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In ecology, the competitive exclusion principle, sometimes referred to as
Gause's law of competitive exclusion or just Gause's law.
gauses exclusion principle states that when two closely related
species will compete with each other for the same resources , then the
superior one will get acess to the same and the inferior one will get
eliminated by the same process.
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Competitive Exclusion Principle:

The principle has been variously named after its principal authors – Gause's principle (Lack, 1944), Volterra – Gause principle (Hutchinson, 1957) and Hardin's competitive exclusion principle. Gause's competitive exclusion principle states that no two species can coexist if they occupy the same niche. In other words, an ecological niche cannot be simultaneously and completely occupied by stabilized populations of more than one species.

In his classic experiment Gause (1934) first grew Paramecium caudatum and Paramecium Ha in separate cultures and found that each species grew in numbers according to the logistic equation. However, P. aurelia grows in numbers more quickly than P. caudatum and shows more individuals in the same volume of culture medium.

But when he grew the two species together in same culture volume, he observed that initially both species grew in numbers, but eventually P. caudatum declined and became extinct (Fig. 3.6). He repeated has experiment and found that P. aurelia always won the competition between the two species. Gause attributed the result to the nee of 'but a single niche in the conditions of the experiment'.
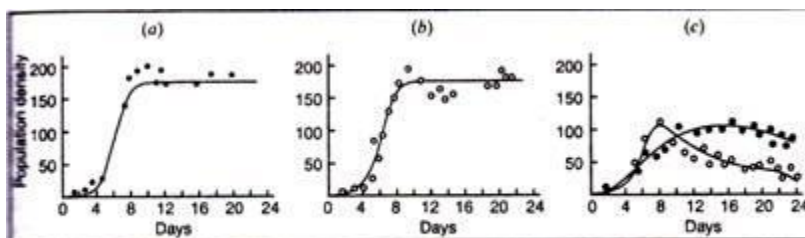

Fig. 3.6. Competition between two species of *Paramecium*. (a) *P. aurelia* alone; (b) *P. caudatum* alone; (c) both species together in the same culture (from Gause, 1934)

There are other examples illustrating the principle of Gause. Park(1948,1954,1962) conducted laboratory experiments on two species of flour beetle, Tribolium confusum and Tribolium castaneum. He found that in mixed cultures one species always "wins" over another. But it depended on the environmental conditions. T .castaneum always wins (or T. confusum becomes extinct) under conditions of high temperature (34°C) and high humidity (70% R.H), while T. confusum always (T. castaneum becomes extinct) under cool-dry climate, i.e., under conditions of low temperature and low humidity (30% R.H.). Under some different environmental conditions (Table 3.1) time's one species survived, sometimes the other. This leads us to conclude that species can coexist even in the face of interspecific competition provided that their niches do not overlap too much.

Table 3.1. Results of competition between two species of flour beetle under different laboratory conditions (after Park, 1954).

Temp.	Relative Humidity	% of times T. confusum wins	% of times T.castaneum wins
24°C	30%	100	0
24°C	70%	71	29
29°C	30%	87	13
29°C	70%	14	86
34°C	30%	90	10
34°C	70%	0	100

Competition and Character Displacement:

Character displacement is defined as the divergence in the characteristics of two otherwise similar species where their ranges overlap, caused by the selective effects of competition between the species in the area of overlap.

In the phenomenon of character displacement, the character traits of two closely related species differ more when they occur in sympatry (two species coexisting within the same geographic area) than in allopatry (when their distributions do not overlap, they are said to be allopatric). The ground finches (Geospiza spp.) of Galapagos Islands, first described by Darwin, furnish an example of character displacement. Character displacement occurs when inter-specific competition results in natural selection causing changes in the morphology of two closely related species.

PREDATOR-PREY DYNAMICS: LOTKA-VOLTERRA

Introduction: The Lotka-Volterra model is composed of a pair of differential equations that describe predator-prey (or herbivore-plant, or parasitoid-host) dynamics in their simplest case (one predator population, one prey population). It was developed independently by Alfred Lotka and Vito Volterra in the 1920's, and is characterized by oscillations in the population size of both predator and prey, with the peak of the predator's oscillation lagging slightly behind the peak of the prey's oscillation. The model makes several simplifying assumptions: 1) the prey population will grow exponentially when the predator is absent; 2) the predator population will starve in the absence of the prey population (as opposed to switching to another type of prey); 3) predators can consume infinite quantities of prey; and 4) there is no environmental complexity (in other words, both populations are moving randomly through a homogeneous environment).

Importance: Predators and prey can influence one another's evolution. Traits that enhance a predator's ability to find and capture prey will be selected for in the predator, while traits that enhance the prey's ability to avoid being eaten will be selected for in the prey. The "goals" of these traits are not compatible, and it is the interaction of these selective pressures that influences the dynamics of the predator and prey populations. Predicting the outcome of species interactions is also of interest to biologists trying to understand how communities are structured and sustained.

Question: What are the predictions of the Lotka-Volterra model? Are they supported by empirical evidence?

Variables:

P   number of predators or consumers

N   number of prey or biomass of plants

t   time

r   growth rate of prey

a'   searching efficiency/attack rate

q   predator or consumer mortality rate

c   predatorís or consumerís efficiency at turning
   food into offspring (conversion efficiency)

Methods: We begin by looking at what happens to the predator population in the absence of prey; without food resources, their numbers are expected to decline exponentially, as described by the following equation:

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

(1)

This equation uses the product of the number of predators (P) and the predator mortality rate (q) to describe the rate of decrease (because of the minus sign on the right-hand side of the equation) of the predator population (P) with respect to time (t). In the presence of prey, however, this decline is opposed by the predator birth rate, ca_iPN, which is determined by the consumption rate (a_iPN, which is the attack rate[a'] multiplied by the product of the number of predators [P] times the number of prey [N]) and by the predatorís ability to turn food into offspring (c). As predator and prey numbers (P and N, respectively) increase, their encounters become more frequent, but the actual rate of consumption will depend on the attack rate (a_i). The equation describing the predator population dynamics becomes

$$\frac{dP}{dt} = ca'PN - qP$$
.

(2)

The product $ca'P$ is the predator's numerical response, or the per capita increase as a function of prey abundance. The entire term, $ca'PN$, tells us that increases in the predator population are proportional to the product of predator and prey abundance.

Turning to the prey population, we would expect that without predation, the numbers of prey would increase exponentially. The following equation describes the rate of increase of the prey population with respect to time, where r is the growth rate of the prey population, and N is the abundance of the prey population:

$$\frac{dN}{dt} = rN$$

(3)

In the presence of predators, however, the prey population is prevented from increasing exponentially. The term for consumption rate from above (*aiPN*) describes prey mortality, and the population dynamics of the prey can be described by the equation

$$\frac{dN}{dt} = rN - a'PN$$

(4)

The product of a' and P is the predator's functional response, or rate of prey capture as a function of prey abundance (see TYPE I or TYPE II functional response modules). Here the term $a'PN$ reflects the fact that losses from the prey population due to predation are proportional to the product of predator and prey abundances.

Equations (2) and (4) describe predator and prey population dynamics in the presence of one another, and together make up the Lotka-Volterra predator-prey model. The model predicts a cyclical relationship between predator and prey numbers: as the number of predators (P) increases so does the consumption rate ($a'PN$), tending to reinforce the increase in P. Increase in consumption rate, however, has an obvious consequence-- a decrease in the number of prey (N), which in turn causes P (and therefore $a'PN$) to decrease. As $a'PN$ decreases the prey population is able to recover, and N increases. Now P can increase, and the cycle begins again. This graph shows the cyclical relationship predicted by the model for hypothetical predator and prey populations.
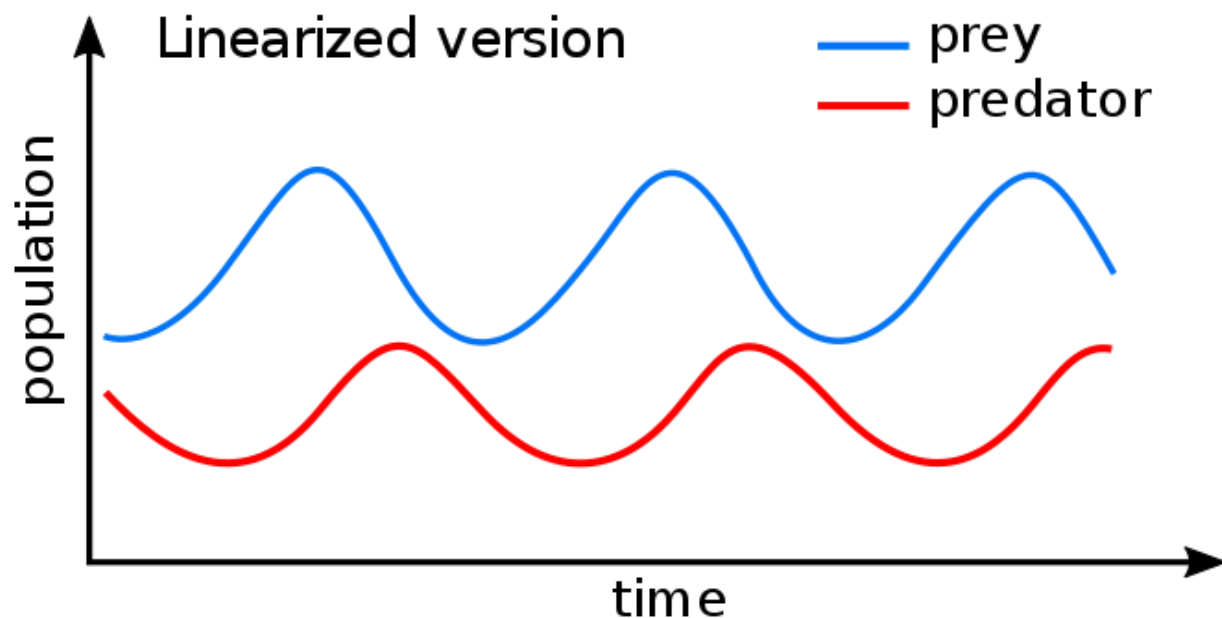
Huffaker (1958) reared two species of mites to demonstrate these coupled oscillations of predator and prey densities in the laboratory. Using *Typhlodromus occidentalis* as the predator and the six-spotted mite (*Eotetranychus sexmaculatus*) as the prey, Huffaker constructed environments composed of varying numbers of oranges (fed on by the prey) and rubber balls on trays. The oranges were partially covered with wax to control the amount of feeding area available to *E. sexmaculatus*, and dispersed among the rubber balls. The results of one of the many permutations of his experiments are graphed below. Note that the prey population size is on the left vertical axis and the predator population is on the right vertical axis, and that the scales of the two are different (after Huffaker, 1958 [fig.18]).
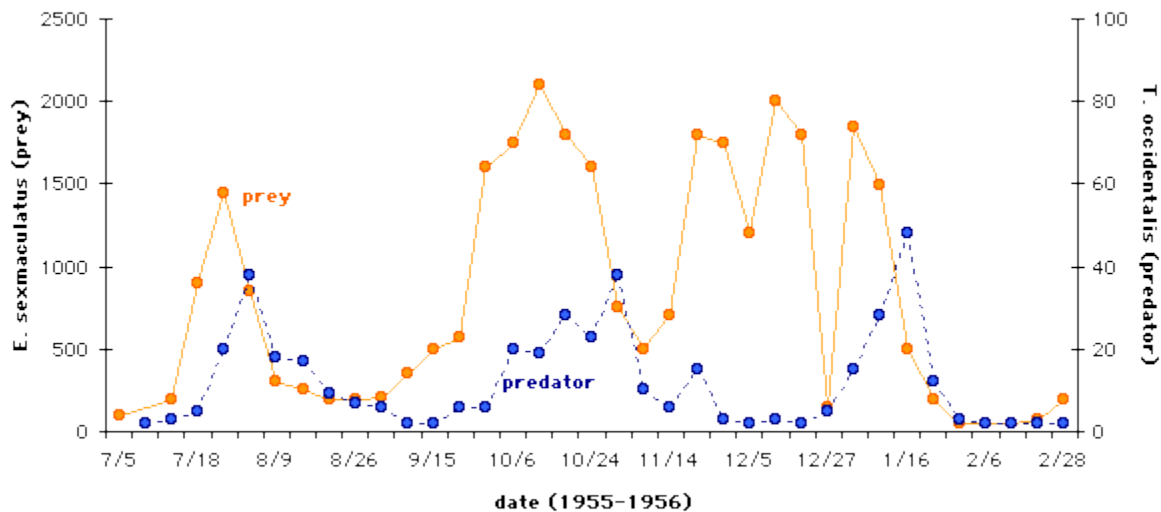
Interpretation: It is apparent from the graph that both populations showed cyclical behavior, and that the predator population generally tracked the peaks in the prey population. However, there is some information about this experiment that we need to consider before concluding that the experimental results truly support the predictions made by the Lotka-Volterra model. To achieve the results graphed here, Huffaker added considerable complexity to the environment. Food resources for *E. sexmaculatus* (the oranges), were spread further apart than in previous experiments, which meant that food resources for *T. occidentalis* (i.e., *E. sexmaculatus*) were also spread further apart. Additionally, the oranges were partially isolated with vaseline barriers, but the prey's ability to disperse was facilitated by the presence of upright sticks from which they could ride air currents to other parts of the environment. In other words, predator and prey were not encountering one another randomly in the environment (see assumption 4 from the Introduction).

Conclusions: A good model must be simple enough to be mathematically tractable, but complex enough to represent a system realistically. Realism is often sacrificed for simplicity, and one of the shortcomings of the Lotka-Volterra model is its reliance on unrealistic assumptions. For example, prey populations are limited by food resources and not just by predation, and no predator can consume infinite quantities of prey. Many other examples of cyclical relationships between predator and prey populations have been demonstrated in the laboratory or observed in nature, but in general these are better fit by models incorporating terms that represent carrying

capacity (the maximum population size that a given environment can support) for the prey population, realistic functional responses (how a predator's consumption rate changes as prey densities change) for the predator population, and complexity in the environment.

Predator-Prey Population Cycles

Predator and prey populations exhibit fluctuations described as the predator "tracking" the prey. The classic example is the snowshoe hare and lynx populations. Note that the lynx population (green) peaks slightly behind the hare population (blue), which is the lynx's primary food source. The hare cycle is mainly driven by excess predation by the lynx, but other factors, such as a winter food shortage, may also be important