

## ***Predation part 2***

Functional Response

Numerical Response

Offtake = product of functional and numerical responses

Cycles and stability

Last time, used simple models (fixed quota, fixed effort, Lotka-Volterra) to describe population dynamics of predator-prey interactions.

Today, take another approach to predator-prey interactions. First describe how a single predator responds to change in prey density. From this, build to a realistic description of population dynamics of predator-prey interactions.

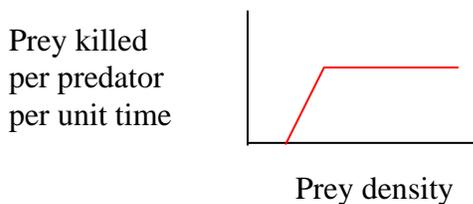
A real predator does not harvest at a fixed rate or with a constant effort. In nature, the rate of harvest by a predator population is determined by two attributes of the predator's response to changes in prey density: ***functional response*** and ***numerical response***.

### ***Functional Response Curves***

**Relates a single predator's prey consumption rate to prey population density**

English entomologist, Solomon, described 3 general classes of functional response.

**Type 1 Functional Response.** Linear increase in consumption rate until satiation, then no change in consumption rate above satiation. In this case, satiation = predator does not need to, or physically cannot, eat at a higher rate.

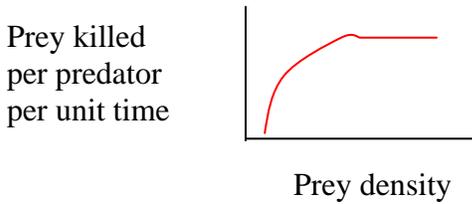


Rare in nature.

Filter feeders provide an example. Intake increases with density of food in water, up to the point at which the filtering apparatus is working at top speed.

(Fig. 9.8 Begon et al: *Daphnia* feeding on *Saccharomyces* yeast)

**Type 2 Functional Response.** Consumption rate increases at a decelerating rate, gradually leveling off at maximum rate.



Common in nature.

At low prey densities, predators take prey in an almost constant-effort fashion: if prey density doubles, then predator locates them twice as often and kills them at twice the rate. Thus, rate of consumption increases almost linearly at low prey density.

As prey density increases, searching for prey becomes a less important limit on the rate of predation. Prey are easy to locate, and rate of consumption is more heavily affected by *handling time*, the time it takes to catch, subdue, kill and eat a prey item, once prey located.

As searching becomes less important and handling becomes more important, the rate of consumption shows decelerating rate of increase. (still increases, but less quickly)

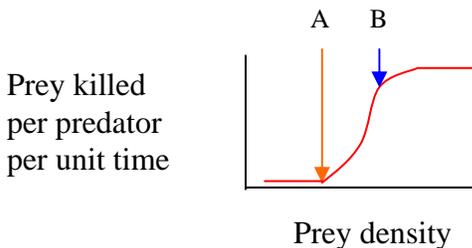
Eventually, search is not limiting at all, and rate of consumption levels off at upper limit determined by handling time alone.

Examples:

(Fig. 16.2 and 16.3 Smith and Smith: weasels and rodents)

(Fig. 9.6b Begon et al: bank voles and willows)

**Type 3 Functional Response.** Sigmoid increase in consumption rate as prey density increases.



Common in nature.

**Three processes (at least) cause type 3 functional responses.**

## 1. When prey are rare, predator has little opportunity to learn:

- a. Where to find them.
- b. How to catch and kill them.

Most active predators must form a *search image* - it is easier to find something if you know precisely what you are looking for. You've probably experienced this yourself, and experiments suggest that it is true for many animals - search times go down as familiarity with the 'target' goes up. This is more important for generalist predators (with many prey types) than for specialists.

Predators with *specialized capture or killing techniques* must learn how to apply these techniques to each prey type.

E.g. many cats kill prey larger than themselves by inserting canines between vertebrae and disarticulating the spine (this is why they have many, sensitive nerves in canines — let them feel the placement of their teeth). They must learn exactly where to bite, to kill prey before it injures them.

Result of these effects is a threshold ( $A$ ) prey density:  
 Below threshold predator essentially ignores that prey species  
 Above threshold, harvest rate quickly jumps to something substantial

(Overhead: Begon et al Fig 9.2 e: learning in dragonflies preying on mayflies and tubifex worms)

(Overhead: AWD cumulative diet - low density prey species rarely taken, though similar to high density prey that are killed often.)

As prey density increases above  $A$ , handling time becomes increasingly imp't, as described for type 2. Above threshold  $B$  consumption reaches upper limit set by handling time alone.

## 2. Predator switching. Switching prey types as function of relative prey density.

Different prey may occupy different microhabitats, or may require different hunting methods (e.g. solitary or group hunting), so that predator must focus only on one. Predator will forage in microhabitat that is most profitable. If prey species is rare, predator will do better to forage in another microhabitat (or with another method), and will ignore prey completely. As prey becomes more common, eventually profitable for predator to switch to hunting them.

(Overhead: Begon et al Fig. 9.2b: Guppies switching between tubifex worms (on bottom) and fruitflies (on surface))

(Overhead: Begon et al Fig 9.2d: Sticklebacks feeding on two insect prey - also demonstrates **learning** - with increase of given prey type, switching gets stronger in later trials)

**3. Prey refuge.** There may be a limited number of safe places, in which prey are not vulnerable to predation. As prey become common, some must use unprotected areas.

E.g. deer 'yards' in boundaries between wolf home ranges in N. Minnesota.  
Small fish using anemones as refuges.

### *Numerical Response Curves*

**Relates number of predators to number of prey.**

(Overhead: Fig 16.7 Smith & Smith).

In addition to functional response, predator numbers might change as prey increase. This can be via:

1.  $\uparrow$  in predator reproduction & survival
2. Aggregation of predators in prey hot-spots.

Most likely numerical responses are:

1. Direct response - predator  $\#\# \uparrow$  as prey  $\#\# \uparrow$
2. No response - no  $\Delta$  in predator  $\#\#$  as prey  $\#\# \uparrow$  (entire response is functional).

Can also see:

3. Inverse response - predator  $\#\# \downarrow$  as prey  $\#\# \uparrow$ .

(Overhead 16.9 Smith & Smith - inverse numerical response of weasels to rodents.)

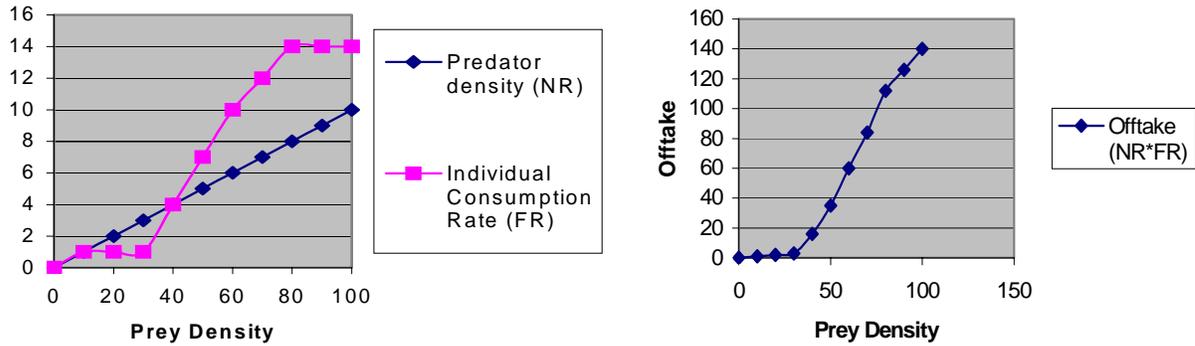
What would cause an inverse response?

(Overhead: Fig. 15.9c Pianka - inverse response is due to out-of phase cycles)

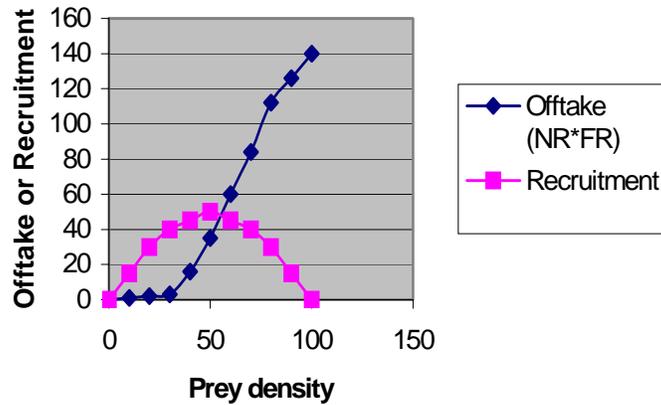
**Predator offtake from functional and numerical responses**

Offtake  
as function of prey density = functional response \* numerical response

Total prey killed/time = prey killed/predator/time \* number of predators



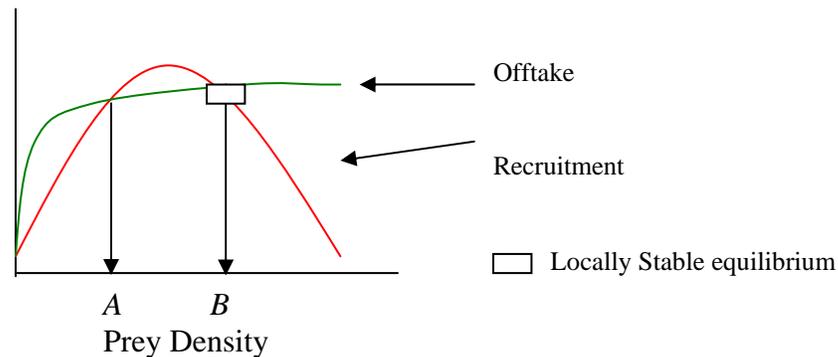
After determining offtake, can plot against recruitment (as in last lecture) to determine predator prey dynamics.



An important point emerges: **Predators with Type 3 functional response are unlikely to drive prey to extinction.** When offtake exceeds recruitment, prey density drops, and this leads to a sharp decline in offtake, allowing the prey to recover rather than dropping to zero.

(The plot looks very similar to one for a fixed effort harvest. Actually the sigmoid offtake curve is even less likely to cause an extinction than a (straight-line) fixed effort harvest, b/c the decline in offtake occurs more rapidly, at higher prey density, than is the case with a linear offtake. Compare this figure to the figure from last lecture for fixed effort, and to fixed quota.)

**Predators with Type 2 functional response are more likely to drive their prey to extinction.**



There is a locally stable equilibrium at prey density  $B$ .

If prey density is between  $A$  and  $B$ , then recruitment  $>$  offtake and prey density increases to  $B$ .

If prey density is above  $B$ , offtake  $>$  recruitment and prey density decreases to  $B$ .

But, if density happens to drop below  $A$ , then offtake  $>$  recruitment and prey are driven to extinction.

Compare this figure to figure showing fixed quota harvest from last lecture.

### ***Data on Predator-Prey Cycles.***

1. Models (Lotka-Volterra, Rosenzweig-MacArthur) suggest that predator prey dynamics can be inherently cyclical.
2. And there are examples from simple laboratory set-ups (no other ecological processes complicating matters) that show these cycles.

(Overhead: Fig. 15.10 Pianka prey and predator are 2 spp of orange mites)

(Overhead: Fig 21-4 Ricklefs prey = Azuki bean weevils. predator = braconid wasp)

4. But these cycles are not at all common in nature, because other ecological processes affect the dynamics. A few examples of cycles in nature do exist.

(Overhead: Fig 1. Peterson & Page 1988 - wolves and moose on Isle Royale. Isolated, one predator-one prey system).

(Overhead Fig 18-4 Ricklefs: 10 yr cycle of lynx and snowshoe hare from trapping data, over huge area from Alaska to Newfoundland)

(Overhead: Fig 16.15 Smith & Smith - lynx and hare data not from same places; more detailed analysis suggested that hares were eating lynx! Need to incorporate changes in food for hares to fully explain this cycle. Much of the hare decline is caused by *decline in birth rate (food)*, rather than *increase in death rate (predation)*).

(Overhead: Fig 10.5 Begon et al. - even better explanation of cycles when dynamics of second prey - ruffed grouse - are considered).

Why is (relatively) stable coexistence of predators and prey more common than cycles, in nature? Many factors can stabilize dynamics. Two major ones are:

1. Both the predator and prey are influenced by *other* ecological interactions. E.g. many predators are prey themselves. Many prey are limited by interspecific competition for food, as well as predation.
2. Many predators take more than one prey, and generalist predators are not tightly tied to the dynamics of any one prey species.

(Overhead: Figure 10.1a, Begon et al: Owl (generalist) and two spp of rodent)