameters are taken from transient cyclic solutions found in McCann & Yodzis (1995).

parameter set gives point attractor solutions for the food-chain system (McCann & Yodzis 1995).

Interestingly, throughout the range in ω , the solutions to system (2) remain stable (figure 4*a–c*). Pimm & Lawton's (1) results suggest that the point attractors are likely to become unstable as omnivory is added to the system—this is not the case for a wide range in the strength of omnivory. There is, how-

Figure 4. For a range of values of the parameter, ω , a set of local minima are taken from solutions to system (2) discussed in the text for: (a) the top predator, P ; (b) the intermediate consumer, C ; and (c) the resource, R . All other parameters are held constant at $x_C = 0.40$, $x_P = 0.08$, $y_C = 2.009$, $y_{PR} = 2.00$, $y_{PC} = 2.876$, $R_0 = 0.161\,29$, $R_{02} = 1.50$, $C_0 = 1.50$. These parameters are taken from transient cyclic solutions found in McCann & Yodzis (1995).

ever, a point of conflict with our previous results. The question of persistence is not as clear. The resource equilibrium density declines (figure 4c) throughout the range of ω and the top predator density, P , declines after $\omega = 0.25$. The system, in this sense, may become less persistent.

6. CONCLUSION

Our results suggest that omnivory, generally speaking, locally stabilizes and enhances persistence of a three-species food web. Stability here refers to the following: an unstable equilibrium tends to become locally stable with the addition of omnivory. Additionally, omnivory tends to bound the minima attained by non-equilibrium attractors further away from zero. This bounding effect may be responsible for invoking a period-doubling reversal and inhibiting chaos in system (2). Stone (1993) noted a similar result when spatial structure, in the form of metapopulations, is added to a discrete single species model. In Stone's investigation, individual populations were not allowed to drop below a preset floor—in other words, the model dynamics were forced to behave in a well-bounded fashion. Ruxton (1993) suggested that this preset floor invokes the period-doubling reversal and that Stone's result therefore occurs without any biological-motivated mechanism. Our results are consistent with Stone (1993), and yet the result is based upon a clear biological mechanism. In this case, omnivory acts to raise the floor in population densities attained by the solutions and, in doing so, inhibits chaotic dynamics in simple food webs.

The results presented here may have repercussions for more complex model communities. For example, May (1973) found using Lotka–Volterra models that increased multispecies trophic complexity (i.e. more species and more links) makes for lower stability. Our results suggest that adding some omnivory ought to do the exact opposite: up to some maximum amount of strength, omnivory (i.e. increased system complexity in terms of number of links) tends to stabilize a three-species food chain. Of course, our result is preliminary.

Some words of caution are necessary. As noted in figure 3b, relatively strong omnivory may cause system (2) eventually to lose its interior attractor (mathematically speaking, the interior attractor collides with a solution on one of the planes in a trans-critical bifurcation). So, when omnivory is too strong it can definitely destabilize in the sense of Pimm & Lawton (1978)—the system suffers the loss of an interior attracting solution. This begs the question: how much omnivory is too much? Some insight into this can be gained by relaxing the assumption that the top predator is less efficient at lower trophic levels. If we allow the top predator, P , to be super efficient at all trophic levels, our results do not qualitatively change; rather, they simply become concentrated into a smaller portion in the ω parameter space (i.e. all the behaviour occurs across a smaller range in ω).

At least for the case of a simple food web, the amount of omnivory required such that the system loses stability depends on how efficiently the top predator exploits lower trophic levels. In general, the more efficient the top predator, the less omnivory the system can withstand. Interestingly, one general

conclusion of optimal foraging theory is that generalist consumers (i.e. omnivores) are less efficient than specialists (see Schoener 1971).

Finally, the same values of ω that increase stability and enhance persistence also appear, in many cases, to promote longer transients and multiple basins (i.e. as more types of fold bifurcations become possible). This is consistent with our suggestion earlier that long transients may play a much larger role in more coupled systems (real food webs). The addition of omnivory may bound dynamic behaviour in food webs but may do so at the cost of promoting transient dynamics. Further research will be needed to clarify if increased coupling does in fact promote the length of transient dynamics in food webs.

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