

# Schoener Exam

Carl Boettiger

June 9, 2008

## Question 1

Volterra predator prey dynamics begin with the simple form (in the notation of Schoener, (1974)):

$$\frac{dF}{dt} = rF - \alpha FN \quad (1)$$

$$\frac{dN}{dt} = \alpha\beta FN - dN \quad (2)$$

$F$  is prey density,  $N$  the predator density,  $r$  is prey growth rate,  $\alpha$  is frequency of prey-predator encounters that result in prey death,  $\beta$  is conversion efficiency of a dead prey into new predators, and  $d$  the death rate of predators.

This model has neutrally stable cycles, which are thought not to be very realistic as they are never convincingly observed in nature. Because they are neutrally stable, any perturbation would simply move the system to a different amplitude cycle, rather than allow it to return to its original cycle.

The first modification we consider is to add logistic growth to the prey. This follows MacArthur and Levins (1967) model of a resource-consumer model (which they used to derive their resource overlap), and also appears in May and MacArthur 1972:

$$\frac{dF}{dt} = rF \left(1 - \frac{F}{K}\right) - \alpha FN \quad (3)$$

The Predator dynamics remain unchanged. Prey now exhibit density dependence as well as predation, which tips the model to a single stable

state. The approach to the single stable state could be a spiral (damping oscillations) or a direct approach (overdamped). Some experimental evidence supports this common model.

For instance, Luckenbill's (1973) study analyzed by Harrison (1995) is a predator prey laboratory system consisting of the protists *paramecium* and *didinium*. Luckenbill found that increasing resources of the prey species destabilized the system, which he called "The Paradox of Enrichment." This can be partly explained by the logistic term we just added, as increasing carrying capacity of prey,  $K$  by adding resources, effectively removes the nonlinear term that we had, removing the stable state. To understand how this can become totally unstable, we consider another effect.

So far we have modeled predation with a (Holling) Type I response: linear in  $F$ . We can replace this with a Type II response, which can mechanistically derived by considering the handling time and search time of predators. This models predator saturation. The equations take on the following form:

$$\frac{dF}{dt} = rF - \alpha \frac{F}{U + F} N \quad (4)$$

$$\frac{dN}{dt} = \alpha \beta \frac{F}{U + F} N - dN \quad (5)$$

(See figure 1 for a diagram of the types of functional responses). Here  $U$  measures the relative saturation of predators. If predators have long handling times relative to search times,  $U$  is quite large relative to  $F$  and they don't saturate very quickly. In the limit of large  $U$  the model becomes Type I again. Meanwhile, for small  $U$ , the predators can saturate. For the moment, our equation doesn't have logistic growth of prey, so saturating the predators means that the system becomes unstable, the neutral limit cycles will instead spiral out to extinction.

Luckenbill tested this effect too by adding methyl cellulose to the medium. This slowed down the rate predators could move, making the predators less likely to be saturated with prey, (effectively removing the type II curve), which he found was stabilizing.

Considering the logistic model and the Type II model together, we can get stable limit cycles: where the population densities oscillate over time, returning to the same amplitude oscillation if perturbed. Original evidence for stable oscillations in predator-prey dynamics dates back to the Hudson Bay company trapping data on Lynx and hare abundances, which were thought to show stable limit cycles.

This system has been investigated much today, including the very large scale, 8 year study by Krebs (1995), with predator exclosures and supplemented resources, which showed abundances of hare increasing with more food and with fewer predators. However, when both were presented together, the response was more than expected (11 fold, compared to individually only 3-fold responses), which suggests aspects not in the model (such as behavioral change where hare also forage more without predators).

If predators have access to an alternate food resource, then the Type II model may be inappropriate, and can be replaced with a Type III response, as shown by van Baalen et al.

$$\frac{F^a}{U^a + F^a} \quad (6)$$

A type III response can be stabilizing or destabilizing, as shown by Oaten and Murdoch (1975): it is stabilizing when the per capita risk increases with increasing number of prey. The van Baalen work demonstrates that this can be an appropriate model for prey switching, and can stabilize the predator-prey system as predicted by Oaten and Murdoch.

## Question 3

### A

Apparent Competition (see diagram, Figure 2) results when two prey items are consumed by the same predator. The two appear to be in competition, as increasing the abundance of one, increases the abundance of the predator, and thus increases predation on the second prey species, hurting the species. The concept and early models were first put forward by Holt (1977, 1984) which demonstrated the idea with simple differential equation models and then put forward the idea of prey aggregation.

One of the most elegant examples of apparent competition can be found in Schmitt (1987). Our two prey species are bivalves and gastropods. They have a variety of predators, including octopus and lobsters, who can all be thought as an effectively equivalent predator guild. The predators prefer the bivalves, who live higher up along the rocky reef, over the gastropods, living lower down by the floor. Schmitt moves bivalves down to the floor with the gastropods, and finds that the predators not only follow to eat the bivalves,

but also eat more gastropods as well, supporting theoretical predictions about the role of aggregate response.

To understand the interaction in Figure 2, we classify it as apparent competition based on the sign of the impact species 1 has on species 2. The difficulty of this approach is that it confounds mechanisms – apparent competition is a predation mechanism, yet is being classified with other competition mechanisms. The weakness of this approach is discussed in Abrams (1987), who argues for more mechanistic definitions rather than the sign method. Chaneton and Bonsall (1995) revive the attention to the subject of apparent competition in a review paper, but find that most interactions are only weak, almost (0,-) rather than (-,-), which they subscribe to very different relative abundances of the prey (manipulating the less abundant one has little impact on the system, since it wasn’t a large part of the predator diet to begin with).

## B

Food webs consist of many more interactions than drawn in the simple diagram of Figure II. The prey may also be competing for resources, one of the prey may predate on the other (making this intraguild predation), and most importantly, many more species are usually involved, such as the dynamics of the primary producers that the prey are eating, more trophic levels, etc. Many attempts have been made to understand more complicated food webs, with limited success.

A common approach is seen in Huismann and Wessig, which consider a system of coupled differential equations. Primary producers follow the May & MacArthur logistic growth form Eq (3) while their consumers follow (2), and consumers compete with Lotka-Volterra (LV) dynamics. They showed by a variety of simulations that this system was highly unpredictable. Rolke responded the following year with a paper demonstrating that the very same system could be made highly predictable by pulsing resources, not only demonstrating this by simulating the same equations, but also in an experimental system with replicate fouling-plate communities.

The applicability of these LV models to multi-species systems has been questioned in much theoretical and experimental competition literature, such as Vandermeer’s study with four *paramecium* species that showed only qualitative fit, or Neill’s study in microcrustaceans that argued that pairwise parameterizations of LV models did not match the behavior of the many-

species community. Without the ability to parameterize models accurately in pairwise experiments, understanding the dynamics of the whole community becomes even more daunting.

The jury still weighs on the side of unpredictability. Case (1995) showed the importance of transient dynamics and unpredictability in how an invader species could enter a community and have a positive growth rate, drive some residents to extinction and then go extinct itself, leaving no record but a changed community.

Yodzis (1988) considers the general problem of a population whose dynamics are described by coupled differential equations,

$$\frac{d\vec{N}}{dt} = f(\vec{N}) \quad (7)$$

The equilibrium  $\vec{N}_e$  will be shifted slightly by a press perturbation  $I$ :

$$\frac{d\vec{N}}{dt} = f(\vec{N}_e(I)) + I = 0 \quad (8)$$

which will equal 0 at the new equilibrium. To get the response to a perturbation,  $\partial\vec{N}/\partial I$ , we differentiate with respect to  $I$ ,

$$\frac{\partial f}{\partial \vec{N}} \frac{\partial \vec{N}}{\partial I} + 1 = 0 \quad (9)$$

Which we can then solve, noting that  $\frac{\partial f}{\partial \vec{N}}$  is nothing more than the community matrix  $A$  (Jacobian of the coupled system):

$$\frac{\partial f}{\partial \vec{N}} \frac{\partial \vec{N}}{\partial I} = 1 \quad (10)$$

$$A \frac{\partial \vec{N}}{\partial I} = 1 \quad (11)$$

$$\frac{\partial \vec{N}}{\partial I} = A^{-1} \quad (12)$$

Hence the inverse of the community matrix gives the response of the system to a press-perturbation (raise a population above its equilibrium and hold it there). From this Yodzis argues that in many cases the responses will be difficult or impossible to determine. Schmitz (1997) presents a courageous

attempt to test this in a system of grasshoppers, four plant species, and nitrogen resource. Using previous estimates from this familiar system, he parameterizes the differential equation models, evaluates the inverse of the community matrix, and gets qualitatively accurate predictions on the sign of the effect when compared to his experimental press experiment, though the magnitudes are not very accurate. This heroic experiment would be even harder to perform in a larger community with a more complicated food web. For many natural systems, the food web itself is not worked out, let alone the parameterization of all the connections. Work such as Yodzis suggests that even having accomplished these Herculean tasks, the problem remains difficult to its core.