

Lecture 16: Interspecific Competition

Outline

Intraspecific competition = density dependence
Intraspecific and interspecific competition
Limiting resources
Interference vs exploitation
Effects on population growth

- Lotka-Volterra competition equations
- Competition coefficients
- Competitive exclusion vs. density compensation

Facilitation
Apparent competition - two prey species taken by same predator

Last lecture showed that intraspecific competition can decrease survival and reproduction as a population approaches the carrying capacity -- density dependent population growth is due to intraspecific competition. Logistic equation describes sigmoid population growth curve due to intraspecific competition.

(Fig 6.13 Begon et al) Logistic growth in wildebeest population

Logistic equation assumes that interactions with other species have no effect on population growth. (Excepting resource (prey) species, which affect the carrying capacity). But in most real world situations, individuals will face two types of competition:

Competition: *use or defense of a limiting resource by one individual that reduces the availability of that resource to another individual*

if individuals are of same species: ***intraspecific competition***

if individuals are of different species: ***interspecific competition***

Limiting resource: a resource whose availability influences survival or reproduction

Use: if one wildebeest simply eats a patch of a limited food plant, before another wildebeest does, then they are competing with one another even though they never interact directly - this is ***competition by exploitation***

Defense: if one wildebeest physically denies other wildebeest access to a patch of food (e.g. by defending a territory), this is ***competition by interference***.

Important to recognize that the ecological definition of competition is not the same as its common definition, which emphasizes physical contests between individuals. Ecological

competition can occur between two individuals that never even see one another, if they reduce the availability of limited resources for one another.

Competition by interference: effects are strong, but it is relatively uncommon.

Competition by exploitation: effects are usually weaker, but it is much more common.

Effects of interspecific competition on population growth: Lotka-Volterra equations

How do we incorporate interspecific competition into population growth models? Will show this with the equations for continuous breeding.

$dN/dt = rN$ exponential growth with unlimited resources

In this equation, r means r_{\max} , the maximum per-capita growth rate that can be attained under ideal conditions. But we can take intraspecific competition for limited resources into account:

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

so that population growth slows as $N \rightarrow K$ and intraspecific competition becomes more intense. Growth stops when the population reaches carrying capacity.
(when $N = K$, $dN/dt = 0$)

Suppose that the wildebeest in the example above compete with buffalo, as well as competing with other wildebeest. First, add a subscript 'w' to the variables that have to do with wildebeest:

$dN_w/dt = r_w N_w [(K_w - N_w)/K_w]$

If an individual buffalo uses resources (grasses) in exactly the same way as a wildebeest, then the survival and reproduction of wildebeest (dN_w/dt) would be affected by the number of buffaloes in the same way that it is affected by the number of wildebeest. Can incorporate this into the equation easily:

$dN_w/dt = r_w N_w [(K_w - N_w - N_b)/K_w]$

It's unlikely that a buffalo has exactly the same impact on resources as a wildebeest does. Buffalo are much larger, so they consume more grass. Buffalo can also consume coarser grass than wildebeest, so there is not complete overlap in the plant species they consume.

When measuring the impact of interspecific competition on population growth must take into account differences between competing species in:

1. **amount** of resources used
2. **overlap** in the set of resources used

Basically, need to convert buffalo into 'wildebeest equivalents'. Need to determine how many wildebeest would have the same impact on resources (for wildebeest) that one buffalo has. In the equation, this is taken into account by multiplying the number of buffalo by a **competition coefficient**, α_{wb} .

$$dN_w/dt = r_w N_w [(K_w - N_w - \alpha_{wb} N_b)/K_w]$$

Following the same logic used for wildebeest, the equation for buffalo population growth is:

$$dN_b/dt = r_b N_b [(K_b - N_b - \alpha_{bw} N_w)/K_b]$$

This pair of equations for wildebeest and buffalo describe population growth in the presence of both intraspecific and interspecific competition. These are the Lotka-Volterra equations.

Competition coefficients.

1. Competition coefficients have two subscripts, one for each species involved in the competition. By convention, the species affected is listed first, and the species causing the effect is listed second.

α_{wb} - effect *on* wildebeest *of* competition with one buffalo

α_{bw} - effect *on* buffalo *of* competition with one wildebeest

2. In a competitive interaction, the two competition coefficients do not have to be equal. Most cases of interspecific competition are **asymmetric** - the impact of a buffalo on a wildebeest's resources is greater than the impact of a wildebeest on a buffalo's resources, so:

$$\alpha_{wb} > \alpha_{bw}$$

3. Generally, intraspecific competition is stronger than interspecific competition, so competition coefficients are generally less than one. ($\alpha = 1$ when intraspecific and interspecific competition are equally strong). Interspecific competition is usually weaker because two species never use exactly the same resources (they do not have the same **ecological niche**). If you are a wildebeest, most other wildebeest need exactly the same things you do (though there may be differences between the sexes, or among age-classes). Buffalo need some of the same things, but the overlap in resource use is not as complete.

If two species use similar resources, and one of the species (b) is much bigger, then interspecific competition may have a stronger effect than intraspecific competition for the small species (s). In this case, $\alpha_{sb} > 1$. [Example: medium sized carnivores - data next

lecture for competition between lions (150 kg), hyenas (50 kg) and African wild dogs (25 kg)].

What does population growth look like with interspecific competition?

1. **Coexistence with density compensation.** If the two species are similar in competitive ability, then both will show S-shaped population growth. But, growth levels out at a stable population size that is less than the carrying capacity for each species.

(Fig 7.3 Begon et al.)

If either species was removed, then the other would increase to its carrying capacity. A change in density in response to increase or decrease in competitor is called **density compensation**.

2. **Competitive exclusion.** If one species is a much better competitor than the other (so that $\alpha_{12} \gg \alpha_{21}$):

(Fig. 12.5 Pianka)

The poorer competitor goes extinct

The better competitor shows almost logistic growth. Growth is slower than logistic while the other species persists, shifts upward as the other species declines, and eventually reaches K.

When will competition lead to coexistence, and when will it lead to exclusion? If exclusion, which species is excluded? Can answer these questions using Lotka-Volterra equations to plot a **zero-isocline** for each species.

Zero-isocline - On a plot of N_2 vs N_1 , there is a line for each species that shows where population growth is zero. On one side of the line growth is positive, on the other side growth is negative.

To find this line, start with L-V equation:

$$dN_w/dt = r_w N_w [(K_w - N_w - \alpha_{wb} N_b)/K_w]$$

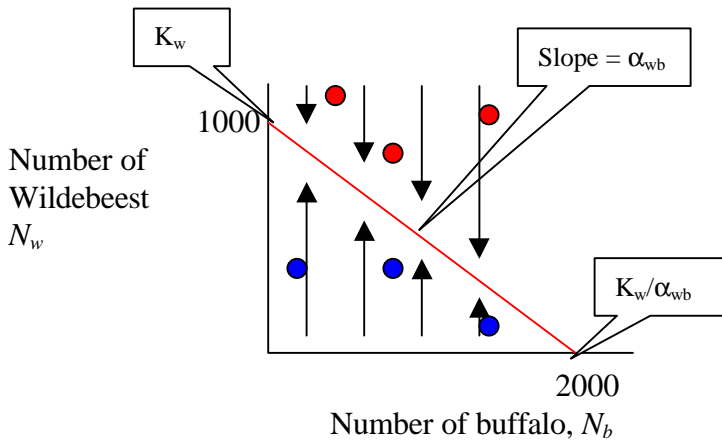
The growth rate for wildebeest (dN_w/dt) will be zero when the term in [] is zero:

$$(K_w - N_w - \alpha_{wb} N_b)/K_w = 0$$

A little algebra (multiply both sides by K_w , add N_w to both sides) gives:

$$N_w = K_w - \alpha_{wb} N_b$$

This is an equation for a straight line on a plot of N_w vs N_b . This line is the zero isocline for wildebeest:



On the isocline, wildebeest numbers stay constant

Above the isocline, wildebeest decline. If the numbers of wildebeest and buffalo were at any of the red points, then wildebeest numbers would drop to the isocline.

Below the isocline, wildebeest increase. If the numbers of wildebeest and buffalo were at any of the blue points, then wildebeest would rise to the isocline.

Can determine the zero-isocline for buffalo just the same way, by starting with the L-V equation for buffalo:

$$dN_b/dt = r_b N_b [(K_b - N_b - \alpha_{bw} N_w) / K_b]$$

And following the same steps as before to get:

$$N_b = K_b - \alpha_{bw} N_w$$

Which is the buffalo population's zero-isocline. For any pair of competing species, plotting both species' isoclines on a plot of N_2 vs N_1 shows the outcome of the competition.

(Figure 12.3 Pianka)

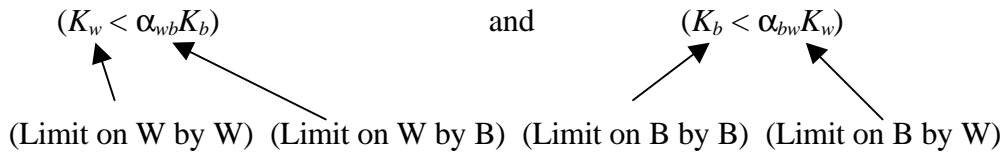
1. If the two *isoclines don't intersect*, then the species with the higher isocline drives the other to extinction. The stable equilibrium is one species at zero and the other at its

carrying capacity. Competitive exclusion, and the same species will win no matter what the initial numbers of each species.

(Fig. 12.3A & 12.3B Pianka)

2. If the two *isoclines do intersect*, there are two possibilities:

A. If each species limits the other's growth more than its own, *unstable coexistence*.



The outcome will be competitive exclusion, with one species at zero and the other at K, but the 'winner' depends on initial numbers of each species.

(Fig 12.3C Pianka)

B. If each species limits its own growth more than it limits the other species' growth, *stable coexistence*

$$(K_w > \alpha_{wb}K_b \text{ and } K_b > \alpha_{bw}K_w)$$

(Fig 12.3D Pianka)

Facilitation. Sometimes, species that use similar resources can have a positive effect on one another. An example comes from the 'grazing succession' in Serengeti. Zebras graze an area first, taking low quality shoots that are too poor for smaller grazers to live on. This stimulates new growth of higher quality, which is then available to gazelles.

Facilitation of this sort can be modeled with the L-V equations, just by making the alpha term positive rather than negative.

Apparent Competition occurs when two species that do not actually compete show density compensation.

(Fig. 11.3 Pianka)

Two species are killed by the same predator (or two plant eaten by the same herbivore). An increase in prey 1 supports a larger predator population, which decreases prey 2. If one was not monitoring numbers of the predator, just monitoring numbers of the two prey, this would look exactly like density compensation due to competition - when one species goes up, the other goes down.

Indirect effect: one species affects the population growth of a second species, although they do not interact directly; the effect is mediated by a third species. Apparent competition is a good example. Indirect effects make it very difficult to identify cause and effect in interspecific interactions.