Predation

Predation

All organisms are subject to various sources of mortality (starvation disease, physical injury, and predation)

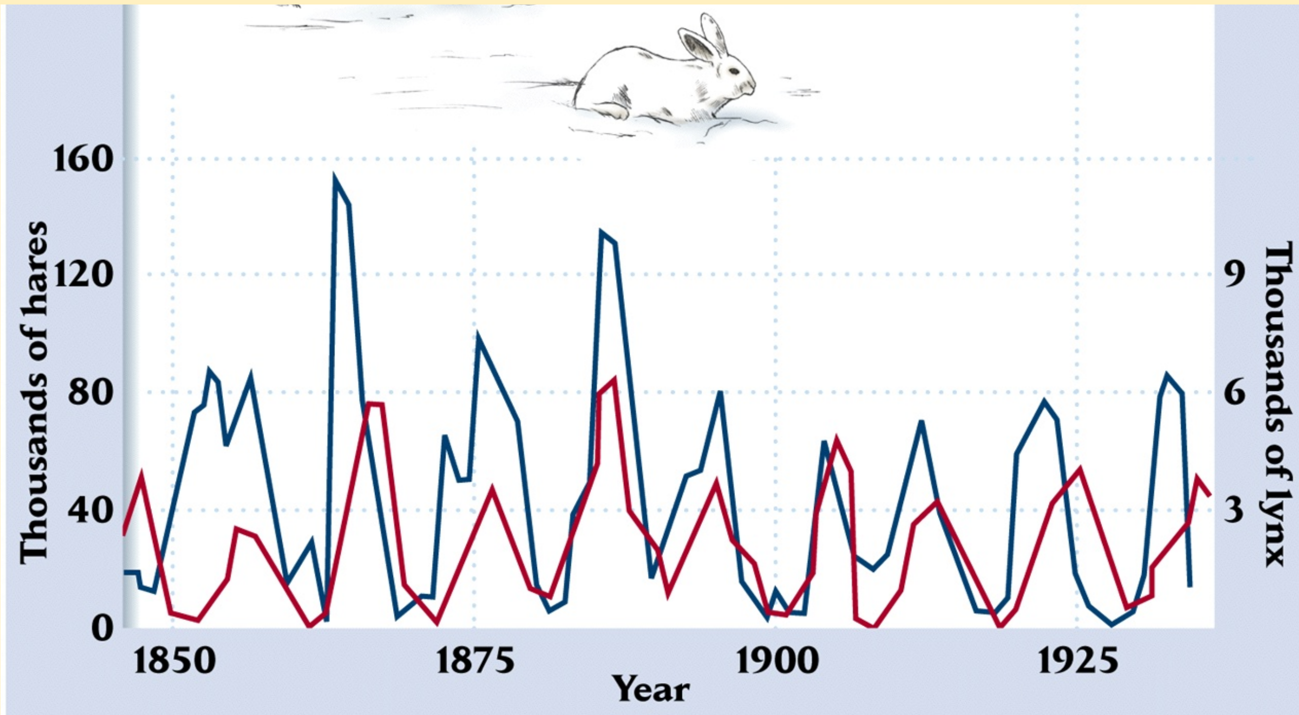
Understanding how much ‘natural’ mortality populations receive is critical to managing populations that we exploit (e.g. fisheries)

Models of predation need to consider predator effect on prey populations, and prey effects on predator population (prey ‘value’ to predator). Also need to consider the time spent searching, subduing and consuming prey.

Predation models

Interested in describing conditions where predators and prey can coexist

Interested in understanding observed fluctuations in predator and prey population densities



Lotka-Volterra predator-prey models

First consider the prey (*V*):

Prey in the absence of predators:

$dV/dt = rV$

Where V = prey (victim) population, r = intrinsic rate of increase

Prey in the presence of predators (P)

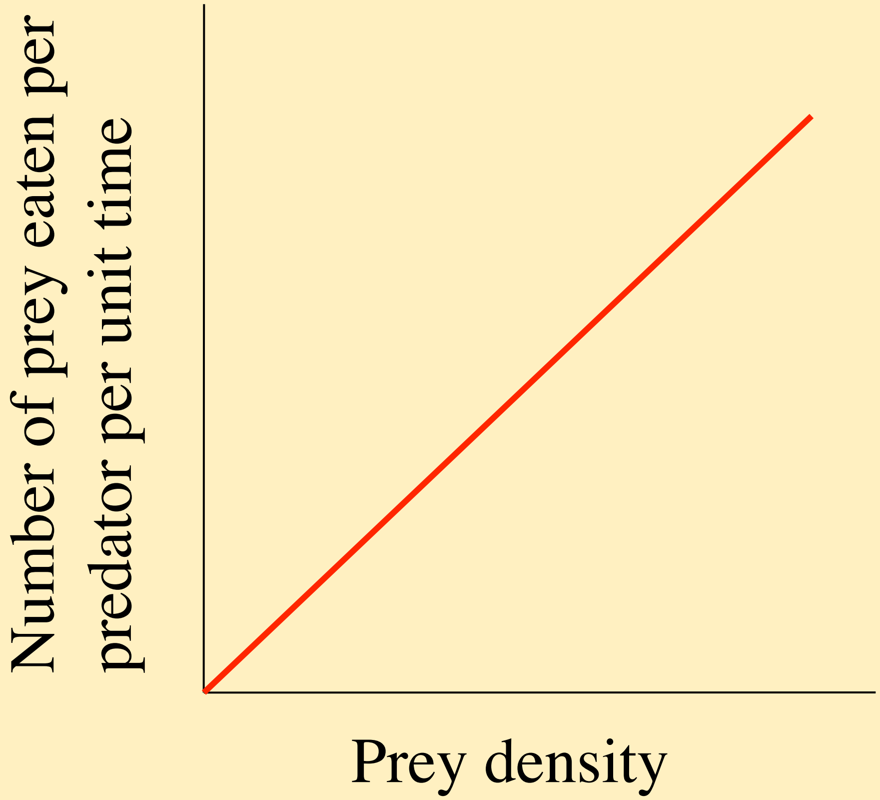
$dV/dt = rV - \alpha VP$

Where αVP is the loss to predators

Loss to predators is determined by the product of predator and victim numbers (assumes predators and prey move randomly through the environment) and the **capture efficiency**, α

α is also measure of the effect of the predator on the per capita growth rate of prey

Here αV also represents the **functional response** of the predator (this describes *how the rate of prey capture is affected by prey abundance*). In this case, the functional response is linear - capture rate increases at a constant rate as prey density increases. The slope of capture rate will be determined by alpha



αV is a linear functional response

Now consider the predator:

In the simplest form of the model, the predator is *specialized* on just one prey species - therefore in the absence of prey, the predator population declines exponentially:

$dP/dt = -qP$ where P is the predator population size, and q is the per capita death rate (*NB: Symbols vary from book to book!*)

No prey – predator population declines at a constant (density-independent) rate determined by q

Positive predator population growth occurs when prey are present as follows:

$dP/dt = \beta VP - qP$

Where β is the **conversion efficiency** - the ability of predators to turn prey into additional per capita growth rate for the predator population.

When β is high a single prey item is valuable (killing a Woolly Mammoth…).

βV is called the **numerical response** of the predator population - *the per capita growth rate of the predator population as a function of the prey population*.

Just like Volterra competition model…

Solve for the equilibrium population sizes of predators and prey, then plot solutions on a state space graph

Start with the prey population…

$dV/dt = rV - \alpha VP$

$0 = rV - \alpha VP$

$rV = \alpha VP$ (oops - we lost the prey population!!)

$r = \alpha P$

… end up with the equilibrium number of predators

Equilibrium $P = r/\alpha$

A specific number of *predators* will keep the prey population at zero growth. How many depends on the ratio of the growth rate of prey to the capture efficiency of the predators.

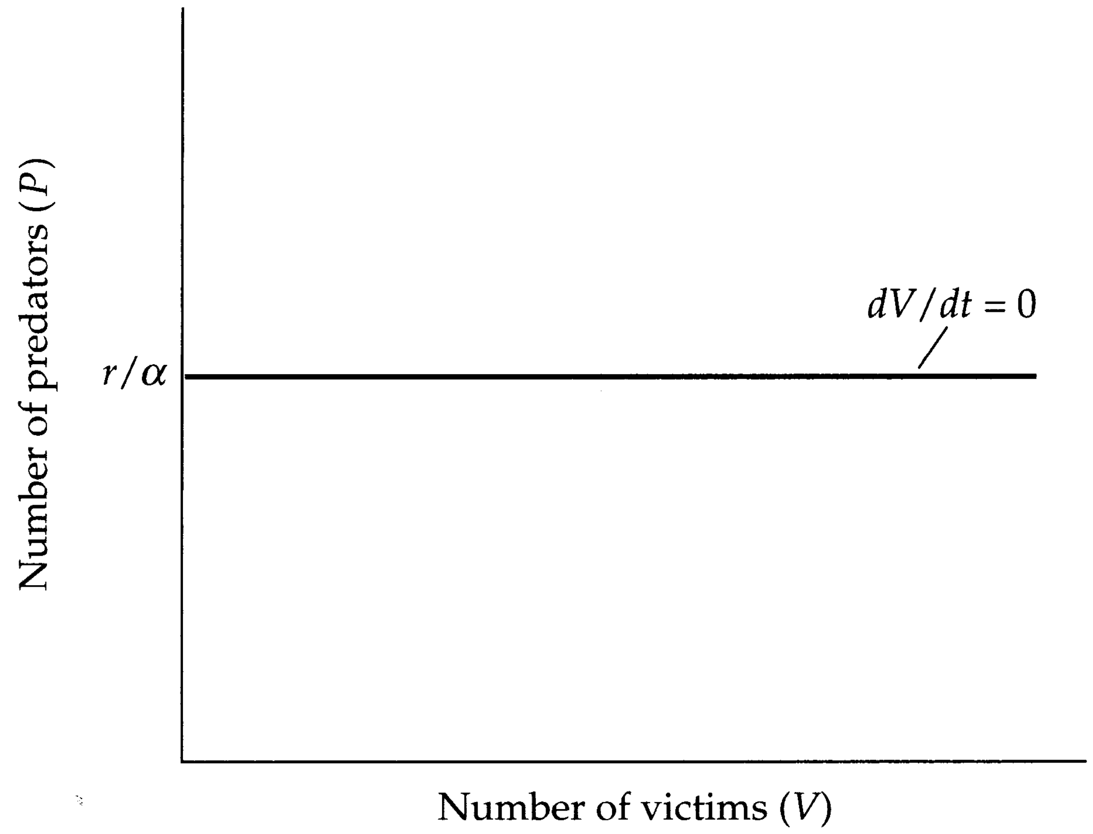
How about the predator population?

$dP/dt = \beta VP - qP$
$0 = \beta VP - qP$
$\beta VP = qP$ (lose the predators)
$\beta V = q$

Equilibrium V (number of prey needed to maintain a constant population of predators) = q/β

Number of prey needed depends on the ratio of the death rate of predators to the conversion efficiency of predators

Can plot prey (V) zero growth isocline in state space



Can plot prey (V) zero growth isocline in state space

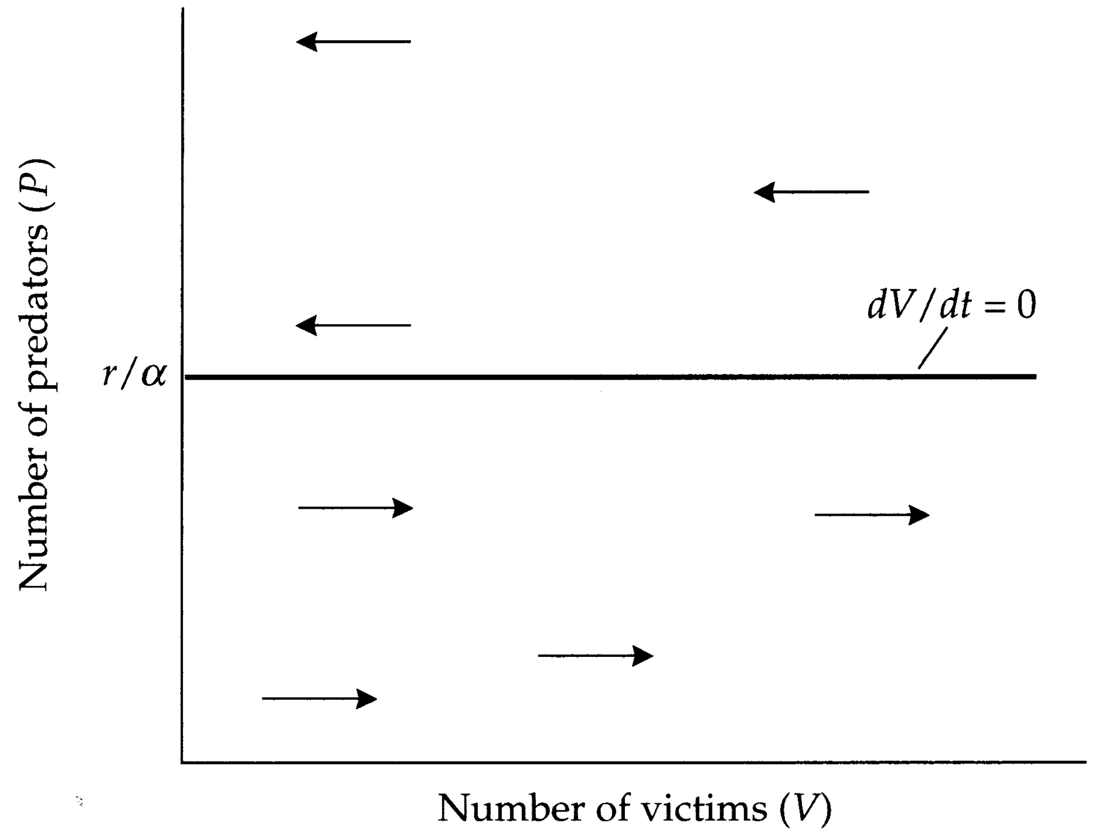
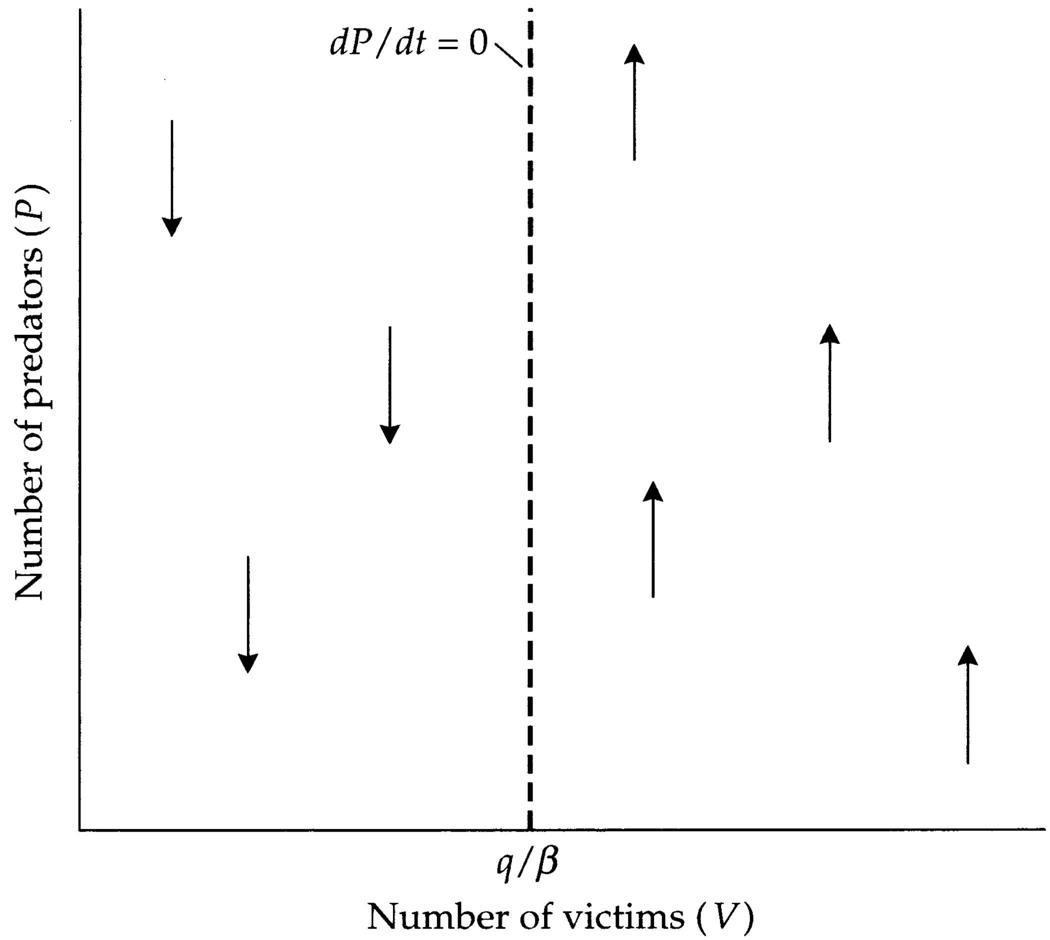


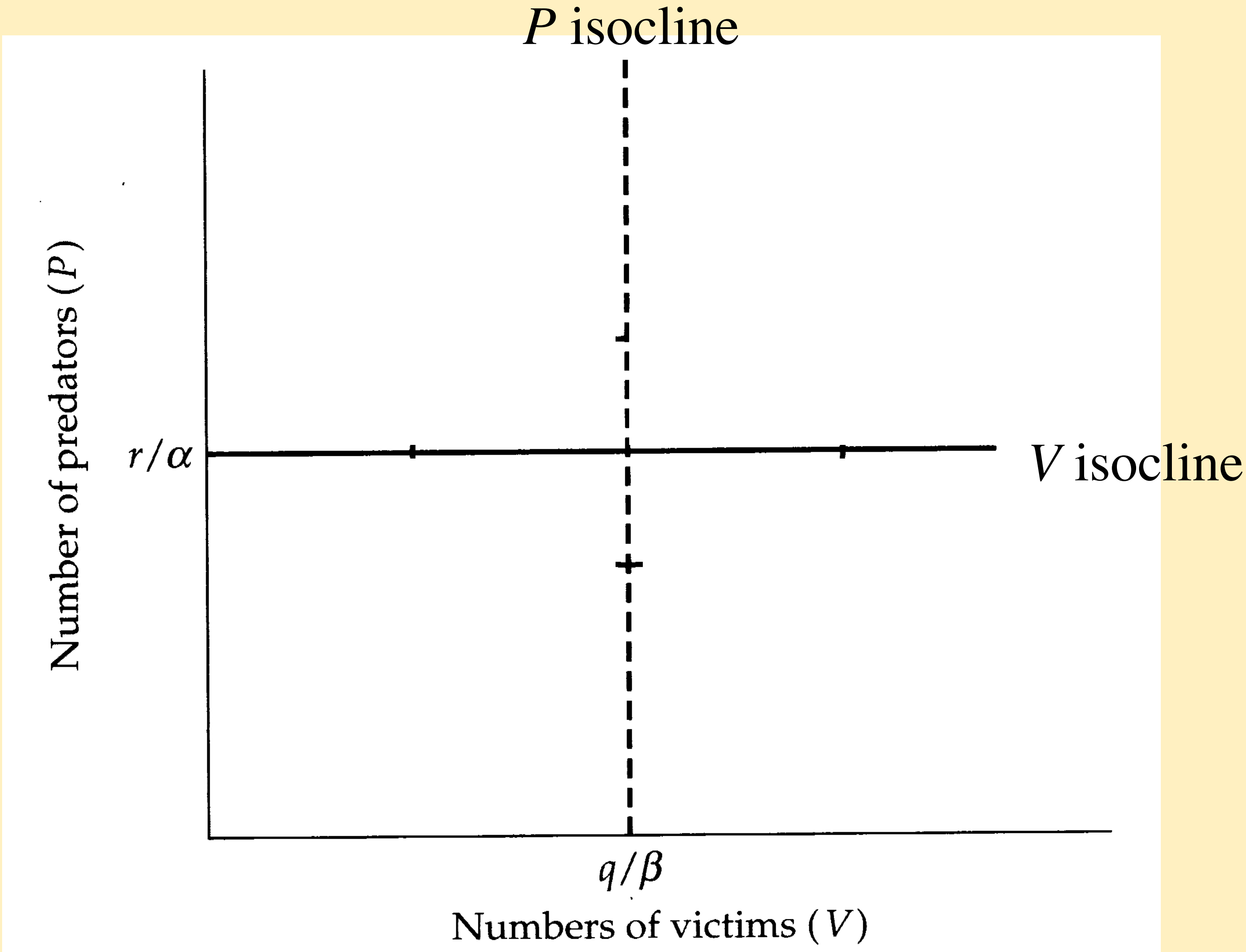
Figure 6.1 The victim isocline in state space. The Lotka–Volterra predation model predicts a critical number of predators (r/α) that controls the victim population. If there are fewer predators than this, the victim population increases (right-pointing arrows). If there are more predators, the victim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

Predator zero growth isocline (notice axes haven't changed)



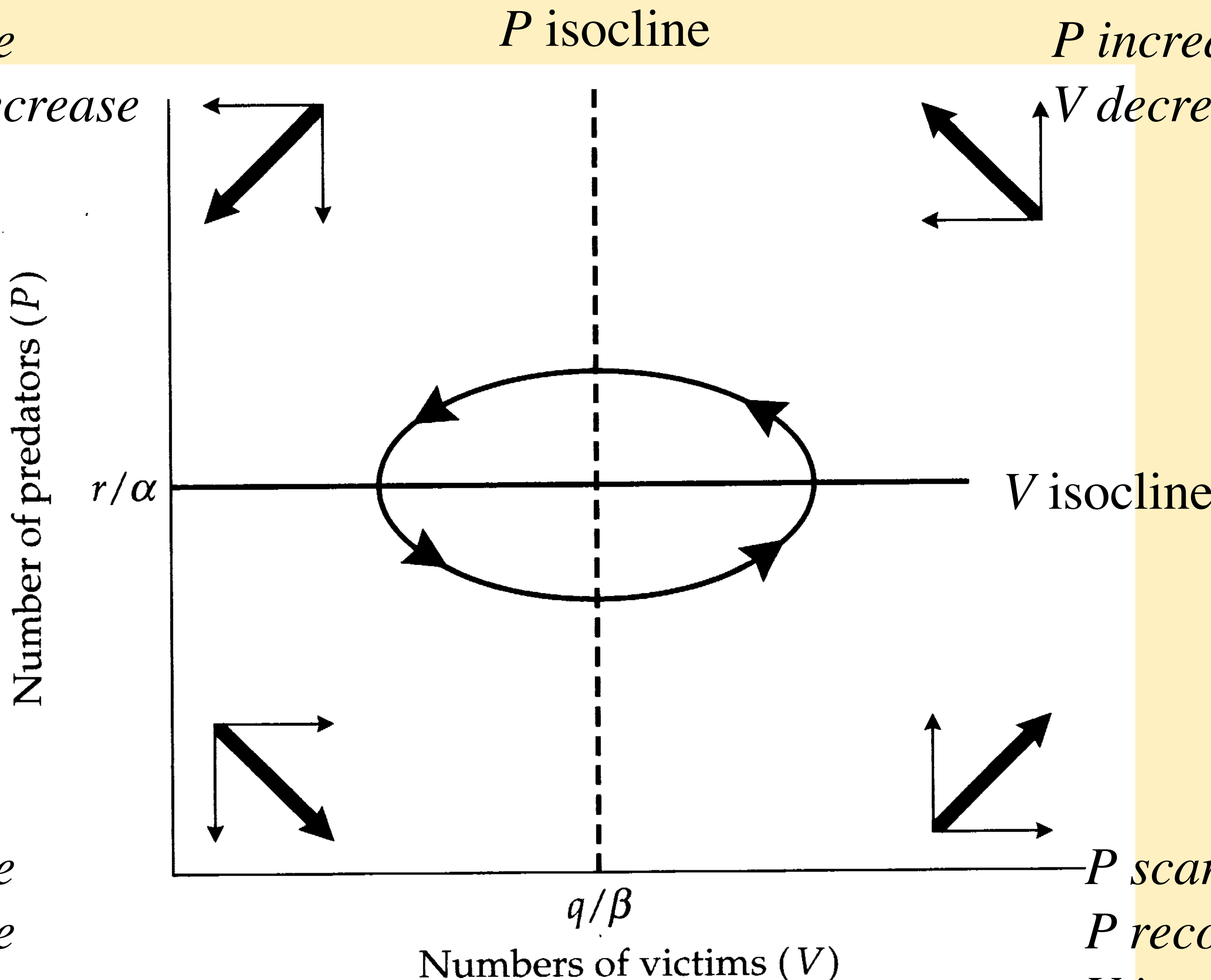
…more than a critical number of prey, then predator population will increase

What will happen to predator and prey numbers if they are *not* at the intersection of the zero growth isoclines?



P abundant
V scarce
P&V decrease

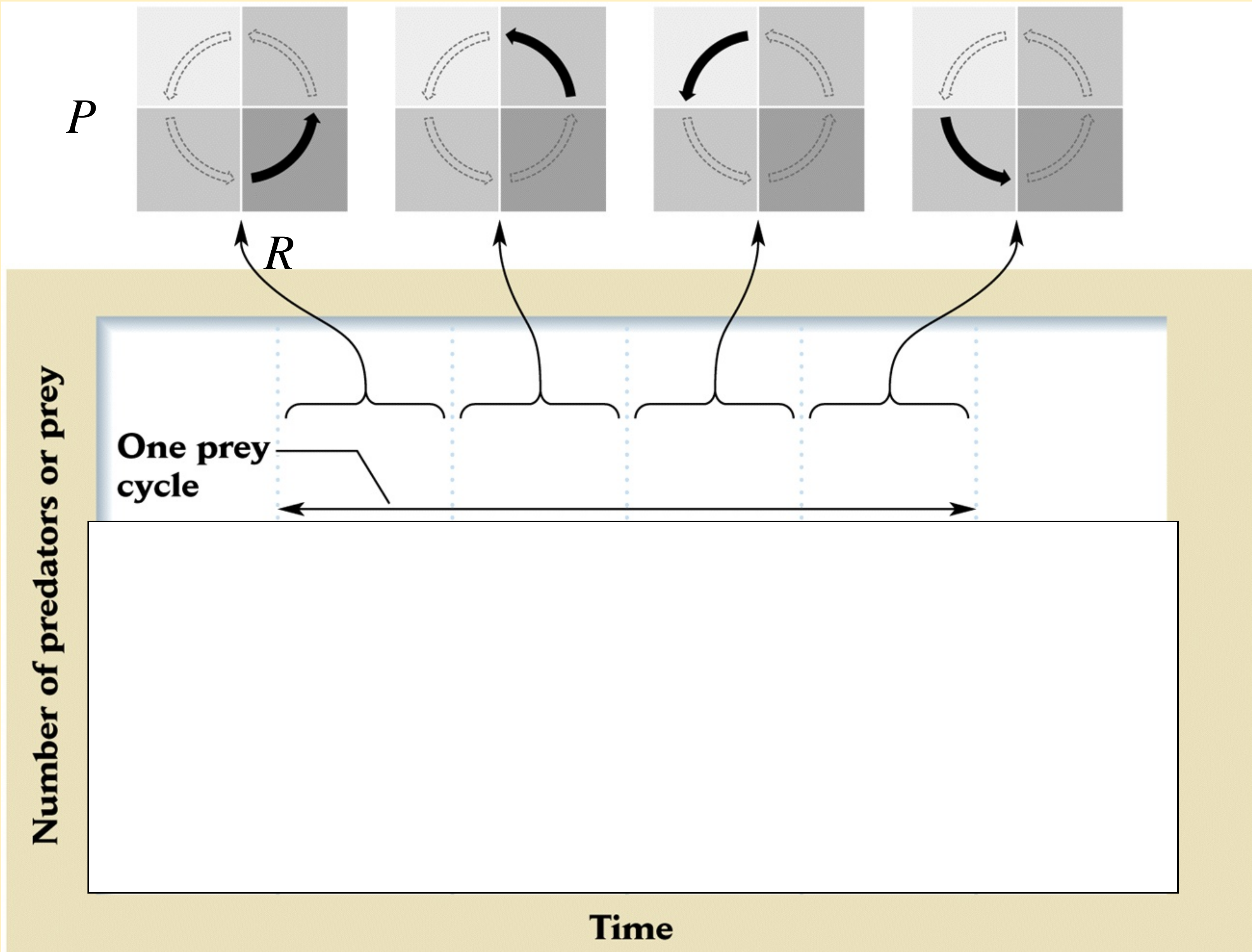
P&V abundant
P increases
V decreases



P scarce
V scarce
V recovers

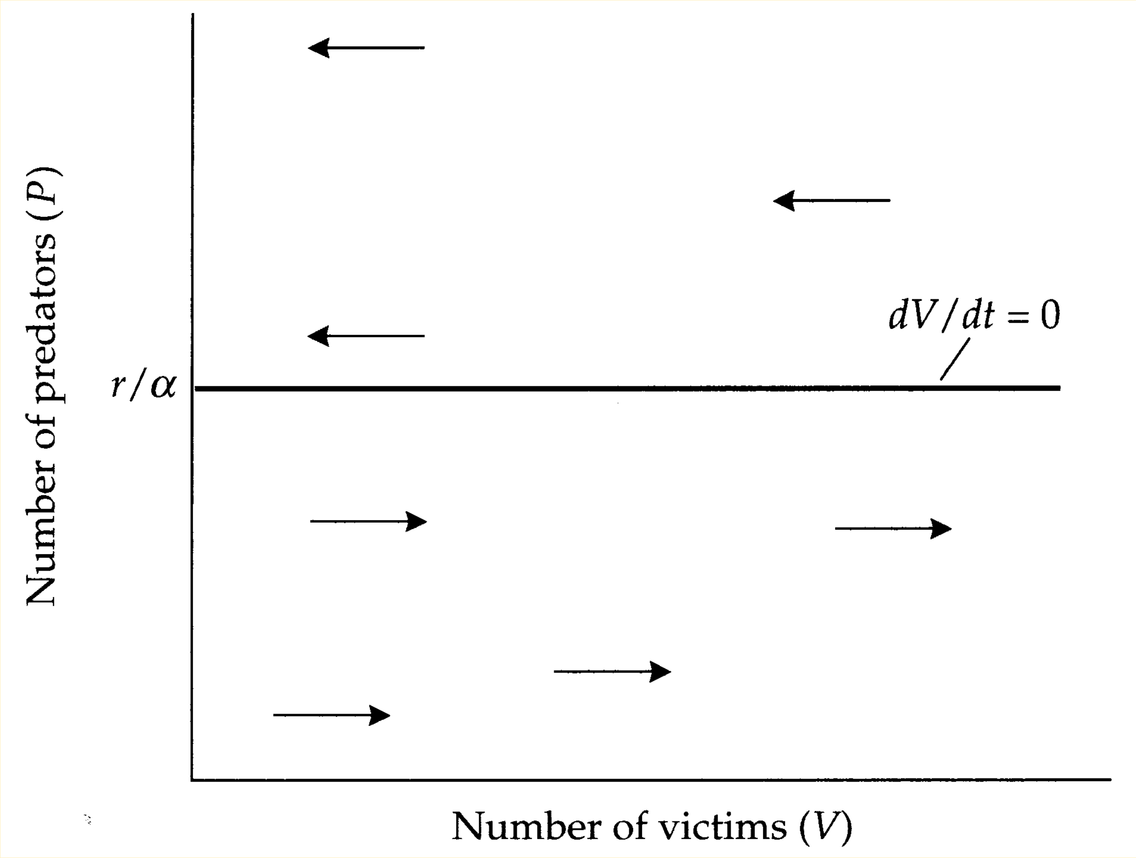
P scarce
P recovers
V increases

Neutral equilibrium cycle



Assumptions of the simple model:

1. Prey population growth is *only limited by predators* (no effect of K)
2. Prey zero growth isocline is *horizontal* - therefore predators can consume an infinite number of prey (doesn't matter how many prey are present, one more predator is enough to drop prey population growth below zero)



Getting (a bit more) real…

Add a prey carrying capacity

$dV/dt = rV - \alpha VP - cV^2$

Where c is a constant

Now prey population growth will slow with increasing abundance even in the absence of predators

How will this alter the slope of the prey zero growth isocline?

There will be some prey density that cannot be exceeded - so zero growth isocline must intercept x axis (prey number)

Prey carrying capacity results in damped oscillations leading to equilibrium predator and prey populations

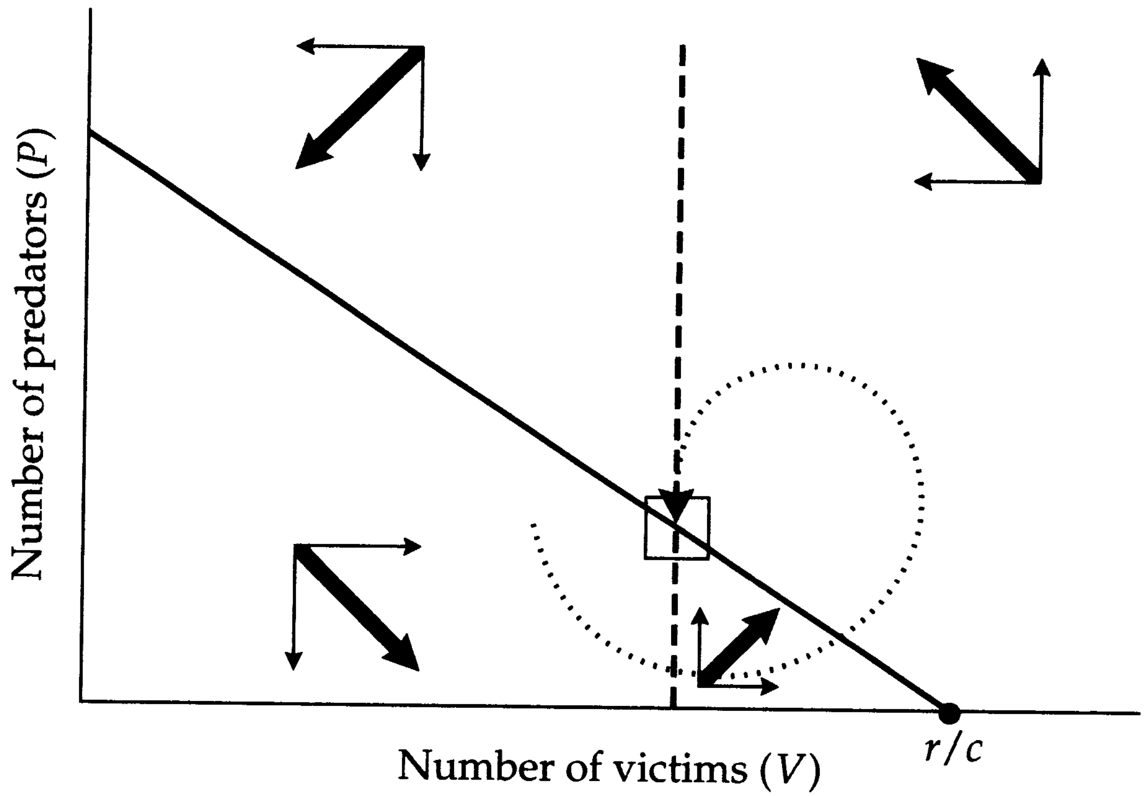


Figure 6.5 The effect of a victim carrying capacity on the victim isocline. The victim isocline slopes downward with a carrying capacity incorporated. The intersection with the vertical predator isocline forms a stable equilibrium point.

Can also make prey capture and consumption more realistic

• Existing model - predators increase prey consumption at a constant rate as prey abundance increases.

• Need to incorporate a non-linear *functional response* of predators to prey as predators are satiated

Holling's model: consider time needed to "handle" each prey (capture and consumption) (= t_h), and time to search for prey (=t_s).

Handling time (t_h), further broken down to:

h = per prey handling time
n = number of prey captured in time t *(capture rate)*
$t_h = hn$

Capture rate (n) in turn depends prey population size (V), capture efficiency (α), and time spent searching (t_s).

$n = \alpha V t_s$ so… $t_s = n/\alpha V$

So total feeding time (t) $= t_s + t_h$

$$= n/(\alpha V) + hn$$

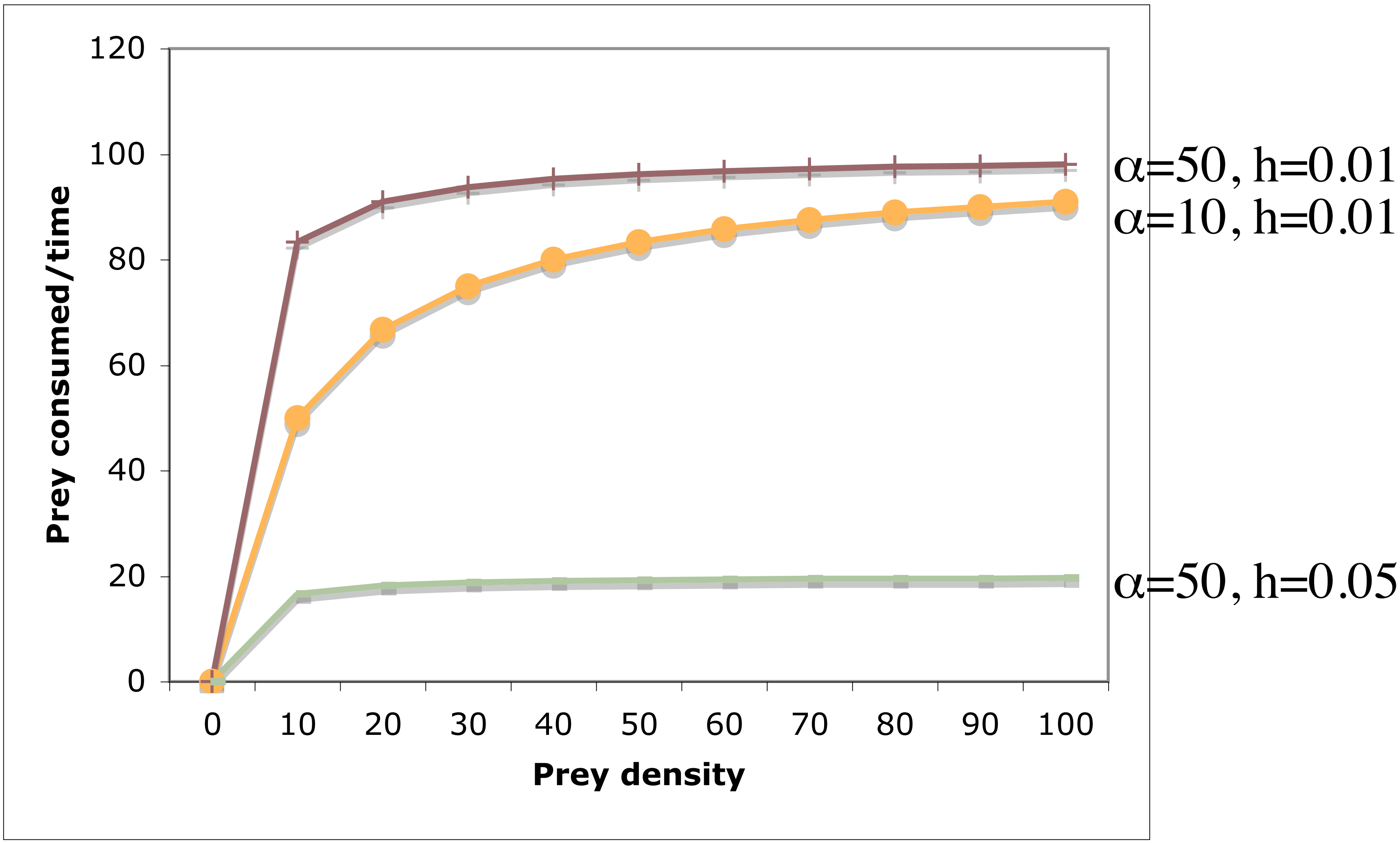
Gives us type II functional response

$n/t = \alpha V/(1+ \alpha V h)$

Type II response: predators can be satiated so that prey captured per predator per unit time reaches an asymptote

(functionally equivalent to Michelis-Menton equation)

High prey densities *n*/*t* determined by *h* (per prey handling time)



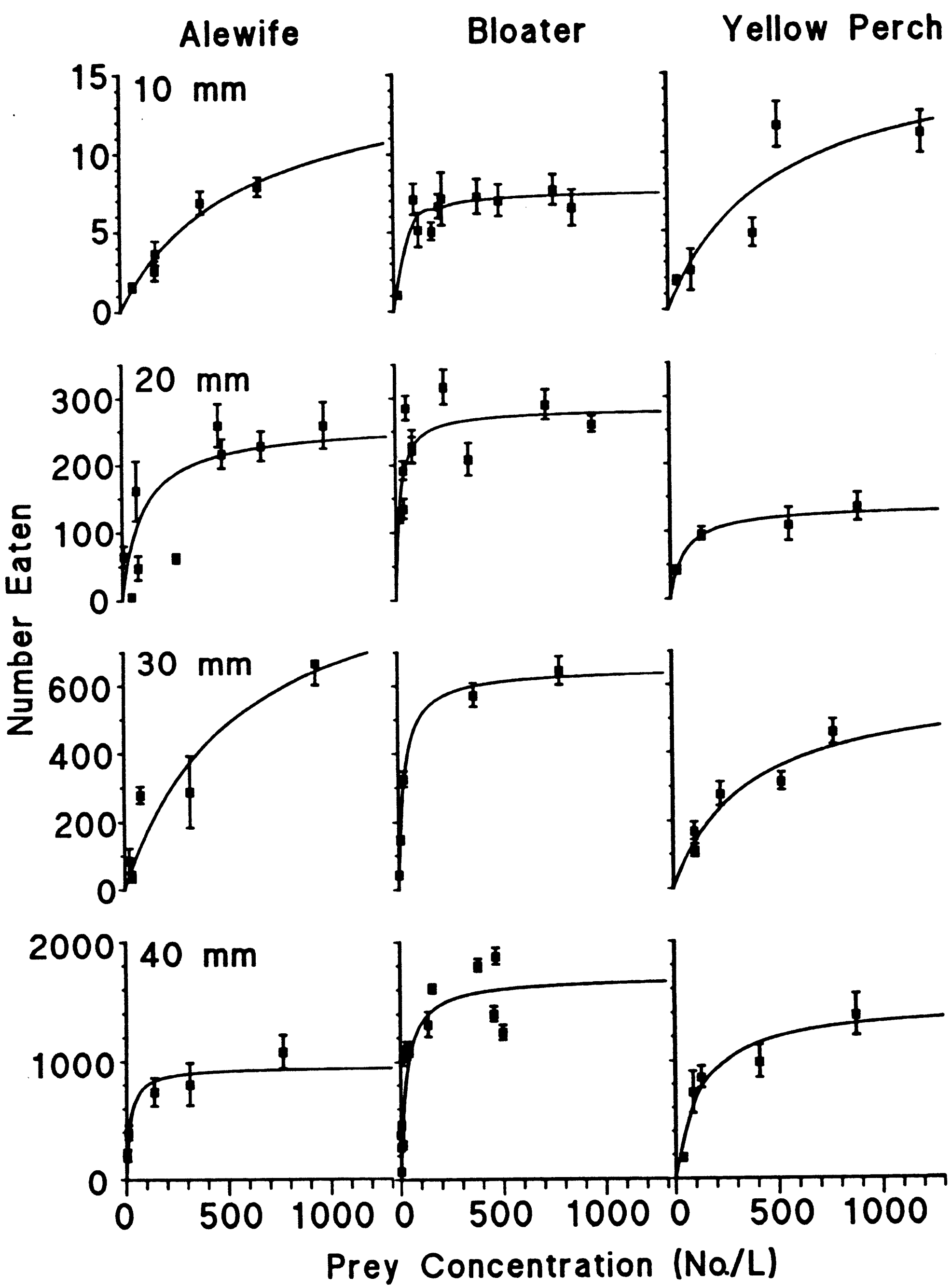
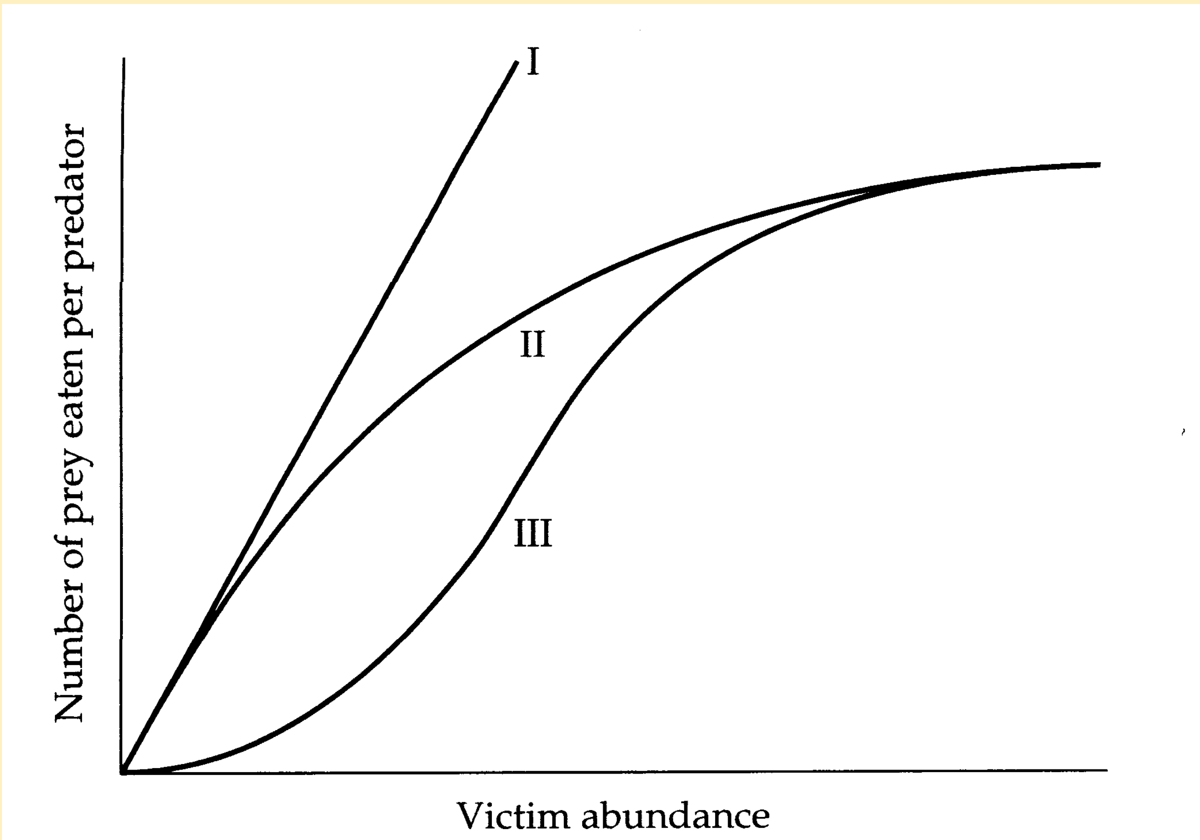


FIG. 1. Nonlinear regression estimates of functional response relationships based on Holling's type II equation (Eq. 1). Individual data are mean gut contents (± SE) of 10 like-sized fish from a single tank trial standardized to a 15-min exposure to a single concentration of *Artemia* prey.

Holling's Type II Functional response fits data on fish predation quite well...

3 different predators,
4 different predator sizes
Single prey species present at constant initial concentration

Sometimes a logistic function (III) better describes predator functional response (low consumption rate at low prey abundance). Why?



Type III might reflect more generalist predator behavior?

Type II or III without carrying capacity are not stable

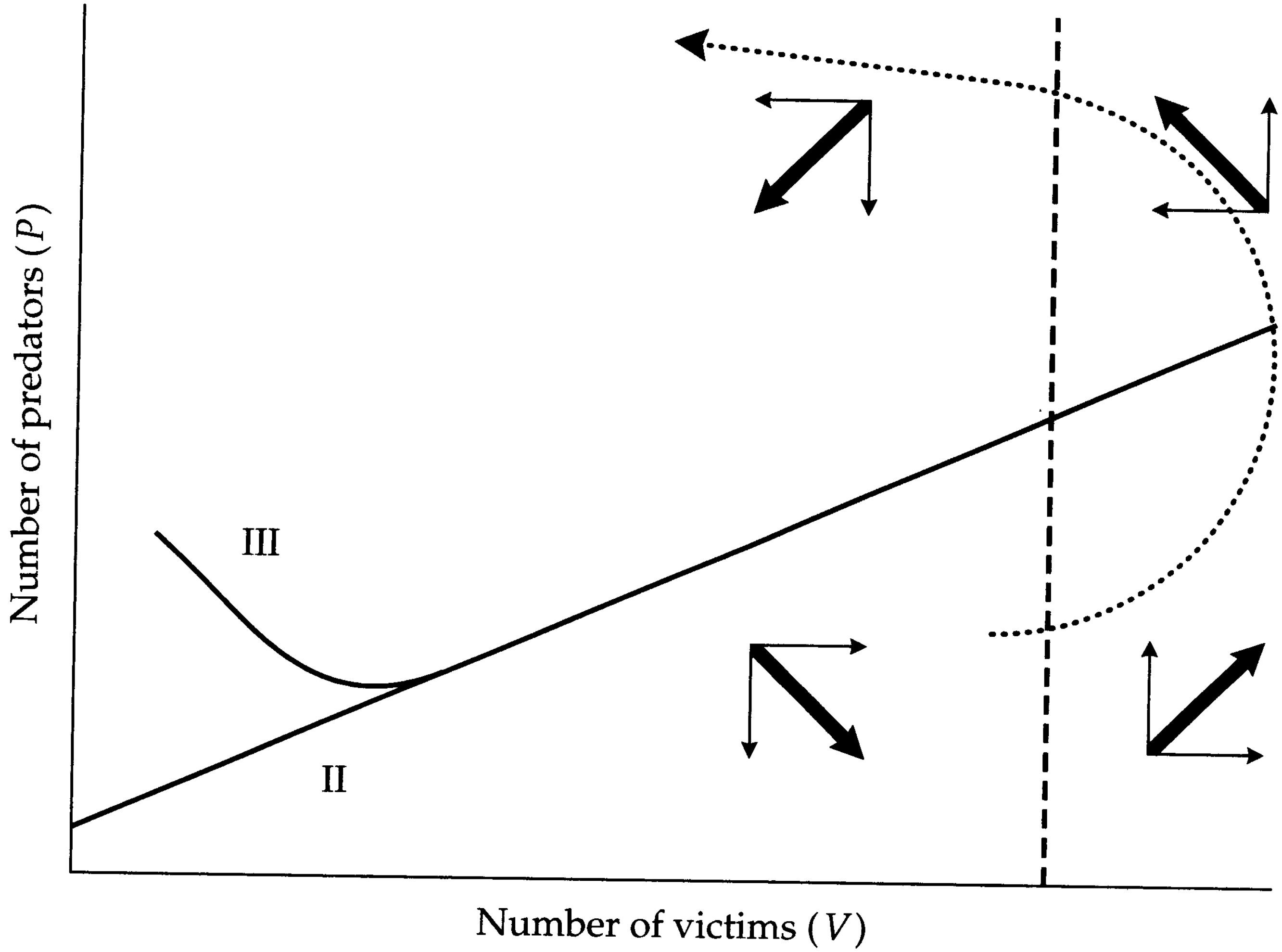
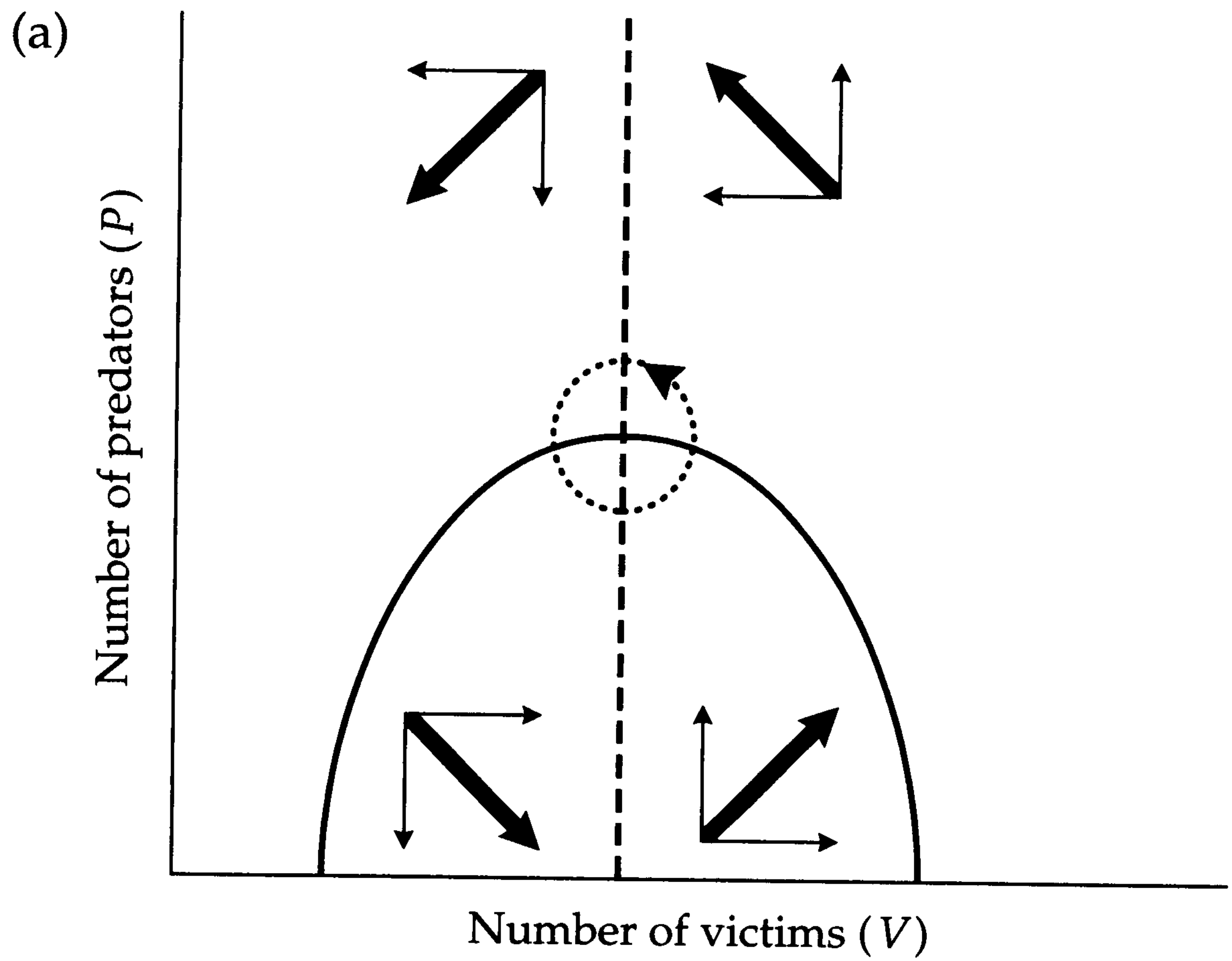
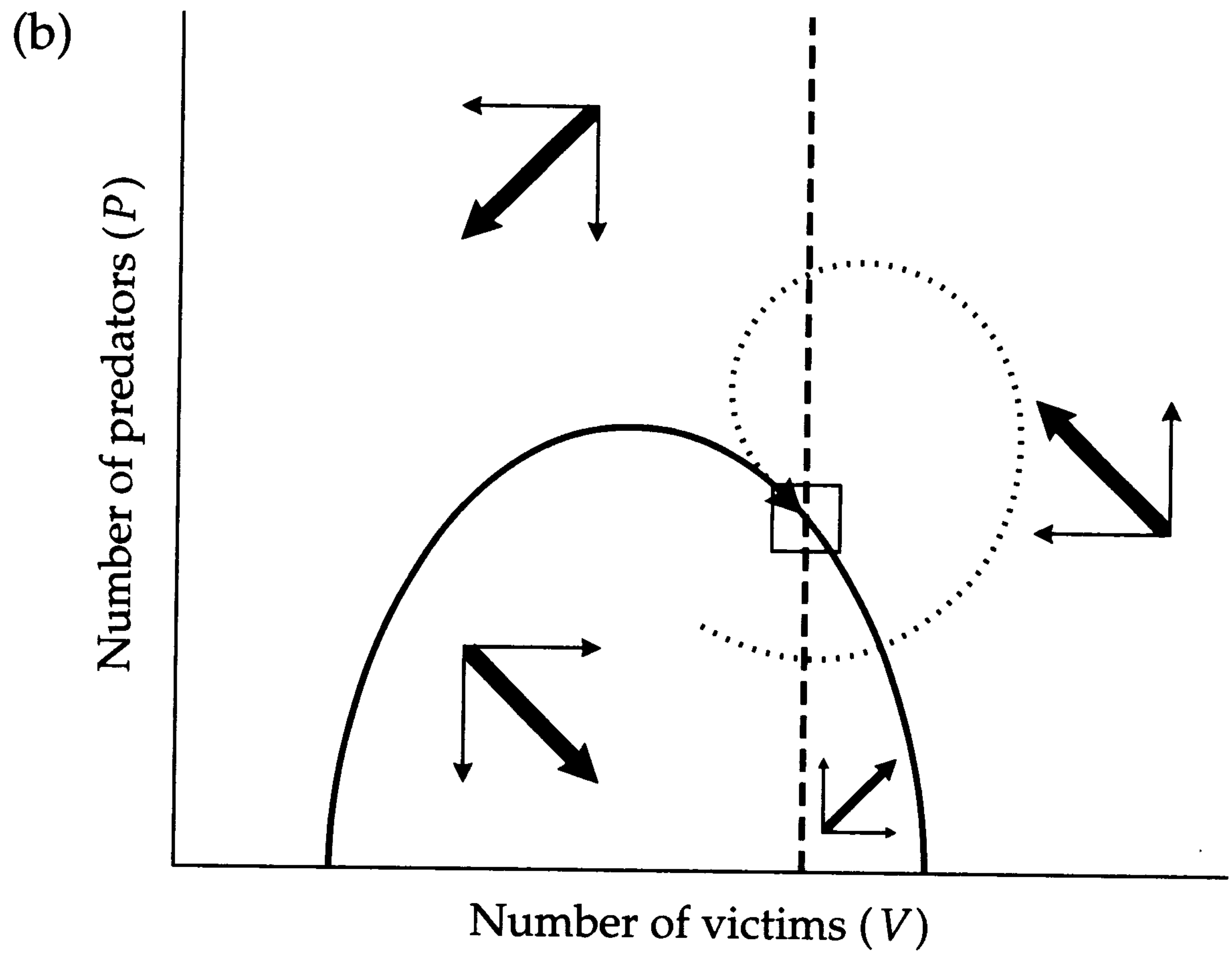


Figure 6.9 Victim isoclines incorporating a Type II or a Type III functional response. The intersection of an increasing victim isocline with a vertical predator isocline generates an unstable equilibrium point.

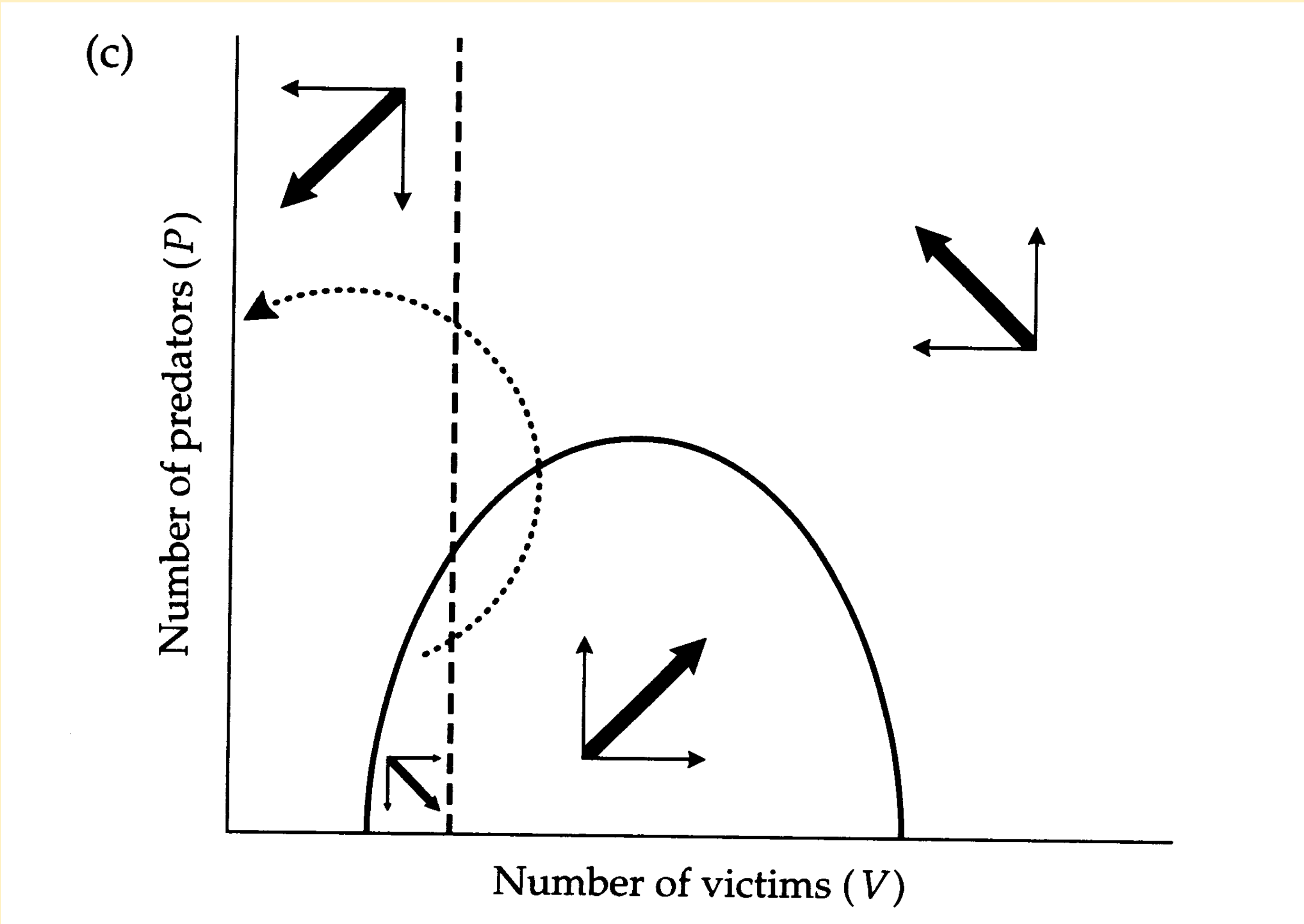
Most appropriate model yields humped prey isocline?



Inefficient predator: populations oscillate to equilibrium point



Efficient predator: stable limit cycle or extinction ("paradox of enrichment")



Greater opportunity for predator to drive down prey density despite increased prey carrying capacity

Paradox of enrichment (Rosenzweig 1971 Science 171:385-387)

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.

…depends on the assumption of a vertical predator isocline

Predation model predictions

- Simplest Lotka-Volterra. Linear functional response no *K* = neutral stability
- L-V model with *K* = stable equilibrium
- No *K*, type II or III functional response = unstable
- Hump shaped prey isocline, vertical predator isocline = neutral stability, stable equilibrium or prey extinction depending on intersection point

Modified - hump prey isocline:

Instead of a hump, the prey isocline may be expected to rise at low prey populations because:

- prey may find spatial refuges from predation at low densities (type III functional response)

- prey may immigrate into habitat containing low prey numbers

- kinked hump isoclines are inherently stable - predators can consume prey only down as far as the remaining prey population present in refuges or to the levels maintained by immigration (where prey isocline approaches vertical)

Effect of prey refuges and/or prey immigration

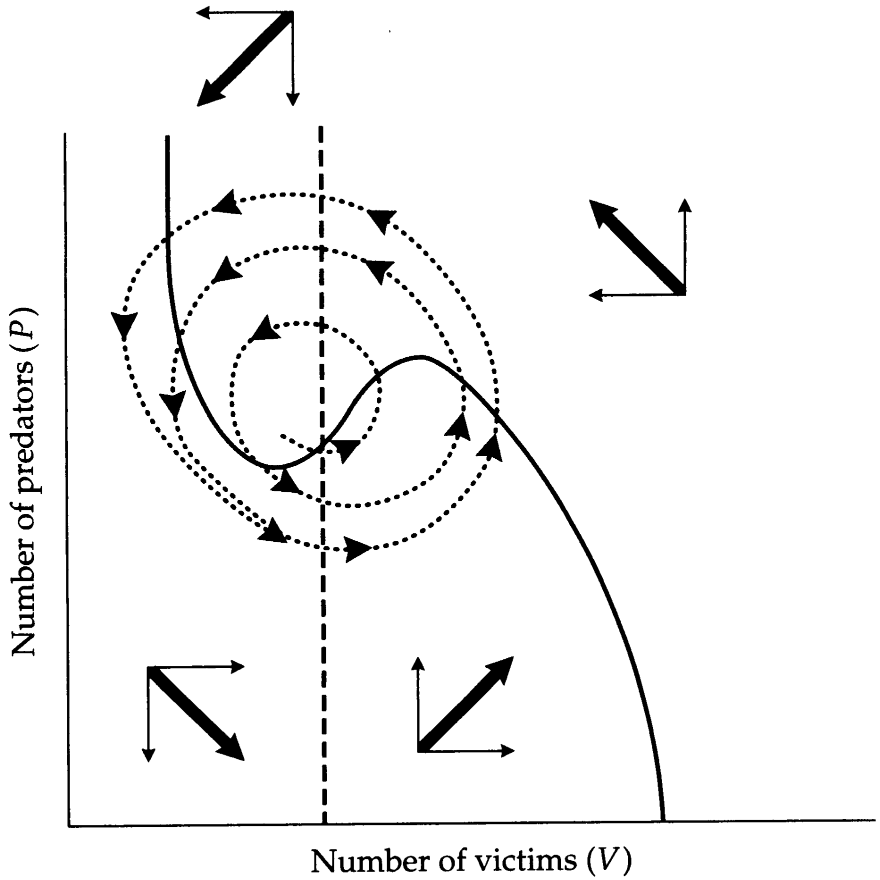


Figure 6.12 Cycling of predator and victim populations because of victim refuges. If there are spatial refuges from predation, the victim isocline becomes vertical at low victim abundance. In this case, the efficient predator cannot overexploit its prey, and begins to starve once all the victims outside of the refuges have been consumed. After the predator population declines below a certain point, the victim population begins to increase again, repeating the cycle.

Changing the predator numerical response:

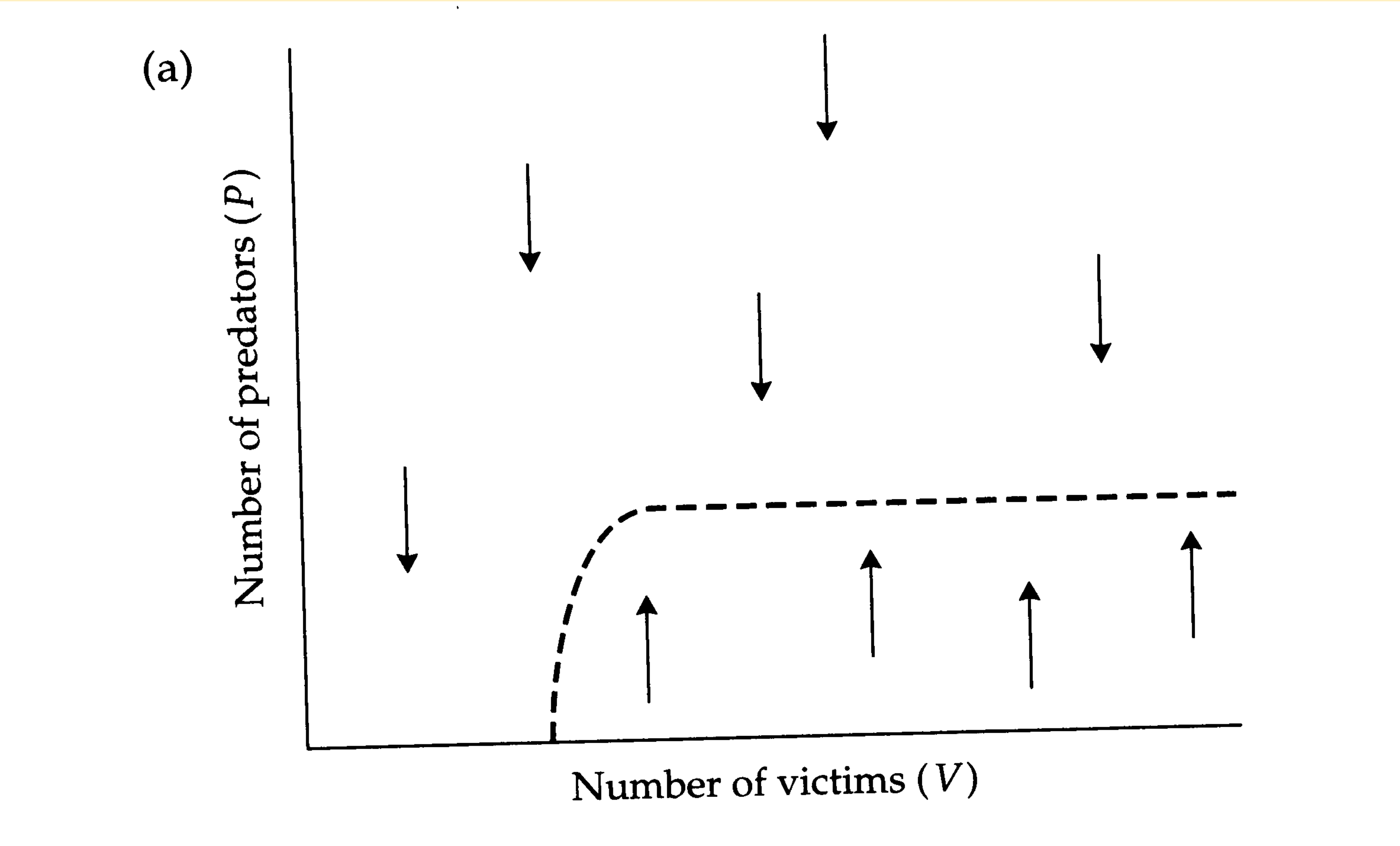
Have so far assumed the predator *numerical response* βV (per capita growth rate of predators as function of prey abundance) is a linear function of prey abundance

But predators may have carrying capacities determined by factors other than prey availability.

- In state space, a carrying capacity will bend the predator zero growth isocline to the right (more prey does not increase predator numbers)

- This will generate a stable equilibrium along the horizontal part of the predator isocline

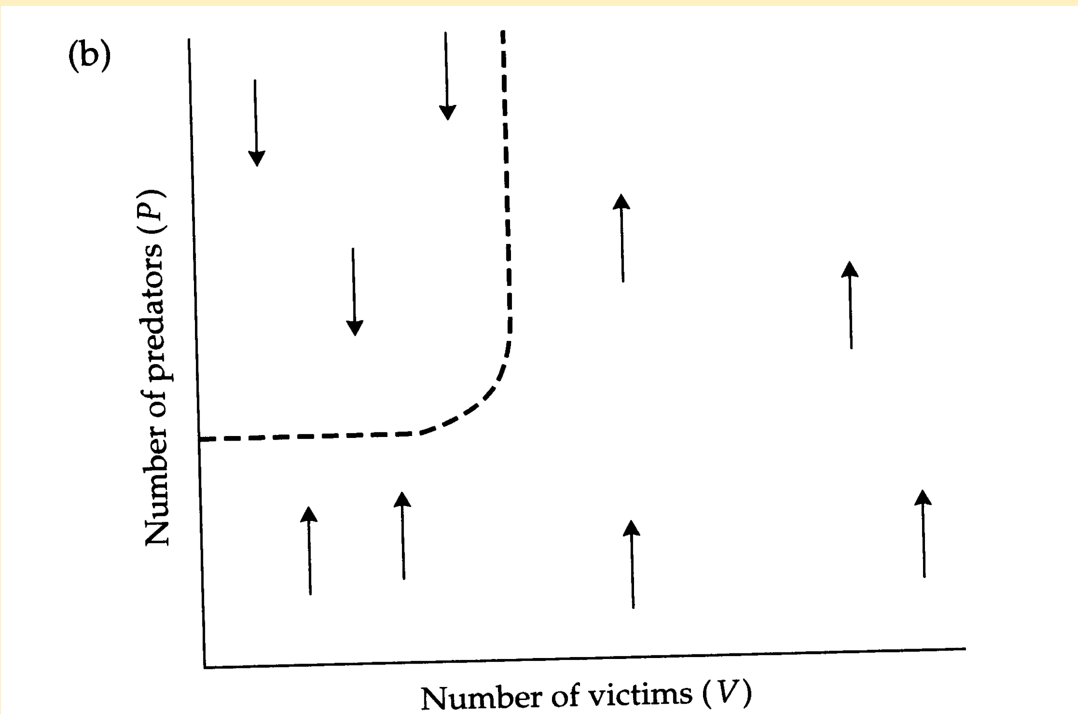
Predator carrying capacity: predator can no longer drive prey to extinction. Stable coexistence



What happens if a predator has multiple prey?

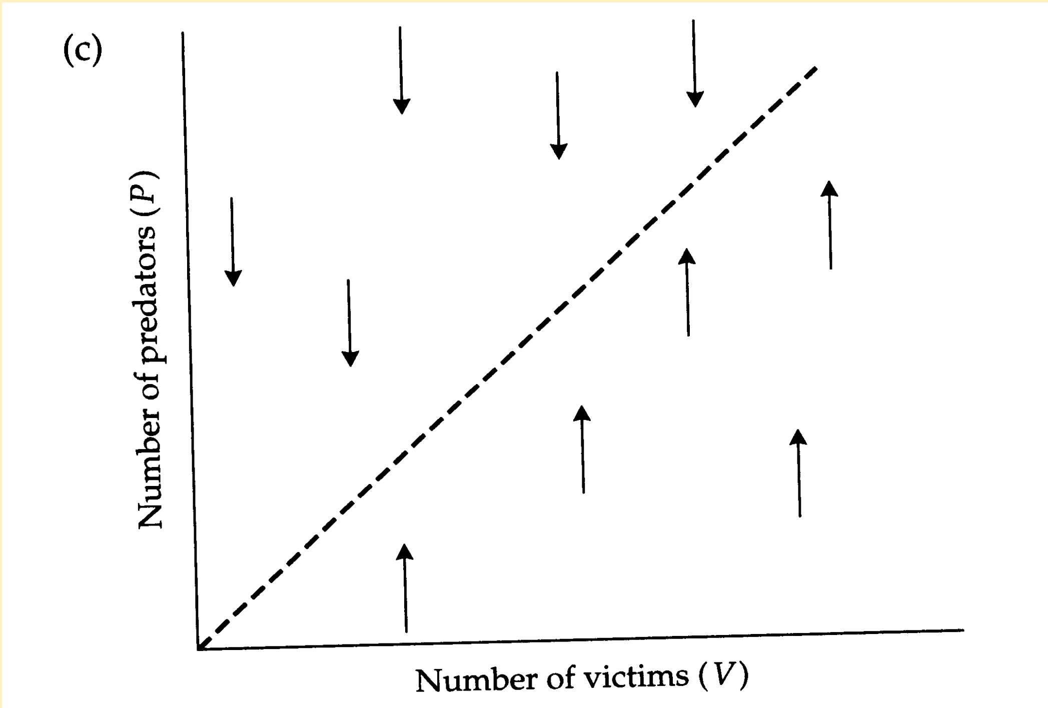
Outcome will depend on whether prey species cycle in concert

If prey abundances are *not* strongly positively correlated then as one prey species becomes scarce, the predator can continue to feed and increase its population size.



Unstable equilibrium
predators drive prey
to extinction

Predator carrying capacity and multiple prey species:



Predator isocline with a positive slope is stable (damped oscillations)

Any factor that rotates the prey or predator isocline in a clockwise direction (ie predator carrying capacity) will tend to stabilize interactions

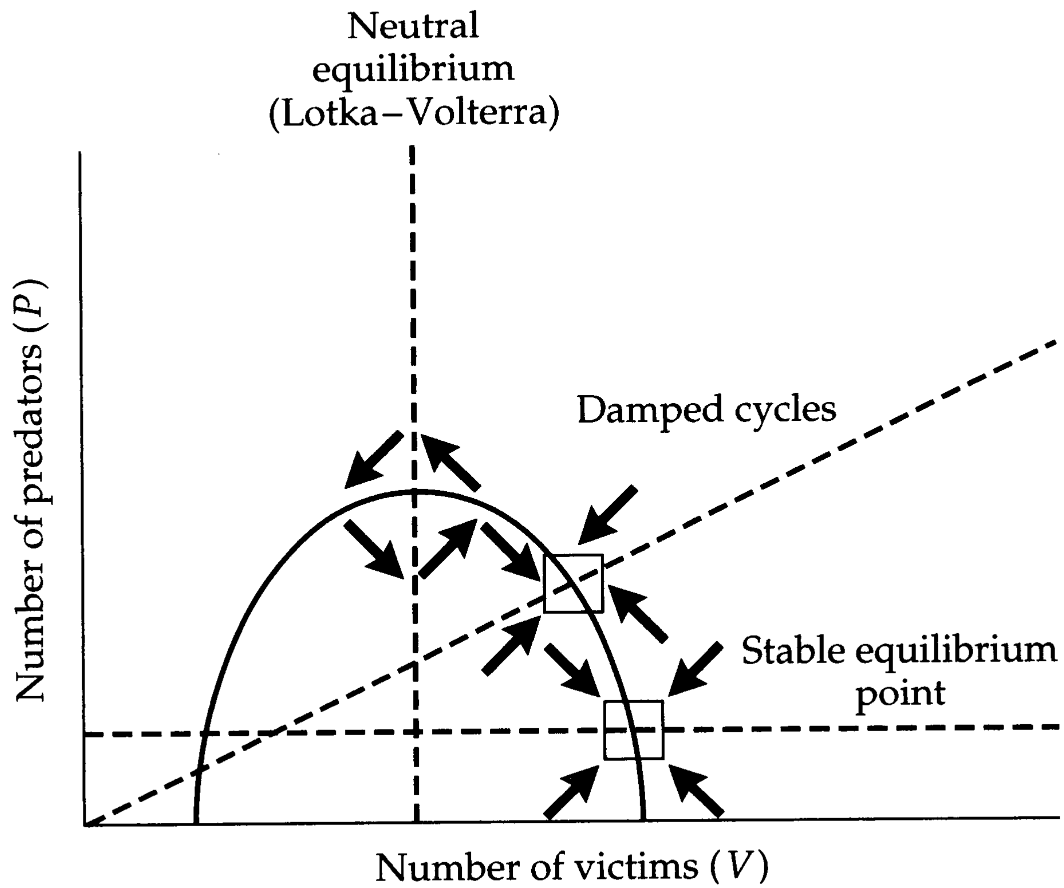


Figure 6.15 Effects of clockwise rotation of the predator isocline. As the predator isocline is rotated, the dynamics change from cycles with a neutral equilibrium, to damped cycles, to a stable equilibrium point. Biologically, the three predator isoclines correspond to a predator that is a complete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

Conclusions: predation models

• Simple predation models generate a variety of behaviors - neutral stability, stable limit cycles, and equilibrium stability.

• Adding predator or prey carrying capacities tends to stabilize models whereas incorporating non-linear functional responses and time lags generally leads to instability.

• Multiple prey species can destabilize populations if it allows predators to over-exploit prey, but predation may also facilitate prey coexistence (Paine paper) - depending on predator preference *and competitive interactions among prey species*

• Simple lab predator-prey experiments most often result in extinction over a short time. This perhaps indicates the importance of *refuges from predators in natural systems*