Lecture 21: Predation Theory

Like competition, predation might influence population growth. On the level of *individuals*, predation clearly has a negative effect (being eaten is pretty negative), but what effect will predation have on the prey *population*?

+/- interactions:

Note that theory to do with predation also applies to parasitism, herbivory on annual plants, and human hunting/harvesting. The common factor is that one species gains and the other loses. Prey try to avoid the interaction, predators maintain the interaction.

Intuitively, might guess that any predation will necessarily reduce prey population size. But this is not necessarily true. Mortality caused by predation can be ***compensatory***. The mortality due to predation often compensates for mortality that would have occurred anyway, due to competition, weather, other factors, so that predation has no effect on population size. On the other hand, mortality due to predation can be ***additive,*** taking individuals that would not have died for other reasons. In this case, the prey population growth rate will be affected unless it can compensate by improved survival and reproduction of other individuals in the population, due to reduced intraspecific competition.

Two processes involved in compensation:

1. *Competing risks* = death by predation of individuals that would have died anyway

(overheads: 2 Figs from USFWS mallard hunting model)

(overhead: Fig 8.9a Begon et al: impact of cheetah predation on TG is less than impact of AWD [assuming equal number so TG killed by each predator], b/c cheetah prey disproportionately on fawns, which have low reproductive value)

2. *Compensatory shift in life-history* = mortality due to predation might be additive (taking individuals that would not have died anyway), but still be offset by improved survival and reproduction among survivors.

(overhead: Fig 8.3 Begon et al, compensatory increase in reproduction by flowers)

(lions: compensatory sex ratio shift in Selous, to >66% male cubs, when adult males are taken by trophy hunting).

If these two components do not completely compensate mortality due to predation, then prey population size is affected.

Predation as extension of logistic pop. growth model.

In absence of predation, the recruitment rate of prey population is:

$dN/dt = rN[(K-N)/K]$

This logistic equation (with linear density dependence) models population growth in Serengeti buffalo pretty well:

(Figs. 74 and 71, Sinclair 1977).

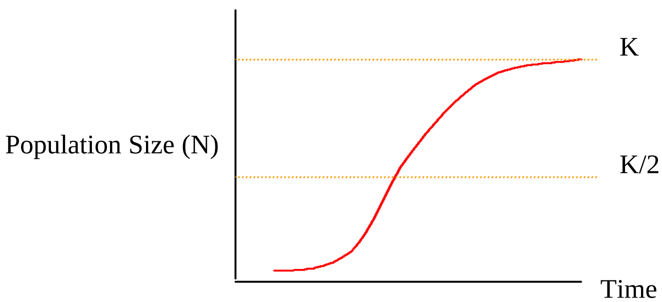
How does recruitment vary with population size, in the absence of predation?

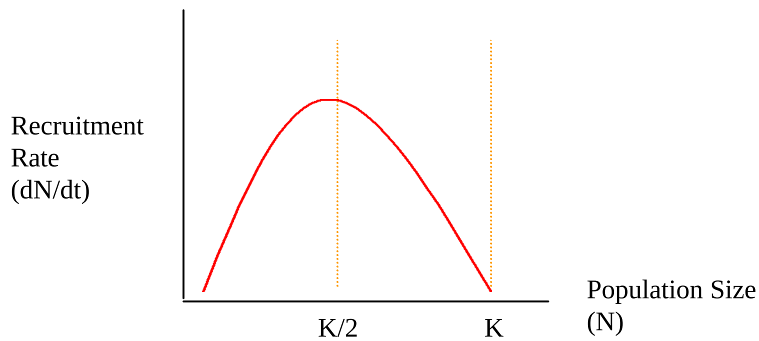
N close to zero: those buffalo that are present reproduce well {(K-N)/K ≈1}, but N is small, so total recruitment (dN/dt) is low.

N close to K: many buffalo present to reproduce, but resources are limited {(K-N)/K ≈ 0}, so total recruitment (dN/dt) is again low.

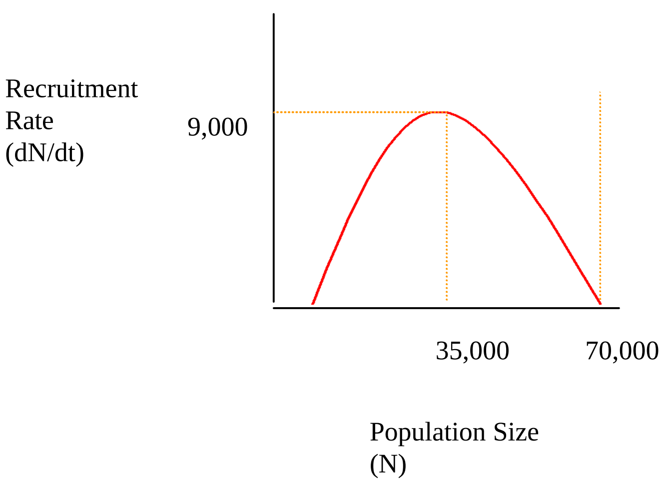
N = K/2: maximum recruitment. Trade-off between number of individuals present and reproductive rate of those individuals.

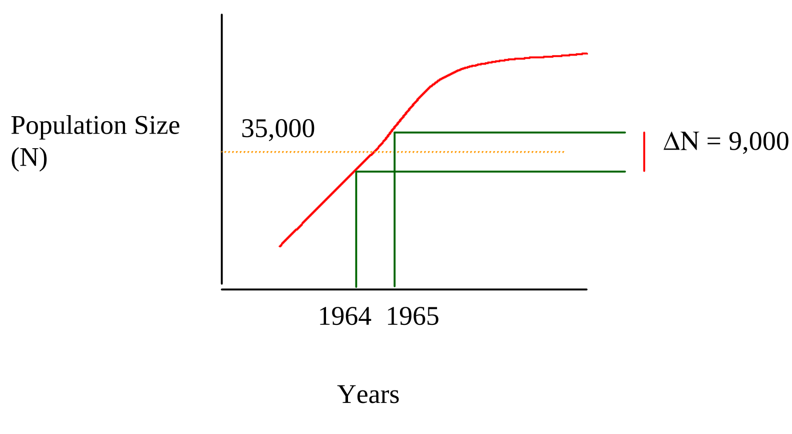
In general:





For Serengeti Buffalo data:





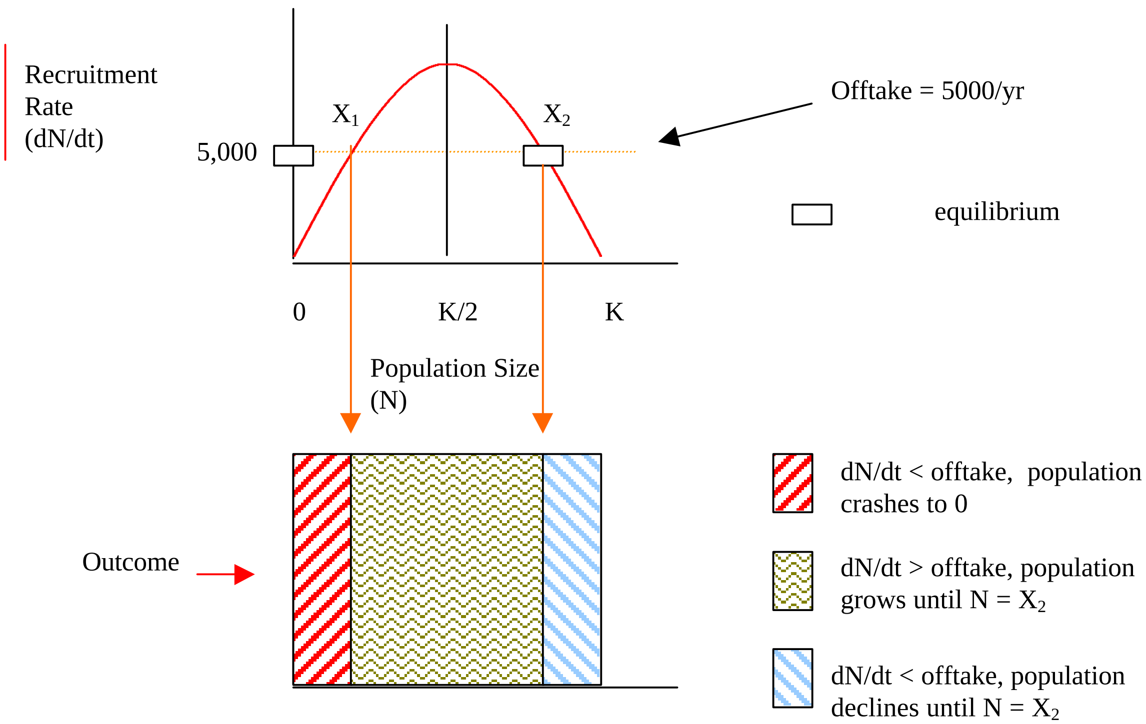
An important note: The logistic model assumes linear density dependence. If density dependence isn't perfectly linear, then max recruitment will not fall exactly at K/2. The recruitment curve will still be an inverted U shape, with a peak at intermediate N, but the location of the peak may fall above or below K/2.

Now, add offtake due to predators to the equation:

dN/dt = rN[(K-N)/K] - offtake

1. Suppose that predators take a *constant number of prey* per year. Note that this model applies to human harvest of animals with a *fixed quota*.

Extending the buffalo example, suppose lions kill 5,000 buffalo annually. Can see the effect on prey population by plotting offtake (harvest, quota) on the recruitment curve.



There are two stable equilibrium population sizes, at N = 0 and N = X_2

If initial population size is less than X1, reach equilibrium at N = 0.

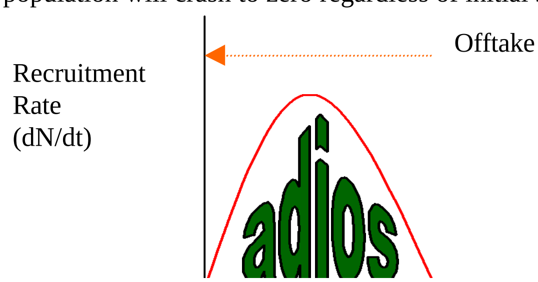
If initial population size is between X1 and K, reach equilibrium at N = X_2.

In red area: population is small enough that recruitment < offtake. Inevitable decline to 0

In green area: Population is at intermediate size, with high recruitment. Recruitment initially exceeds offtake, so population increases. As population grows, recruitment slows (due to ↑ intraspecific comp.) until it exactly balances offtake. Population stabilizes at N = X_2.

In blue area, where population size is near K: Near K the recruitment rate is low, and the offtake by predators exceeds recruitment in this example. Offtake > recruitment means that population will shrink. But ↓N causes ↑ in recruitment (less intraspecific competition). Population will decline until recruitment has increased to balance offtake, then stabilize (at N = X_2).

A final (obvious) point: If the offtake exceeds maximum recruitment, even slightly, then the prey population will crash to zero regardless of initial size.

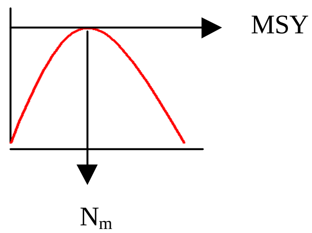


Application to Quota Setting for Hunting and Fisheries:

The theory just outlined seems to suggest a good strategy for setting hunting or fisheries quotas: set a fixed quota that takes exactly the maximum sustainable yield (MSY), where MSY = recruitment rate for N = K/2.

dN/dt

(recruitment rate)



Pop Size (N)

If:

1. We have perfect information about the harvested population's recruitment curve
2. The environment doesn't vary

Then fixed quota harvesting would give consistently high yields. But we never have perfect information, and the environment does vary. Fixed quota harvesting has been a disaster in many cases, because

1. Estimated MSY might be larger than the true MSY (even very slightly)
2. The true MSY will vary from year to year.

If either 1 or 2 is true, then the population is likely to eventually fall to the left of N_m. With a fixed quota equal to MSY, if the population ever drops below N_m, then the harvest will always exceed recruitment, until the population crashes to zero. Fixed quota MSY harvesting has lead to collapse of fish and whale populations, mainly for these reasons.

(Overheads: Fig 16.13 and 16.16 Begon et al.)

Fixed Effort Harvesting: Can avoid overharvest by setting a fixed effort put into harvest, rather than a fixed quota. When the population is large, a fixed effort gives a large harvest. When the population declines, the fixed effort takes a smaller harvest and allows recovery.

(Overhead: Fig 16.14a Begon et al)

Points from fixed effort overhead:

1. There is an optimal effort. Greater effort (or lower effort) gives lower sustained yield.
2. *Unlike* fixed quota, as N drops below N_m, dN/dt exceeds harvest and population recovers.

For most sport hunting, fixed effort is accomplished by selling a fixed number of licenses, regardless of rate of success per license.

Joint Population Dynamics of Predator and Prey

A. Lotka Volterra Model

Coupled equations for pop. growth rate of predator (*P*) and prey (N)

Assume that prey grow exponentially in absence of predation, so

$dN/dt = rN$

Prey are removed at a rate that depends on frequency of encounters between predator and prey. Encounters increase as prey (*N*) increase, and as predators (*P*) increase. More prey are removed as the efficiency (*e*) of predator at finding and killing prey increases.

$dN/dt = rN - ePN$

Predators decline exponentially in absence of prey (*d* = death rate)

$dP/dt = -dP$

Predators are born at a rate that depends on amount of prey consumed (*ePN*, explained above), and the predator's efficiency of converting food into offspring (*f*)

$dP/dt = fePN - dP$

Now have a pair of equations that describes population growth for the prey and for the predator. Can plot the zero-isoclines for these equations to see joint changes in predator and prey populations through time.

(See lecture notes on interspecific competition for a refresher on zero-isoclines, if necessary).

(overhead, Begon et al Fig 10.2)

L-V predation model predicts:

1. Cycles of predator and prey
2. Predator cycles slightly after prey (delayed density dependence, with 1/4 cycle phase shift)
3. 'Neutral stability' of cycles - will cycle indefinitely unless disturbed. If disturbed, will drop into a new cycle with different amplitude and stay in it until next disturbance.

Limitations:

1. Exponential growth of in absence of predator (no intraspecific density-dependence). Pianka gives example that corrects this.

(Overhead: Pianka Fig. 15.3)

2. No effect of intraspecific competition on predator either. Pianka gives example that corrects this

(Overhead: Pianka Fig. 15.7)

3. No predator satiation. The zero-isocline for prey is horizontal, so the same number of predators hold the prey population constant, for the entire range of prey density.

4. Uniform habitat, with no refuges from predation. The simple assumptions about encounter rates can be modified to take into account fact that intensity of predation varies across habitats/locations. This modification tends to stabilize the dynamics, damping or eliminating the cycles observed in L-V model

5. Single predator - single prey system, i.e. the predator specializes on just this prey species, and this prey species is not affected by other competitors. Making the predator a generalist also stabilizes the dynamics

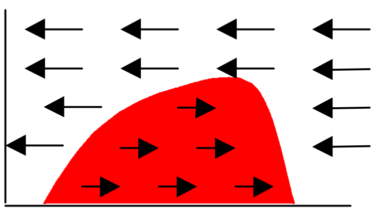
B. ***Rosenzweig & MacArthur's Graphical Model***

Assume that prey:

1. Have a carrying capacity that sets an upper limit on numbers
2. Have a minimum density below which 'Allee effect' - failure to find mates - causes extinction.
3. For all prey densities between these thresholds, there is a maximum predator density that the prey population can support - at this density the prey population is stable.

These three assumptions give a zero isocline for prey, below which prey increase, above which prey decrease:

Number of
Predators



K

Number of Prey

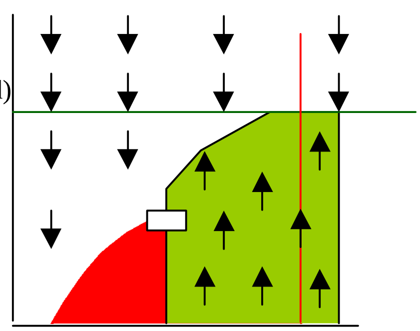
Assume that predators:

1. Have a carrying capacity that sets upper limit on numbers
2. Have a threshold density of prey below which they cannot kill enough to survive and breed.
3. Compete with one another for prey as predator population approaches its carrying capacity.

These assumptions give a zero-isocline for predators:

K(pred)

Number of
Predators

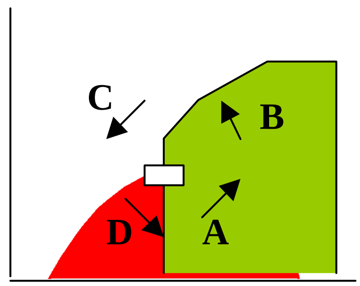


= Equilibrium

K(prey)

Number of Prey

Number of Predators



Number of Prey

Region A:	Prey ↑	Predator ↑
Region B:	Prey ↓	Predator ↑
Region C:	Prey ↓	Predator ↓
Region D:	Prey ↑	Predator ↓

Depending on the rate of ↑ or ↓ for each species, three possible outcomes:

1. Stable cycles
2. Damped cycles
3. Cycles of increasing amplitude, perhaps leading to extinction of predator, or prey (followed by predator).

(Overhead: Fig 15.8 Pianka)