Predator-Prey Models

This is a diverse area that includes general models of consumption:

- Granivores eating seeds
- Parasitoids
- Parasite-host interactions

Lotka-Voterra model prey and predator:

V = victim population

P = predator population

Such that:

$$\frac{dV}{dt} = f(V, P)$$

If predator is only limiting factor for victim population.

Predator-Prey Models

Start $$\frac{dV}{dt} = rV$$

Then add $$\frac{dV}{dt} = rV - \alpha VP$$ losses to predator

Where: α = encounter rate; proportional to killing rate of predator

* αV = functional response (rate of victim capture as a function of victim density)

Predator-Prey Models

Predator

$$\frac{dP}{dt} = g(P,V)$$

If no prey

$$\frac{dP}{dt} = -qP$$

exponential decline

With prey

$$\frac{dP}{dt} = \beta VP - qP$$

Where β is the conversion efficiency of prey into predator offspring

… proportional to nutritional value of individual prey

β V = numerical response

= growth rate of predator population as a function of prey density

Predator-Prey Models

Set $$\frac{dV}{dt} = 0 = rV\text{-}\alpha VP$$

$$rV = \alpha VP$$

$$r = \alpha P$$

So: $$\hat{P} = \frac{r}{\alpha}$$

Notes: 1) solution for V in terms of P

2) $\hat{P}$ some number of predators needed to yield prey growth rate equal to 0

3) Function of victim r AND predator encounter rate such that, greater r requires more predators (*or more efficient predator*) to keep victim population growth in check

Predator-Prey Models

Set: $$\frac{dP}{dt} = 0 = \beta VP - qP$$

$$\beta VP = qP$$

$$\beta V = q$$

So: $$\hat{V} = \frac{q}{\beta}$$

1) Solution in terms of V
2) $\hat{V}$ number of prey needed to sustain P
3) Function of predator death rate and *conversion efficiency*… greater efficiency, less prey needed to sustain P

Predator-Prey Models

Equilibrium solutions yield predator-prey isoclines

Note: isoclines only cross at 90º angles

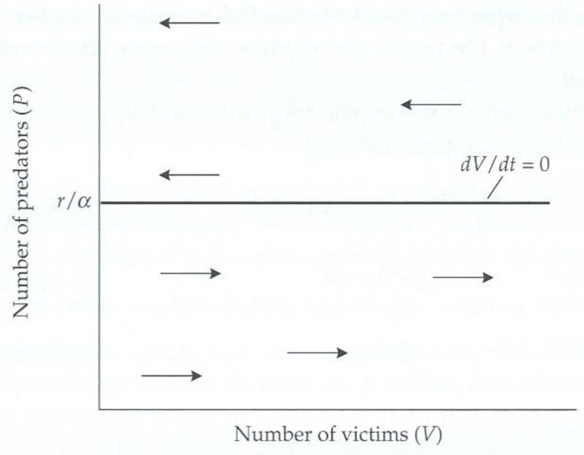


Figure 6.1 The victim isocline in state space. The Lotka–Volterra predation model predicts a critical number of predators (r/α) that controls the victim population. If there are fewer predators than this, the victim population increases (right-pointing arrows). If there are more predators, the victim population decreases (left-pointing arrows). The victim population has zero growth when $P = r/\alpha$.

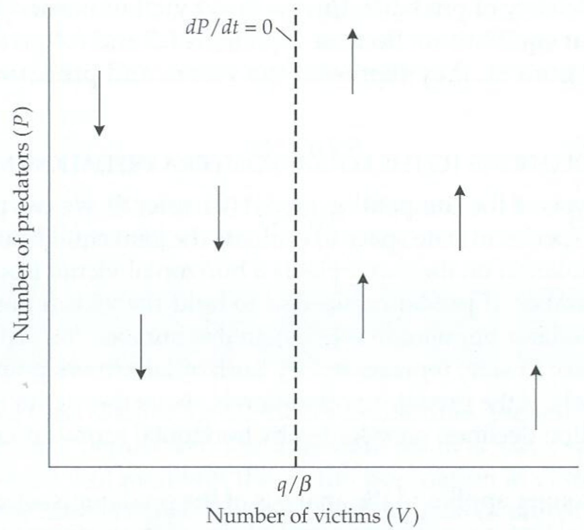


Figure 6.2 The predator isocline in state space. The Lotka–Volterra predation model predicts a critical number of victims (q/β) that controls the predator population. If there are fewer victims than this, the predator population decreases (downward-pointing arrows). If there are more victims, the predator population increases (upward-pointing arrows). The predator population has zero growth when $V = q/\beta$.

Predator-Prey Models

Together, these equations divide the state space into 4 regions.

Prey populations trace on an ellipse unless

1) start precisely at the intersection;

2) start at low initial abundance

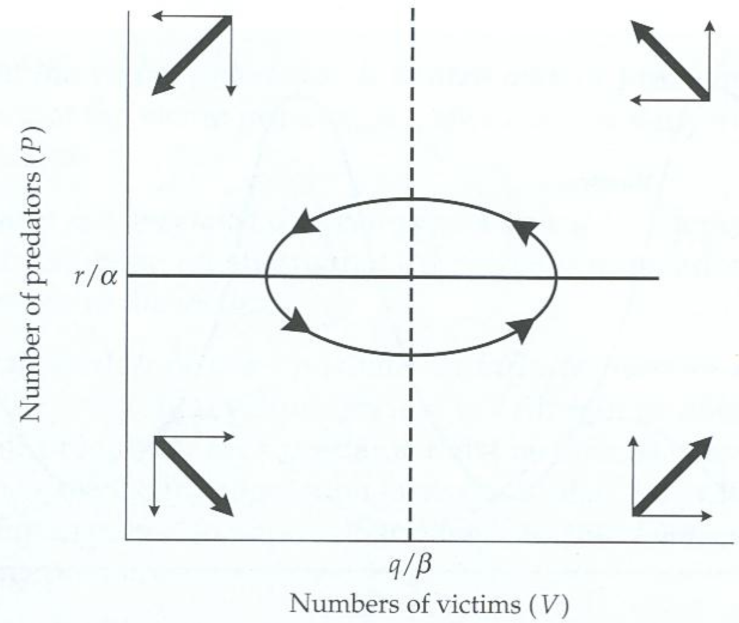


Figure 6.3 The dynamics of predator and victim populations in the Lotka–Volterra model. The vectors indicate the trajectories of the populations in the different regions of the state space. The populations trace a counterclockwise path that approximates an ellipse.

Predator-Prey Models

Note: Yields cycles… closer to intersection of isoclines the less amplitude

Amplitude (A) = neutrall stable, amplitude set by initial conditions

Period

$$c = \frac{2\pi}{\sqrt{rq}}$$

Key is reciprocal control of P and V

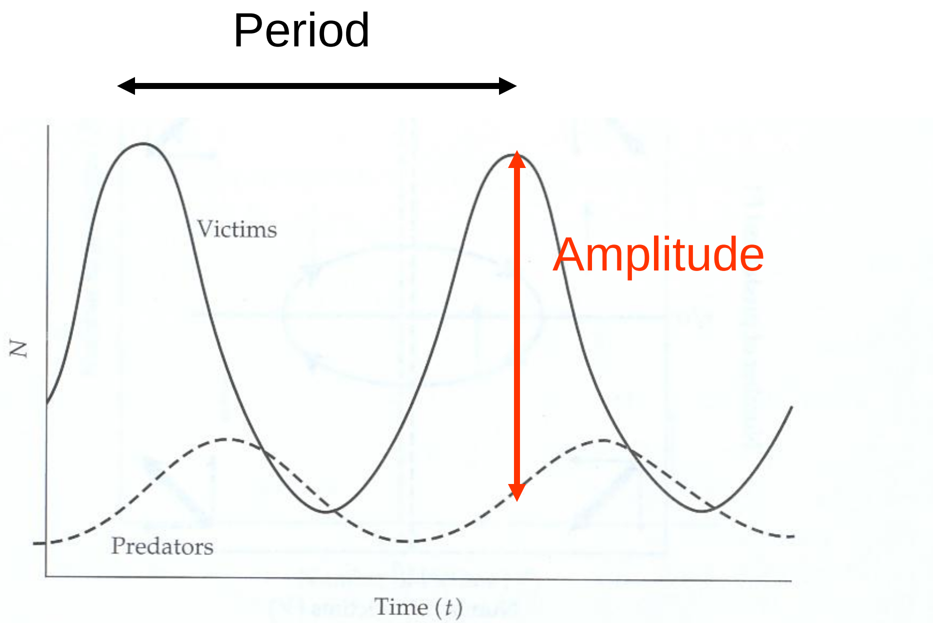


Figure 6.4 Cycles of predators and victims in the Lotka–Volterra model. Each population cycles with an amplitude that is determined by the starting population sizes and a period of approximately $2\pi/\sqrt{rq}$. The predator and victim populations are displaced by one-quarter of a cycle, so that the predator population peaks when the victim population has declined to half its maximum, and vice versa.

Predator-Prey Models

Lotka-Volterra assumptions:

1) Growth of V limited only by P
2) Predator is a specialist on V
3) Individual P can consume infinite number of V
    a. No interference or cooperation
    b. No satiation or escape; type I functional response
4) Predator/Victim encounter randomly in homogeneous environment

Predator-Prey Models

Incorporating carrying capacity for prey

Consider: $$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) = rN - \frac{rN^2}{K} \qquad \therefore\ set\ \ c = \frac{r}{K}$$

Then by substitution $$\frac{dV}{dt} = rV - cV^2$$

Back to prey population

$$\frac{dV}{dt} = rV - \alpha VP$$

$$\frac{dV}{dt} = rV - \alpha VP - cV^2$$

Predator-Prey Models

Incorporating carrying capacity for prey

$$\frac{dV}{dt} = rV - \alpha VP - cV^2$$

$$\frac{dV}{dt} = rV\left(1 - \frac{V}{K}\right) - \alpha VP$$

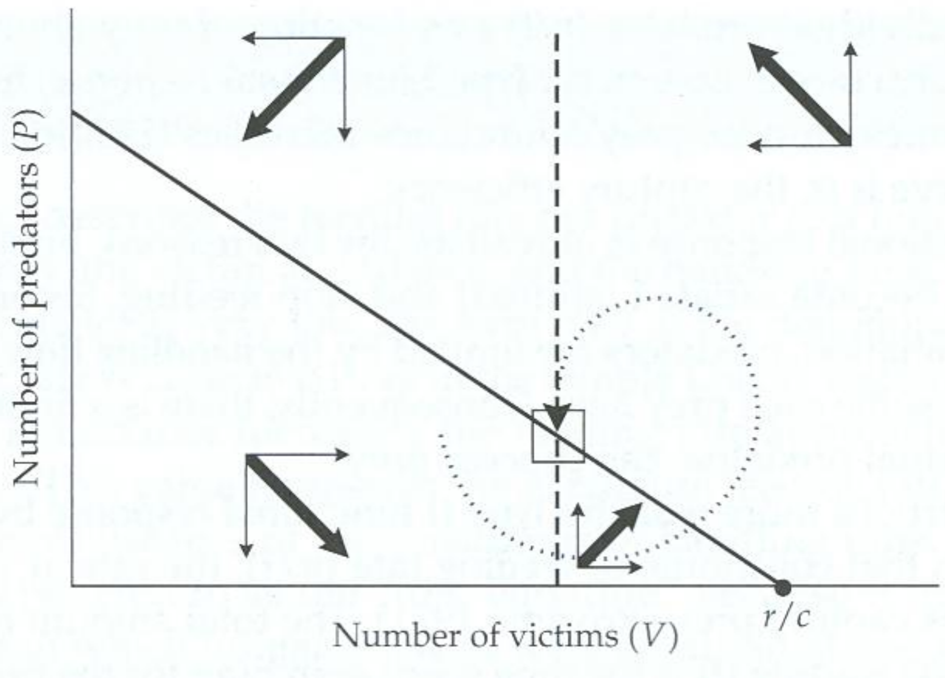
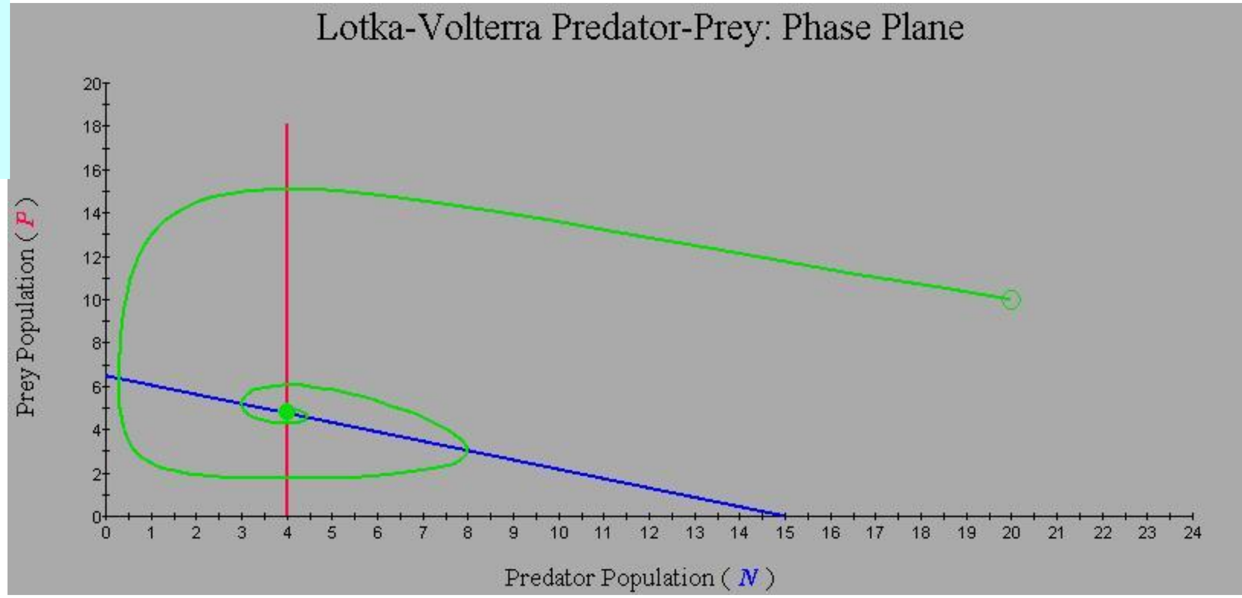
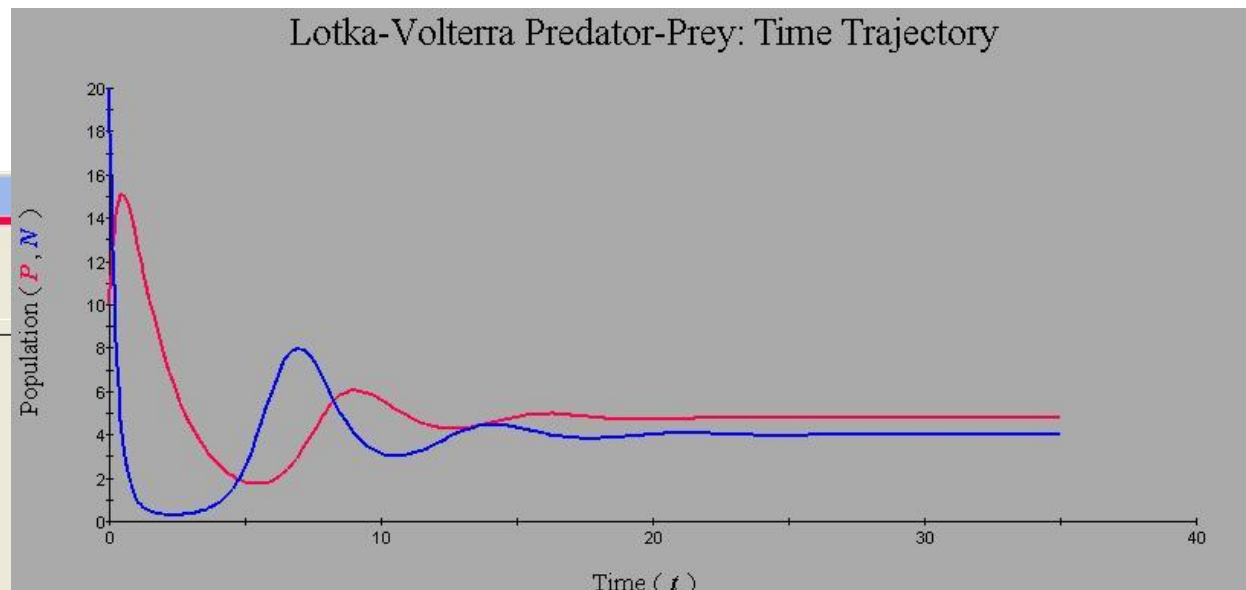


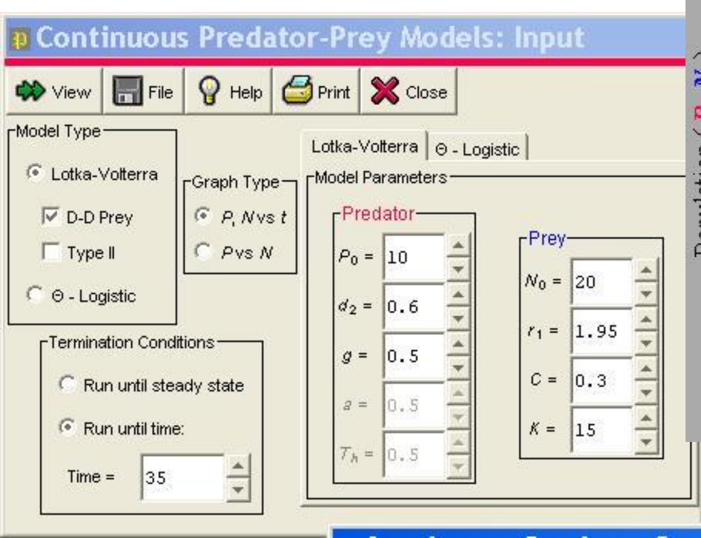
Figure 6.5 The effect of a victim carrying capacity on the victim isocline. The victim isocline slopes downward with a carrying capacity incorporated. The intersection with the vertical predator isocline forms a stable equilibrium point.

Predator-Prey Models

- Lotka-Volterra dynamics with prey density-dependence
- Can yield converging oscillations
- Populus parameters:
  d=rate pred starve;
  g=conversion efficiency of prey to pred recruits
  C=encounter rate







Predator-Prey Models

Functional Response

Lotka-Volterra assumes constant proportion of prey captured.

Called a type I functional response

- no satiation

- no handling time

α: $\Delta y / \Delta x$ = capture efficiency

n=# prey eaten/predator•time

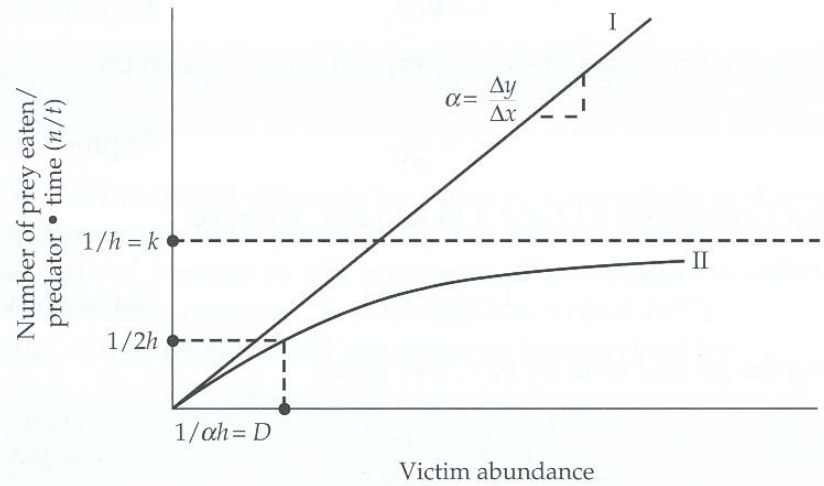


Figure 6.6 The functional response of predators is the feeding rate per predator as a function of prey abundance. The shape of these curves depends on the capture efficiency (α), the maximum predator feeding rate (k), and the victim abundance for which the predator feeding rate is half of the maximum (D).

Predator-Prey Models

Consider a type II functional response:

t = time feeding; t_s=time searching; t_h=time handling

Where $t = t_s + t_h$

h= time handling each item; n = # eaten

$t_h = h \cdot n$

and $n = V\alpha t_s$

$$\therefore t_s = \frac{n}{\alpha V}$$

and by substituting $t = t_s + t_h$

$$t = \frac{n}{\alpha V} + hn$$

Predator-Prey Models

Which can be shown (see text):

$$\frac{n}{t} = \frac{\alpha V}{1 + \alpha V h}$$

In other words…

feeding rate = f(capture efficiency, prey density, handling time)

Thus, at low V, αVh is small and feeding rate approaches $s = \alpha V$ as in the Lotka-Volterra models

Predator-Prey Models

But as V gets bigger, feeding rate approaches:

$$\frac{n}{t} \approx \frac{1}{h}$$

Thus, handling time sets the max feeding rate in the model. Yields asymptotic functional response (fig. 6.6)

FYI: substituting into Lotka-Volterra gives model identical to Michaelis-Menton enzyme kinetics

Type III: asymptotic, but feeding rate or α increases at low V

Figs. 6.7, 6.8

Predator-Prey Models

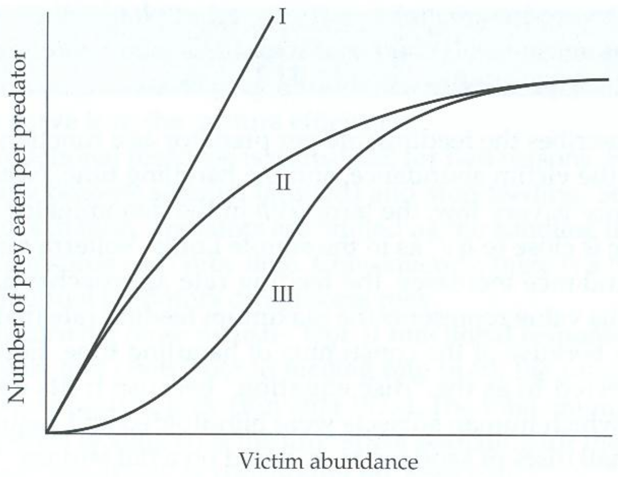


Figure 6.7 Type I, Type II, and Type III functional responses.

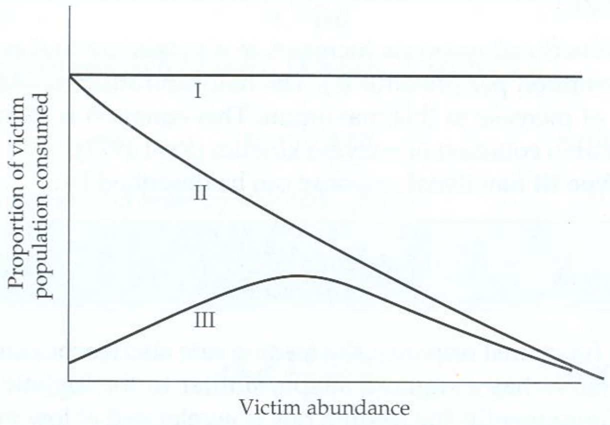


Figure 6.8 The proportion of the victim population consumed by an individual predator as a function of victim abundance.

Predator-Prey Models

Summary: If predator number held constant, no predator can avoid handling time limitation over all V.

Type II and III models are useful & general

Type II & III yield unstable equilibria…

If V exceeds asymptotic functional response, prey escape predator regulation…

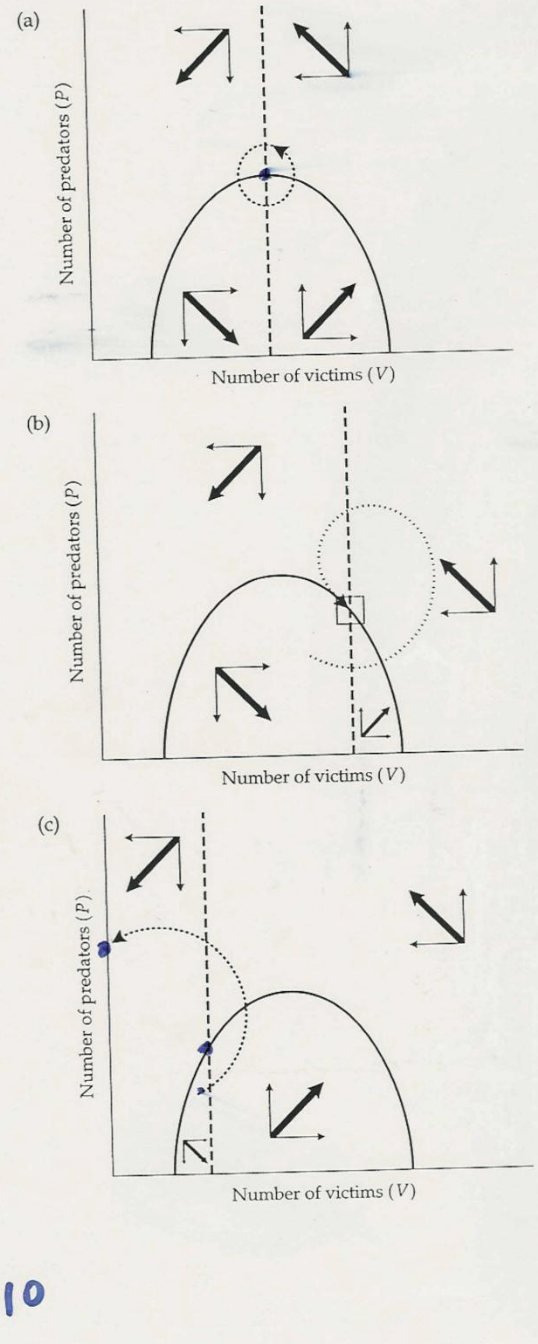
Thus, key is probably numerical and aggregative responses in nature.

Paradox of Enrichment

Victim isocline is humped as in Allee Effect

… example, large prey pops may defend against or avoid predators better

In this case, outcome depends on where the vertical predator isocline meets the prey isocline (fig. 6.10)



Paradox of Enrichment

Outcomes:

At peak, yields cycles

1) To right of peak, converge on stable equilibrium … efficient predator
2) To left of peak, unstable equilib with potential for predator over exploitation
   - Predator too efficient; high α or low q

Option 3 may explain observation called Paradox of Enrichment

-artificial enrichment with nutrients leads to pest outbreaks (fig. 6.11)

Paradox of Enrichment

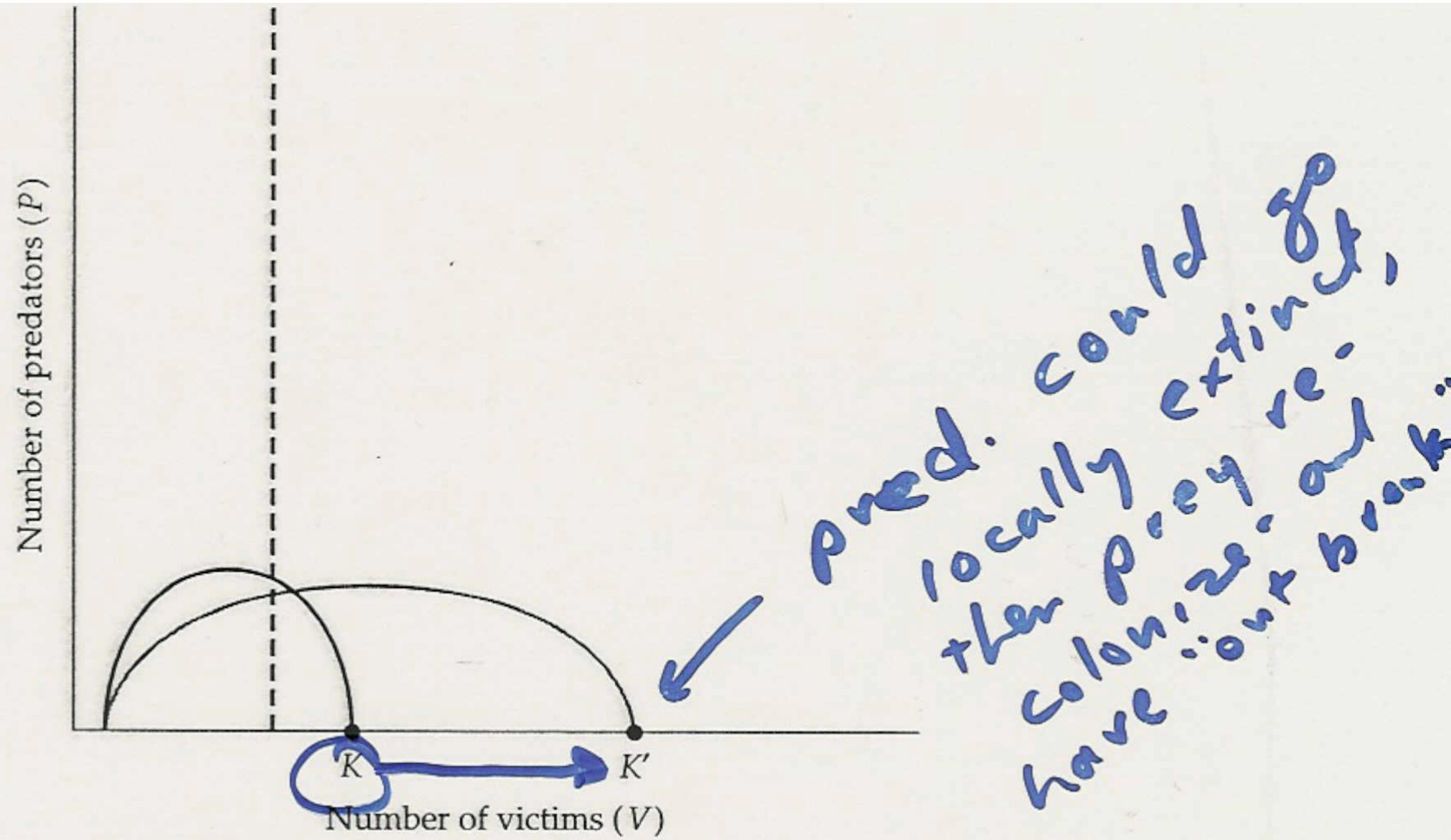


Figure 6.11 The paradox of enrichment. If the victim population has its carrying capacity enhanced from K to K', the system moves from a stable equilibrium to over-exploitation by the predator.

Ratio-Dependent Models

Lotka-Volterra model population response as product of pred and prey populations

$$\frac{dP}{dt} = \beta VP - qP$$

$$\frac{dV}{dt} = rV - \alpha P$$

Michaelis-Menton chemical equation

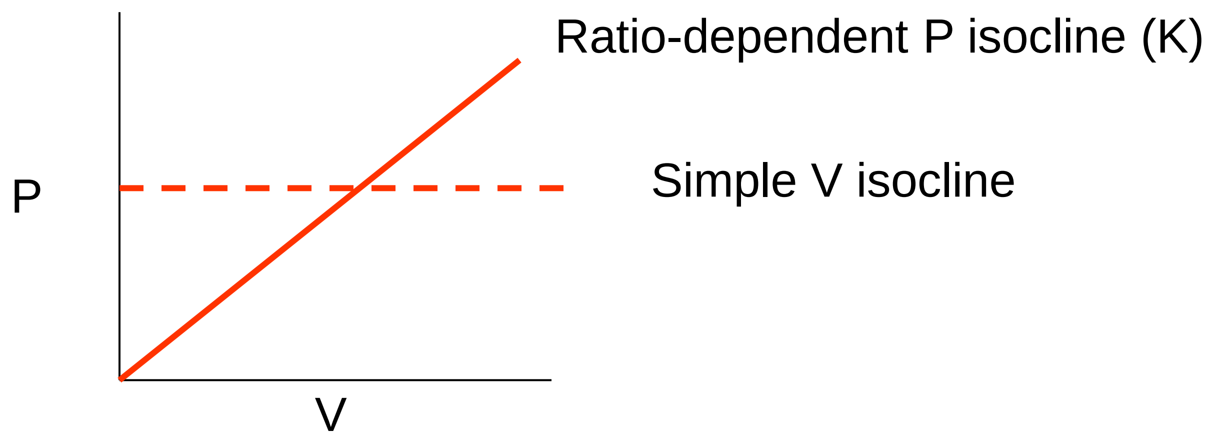
Leslie proposed ratio-dependence (logistic form)

$$\frac{dP}{dt} = \beta P\left\{1 - e\left(\frac{P}{N}\right)\right\}$$

Where e = marginal subsistence demand for prey and N/e is the predator K with constant prey

Ratio-Dependent Models

Basically yields models where predator isocline is a fraction of prey density… prey density sets predator K



Many permutations possible, see Berryman 92

Fig 6.15

Type II functional response yields pred-prey ratio dependence

Ratio-Dependent Models

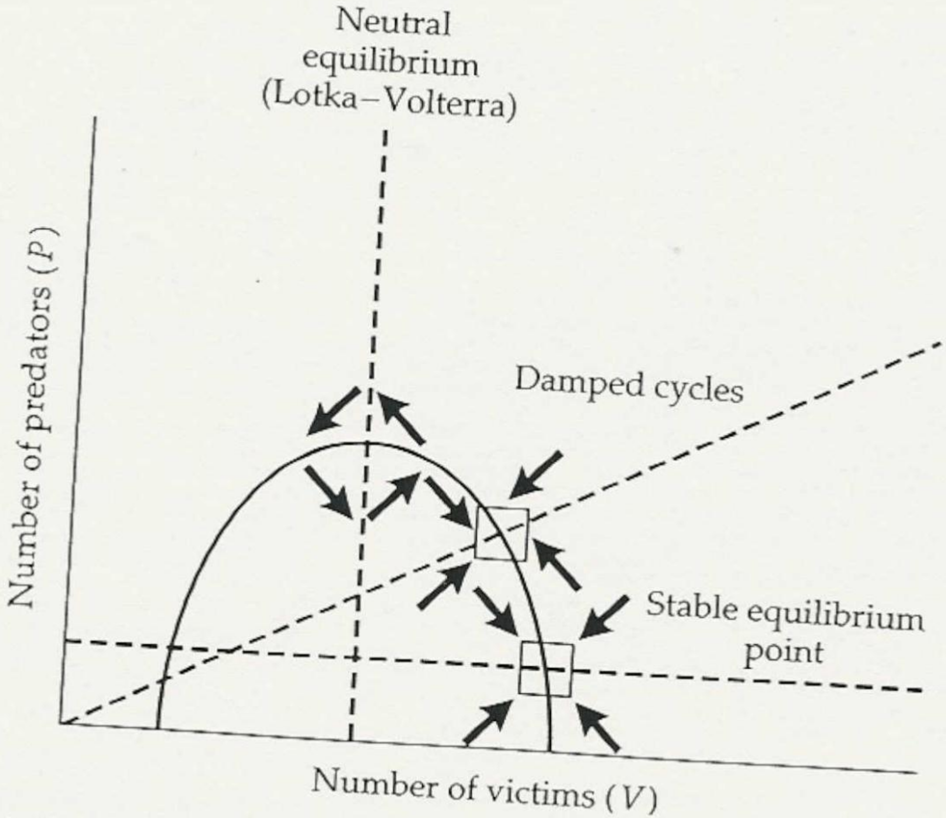


Figure 6.15 Effects of clockwise rotation of the predator isocline. As the predator isocline is rotated, the dynamics change from cycles with a neutral equilibrium, to damped cycles, to a stable equilibrium point. Biologically, the three predator isoclines correspond to a predator that is a complete specialist on the victim, to one whose carrying capacity is proportional to victim density, to one whose carrying capacity is independent of victim density.

Ratio-Dependent Models

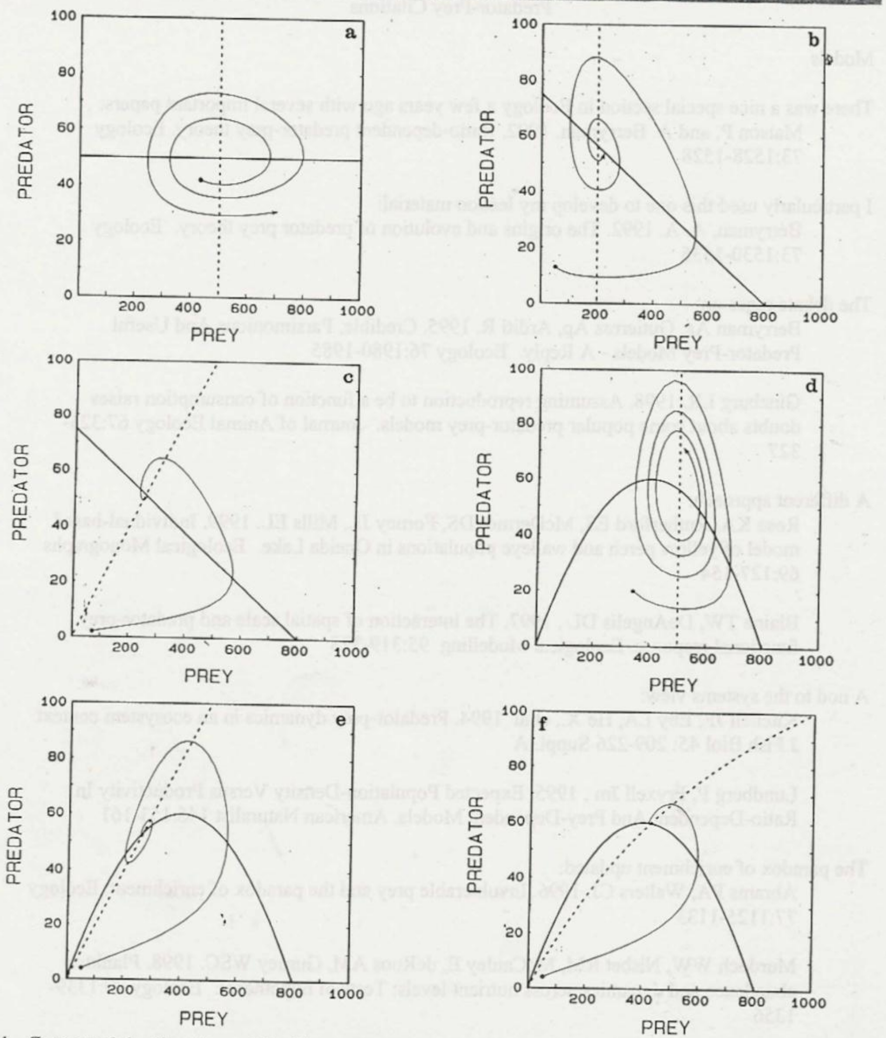


FIG. 1. Zero-growth isoclines for models of interacting prey (——) and predator (- - -) populations. The thin line is a trajectory predicted by the discrete-time per-capita trophic model, Eqs. 8 and 9 (see Berryman 1990); i.e., $N_{i,t} = N_{i,t-1}\exp\{a_i + b_i N_{i,t-1} + c_i Z_i\}$, where $i = 1$ for prey and $i = 2$ for predator, Z_i is the predator/prey ratio, $N_{2,t-1}/(w_1 + N_{1,t-1})$, in ratio models and $Z_1 = N_{2,t-1}$, $Z_2 = N_{1,t-1}$ in Lotka-Volterra models. (a) Lotka-Volterra-Nicholson-Bailey model: $a_1 = 0.2$, $b_1 = 0$, $c_1 = -0.004$, $a_2 = 0.1$, $b_2 = 0$, $c_2 = 0.0002$. (b) L-V-N-B model with *logistic* self-limitation on the prey: prey model with parameters the same as (a) except $a_1 = 0.3$ and $b_1 = -0.0004$; predator model the same as (a) except $c_2 = 0.0005$. (c) *Logistic-*Leslie predator equation: prey model as in (b); *ratio* predator with $a_2 = 0.2$, $b_2 = 0$, $c_2 = -1$, $w_1 = 0$. (d) Holling-Rosenzweig-MacArthur model: *ratio* prey model with $a_1 = 0.3$, $b_1 = -0.0004$, $c_1 = -1$, $w_1 = 0$; predator model as in (a), $a_2 = -0.5$, $b_2 = 0$, $c_2 = 0.001$, $w_1 = 0$. (e) *Logistic* predator–prey model with no predator self-limitation: prey model as in (d); predator model as in (c). (f) *Logistic* predator-prey model with predator self-limitation: prey model as in (d); predator model as in (c) except $b_2 = -0.001$.

Berryman 1992 Ecology 73:1530-1535

Ratio-Dependent Models

Problems from traditional models

- Link fast parameters (foraging) with slow parameters (population growth) [Slobodkin 92]

Functional responses are variable

Very few predators have only one prey type

ETC

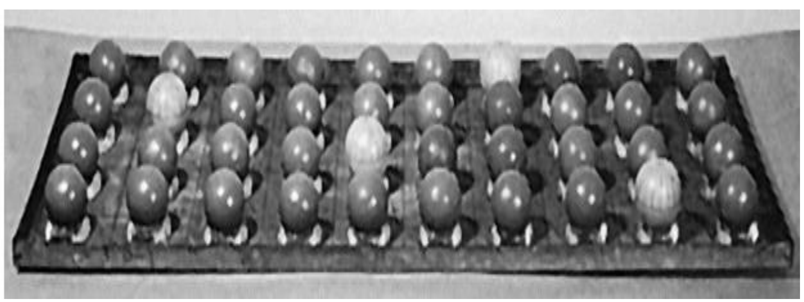
See Arditi and Ginzburg. 2012. How Species Interact. Oxford Univ Press.

Predation for Biological Control?

"Natural Enemies"

Huffaker mites on oranges

Efficient predator drove prey extinct, then went extinct



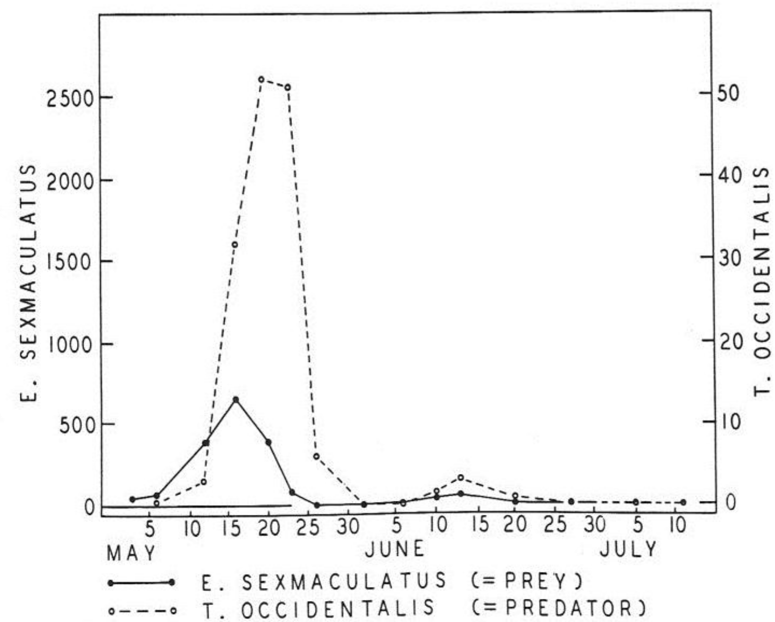


Fig. 11. Densities per orange-area of the prey, *Eotetranychus sexmaculatus*, and the predator, *Typhlodromus occidentalis*, with 6 large areas of food for the prey (orange surface) grouped at adjacent joined positions—a 6-orange feeding area on a 6-orange dispersion (no photograph of this exact arrangement, but it was similar to that of figure 3 except that 6 whole oranges were used; see text, Subsection C, Section II of "Results").

Predator-Prey Metapopulations

By adding spatial complexity to the experiment, made predator inefficient enough to cycle 3-4 times before extinction

Conclusion: Want efficient bio control agent, but efficient predators are unstable!

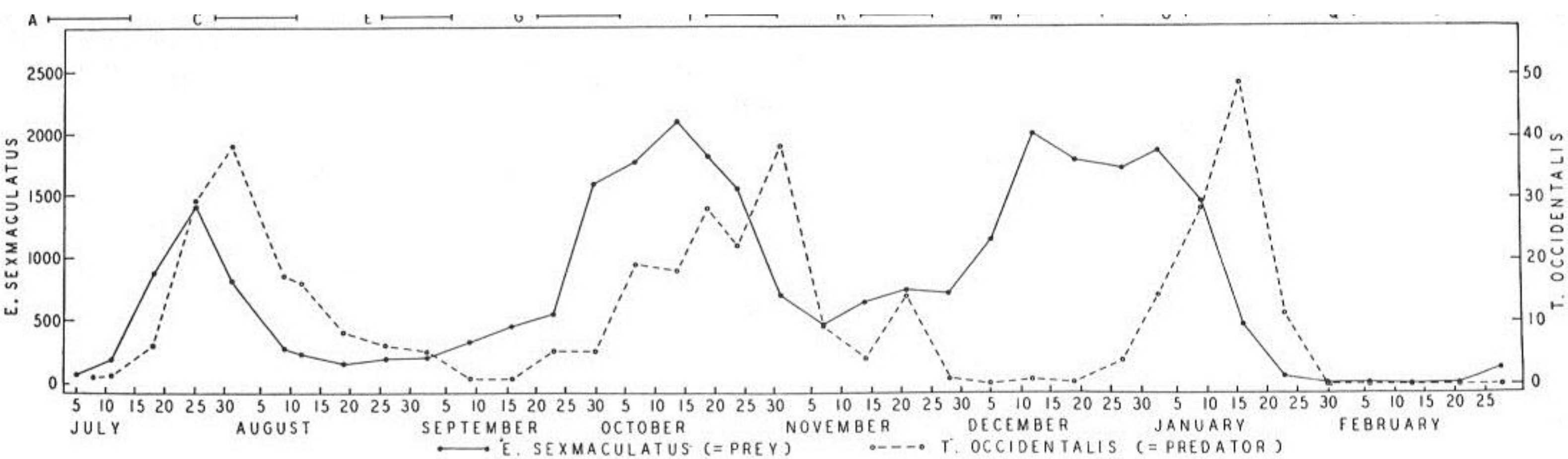


Fig. 18. Three oscillations in density of a predator-prey relation in which the predatory mite, *Typhlodromus occidentalis,* preyed upon the orange feeding six-spotted mite, *Eotetranychus sexmaculatus.*

The graphic record below shows the sequence of densities per orange-area, while the pictorial record, charts A to R, above, shows both *densities* and *positions* within the universe. The horizontal line by each letter "A," "B," et cetera, shows the period on the time scale represented by each chart. A photograph of the arrangement of this universe is shown in figure 5 and a sketch of the complex maze of vaseline partial-barriers in figure 19—a 6-orange feeding area on a 120-orange dispersion (see text, Subsection I, Section II of "Results").

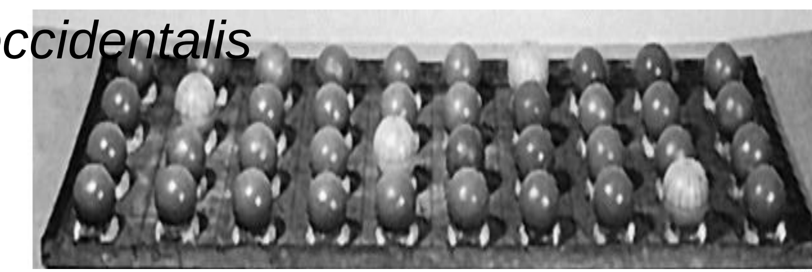
Predator-Prey Metapopulations

Huffaker's 1958 mites on oranges

A: empty orange
B: *E. sexmaculatus* (prey) only
C: *E. sexmaculatus & T. occidentalis* (predator)

A+B+C=1

r_1: per patch *E. sexmaculatus* colonization rate
r_2: per patch *T. occidentalis* colonization rate
r_3: extinction rate of *E. sexmaculatis* & *T. occidentalis*



$$\Delta A = -r_1 AB + r_3 C$$
$$\Delta B = +r_1 AB - r_2 BC$$
$$\Delta C = +r_2 BC - r_3 C$$

$$\hat{A} = (r_2/r_1)\hat{C}$$
$$\hat{B} = r_3/r_2$$