

On Predation

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Predator-victim interactions Relationships between species (the predators) that take advantage of another species, and those that are victimized by them (the prey or victims). Mathematically, let V be the density of the victim species and P be the density of the predator species. Then a predation interaction exists if and only if

$$\partial \ln V / \partial P < 0 \quad \text{and} \quad \partial \ln P / \partial V > 0$$

where $\ln V = \frac{1}{V} \frac{dV}{dt}$, etc.

Originally, predation interactions referred exclusively to species, one of whose individuals killed those of the other for food. Soon it was recognized that such species shared many dynamic properties with others such as parasitoids and their hosts, parasites and their hosts, and herbivores and plants. In fact, the taking of individuals for food is neither necessary nor sufficient to establish the existence of a predation interaction. Some food species, such as predator-resistant gastropods, actually become extinct in the absence of their consumer species, such as starfish, thus receiving a net benefit from their consumer. On the other hand, Batesian model species are damaged by Batesian mimic species although the latter never consume a single molecule of the former.

Predators reduce the populations of their victims. That has led to the persecution of some predator species that compete with humans for resources. But it has also led to the practice of biological control to contain pests and weeds. Often the latter are species that have been introduced to a foreign biological province and escaped their predators.

Predation interactions tend to promote oscillations in the population sizes of the interacting species. But these depend on the presence of a high degree of predator **satiation** (which see) when predator and victim populations are in the

neighborhood of their equilibrium values. If instead, victims compete strongly for their own resources in this neighborhood, predation interactions result in populations that are stable.

Oscillatory dynamics threaten the existence of both predator and victim. Two forces can reduce or eliminate this threat. Predators may require other resources such as shelter. This requirement can limit the amplitude of oscillations. Victims may also have access to refugia where predation rates are diminished and a small population of victims can persist at steady state.

Models of predation Symbolic abstractions of natural, exploitative relationships between species. The exploiter is the predator or enemy; its victim is the prey. Predation models allow deductions about the population dynamics and population sizes of the interacting species.

In the mid-nineteenth century, Herbert Spencer produced the first model of predation. It was purely verbal, but from it he deduced that predatory interactions would likely lead to population oscillations in predator and victim.

In the 1920s, Lotka and Volterra independently produced the first mathematical model of predation. They stripped away all but four of the two species' natural features: b , per capita birth rate of victims; d , per capita death rate of predators; k , predation rate; and β , per capita birth rate of predators per predation event. Then they combined the birth and death rates of each species by assuming their additivity, and wrote a pair of simultaneous differential equations:

$$dV/dt = bV - kVP$$

$$dP/dt = \beta kVP - dP$$

where V and P are the population densities of predator and victim respectively. In this model, notice that in the absence of the predator, the victim density grows infinitely; whereas, in the absence of the victim, the predator becomes extinct.

Inadequate though it may be, Volterra used this model to produce a robust theory of biological control. That theory has weakened only a tiny amount as the model has been improved. Also, the model already suggests many of the central questions that ecologists have asked of predatory dynamics: How do the densities behave? What is the equilibrium point of the system? What is the dynamic stability of the equilibrium point? The answers for this model:

1. Equilibrium point: $(V^*, P^*) = (d/\beta k, b/k)$, where asterisks indicate equilibrium values.
2. Densities of both species oscillate (unless the system is at equilibrium).
3. The dynamics are neither stable nor unstable. The system tends to stay in whatever oscillatory trajectory it finds itself.

In the 1930s, Gause tested this model in his laboratory with mixed results. His systems did oscillate. But the oscillations of *Paramecium* and yeast followed a limit cycle: they had a stable trajectory rather than maintaining their initial trajectory. And the oscillations of *Paramecium* and *Didinium* were unstable unless he reduced the predation rate by adding habitat complexity (in the form of pebbles) to his aquaria.

Adding intraspecific victim competition greatly improved the basic model:

$$dV/dt = bV[(K-V)/K] - kVP$$

$$dP/dt = \beta kVP - dP$$

where K is victim carrying capacity. This model may not even have an equilibrium point in the positive quadrant: predators may become extinct deterministically, leaving their victims at K . But if there is an equilibrium, it will be oscillatory like the basic model. However, the oscillations will converge on equilibrium; the model is stable. Because it is relatively easy to solve, this model is still used in complex, multi-species computer simulations of food webs.

A much better model results from changing the predator functional response (*i.e.*, the rate at which an individual predator kills victims). A non-linear response models predatory hunger and satiation. There are two alternatives:

1. Half-saturation model: $kV/(\chi + V)$, where χ , the half saturation constant, is the victim density at which a predator kills at $k/2$, *i.e.*, half its maximum rate. This response model was conceived independently at least three times. Its most popular form, **Holling's disc equation**, is known as the Type II response. But the Type II and the half-saturation forms are mathematically identical. They are also identical to the Michaelis-Menton equation of enzyme biochemistry.

2. Ivlev model: $k(1 - e^{-cV})$, where c is a constant that is proportional to the predator's search speed.

Incorporating the half-saturation response into the whole model yields:

$$dV/dt = bV[(K-V)/K] - [kVP/(\chi + V)]$$

$$dP/dt = \beta kVP/(\chi + V) - dP$$

This model introduces the possibility of an unstable equilibrium. The Ivlev model may be incorporated in the same way, and also introduces that possibility. Instability in these cases would arise if predators keep the victim population so low at equilibrium that the primary effect of adding more victims would be to satiate predators rather than to add competing victims (see **predator satiation**).

Many other algebraic elaborations of predation models attempt to reconcile empirical work with theory. Some of these concentrate on particular interactions, like sheep and blowflies. Some are more general. The three most noteworthy general models deal with issues of wide application.

Kolmogorov introduced **time lags** to predation models. These make reproduction sensitive to preceding rather than current conditions. Time lags can introduce instability to predatory dynamics. Kolmogorov also analyzed a very general predation model and showed that predatory oscillations can never touch the density axis of either species; oscillations are thus confined to the positive quadrant where neither species becomes extinct. That result depends on two assumptions: strict determinism in the model and its restriction to two species. Stochastic models do allow for extinction of either species. Deterministic multispecies models can also produce extinctions even without stochasticity.

Another class of predation models allows **direct predator interaction**. Previous models tacitly assumed that predators interacted only indirectly by eating each other's food supply. To model direct interactions, a term, ηP , is added to the half saturation constant:

$$dV/dt = bV[(K-V)/K] - kVP/(\chi + V + \eta P)$$

$$dP/dt = \beta kVP/(\chi + V + \eta P) - dP$$

If predators compete directly (by fighting over food or defending territories), $\eta > 0$. But if $\eta < 0$, the interaction is mutualistic. Thus, the model also handles predators that exhibit features like cooperative hunting. Direct competition amongst predators adds stability to the interaction; mutualism reduces stability.

Adding an exponent λ to V in the victim self-limiting term allows that term to fit a variety of curvatures:

$$dV/dt = bV[(K-V^\lambda)/K] - kVP/(\chi + V + \eta P)$$

Models to this point had limited the death rate of predators to a constant d . But without food, predators may all die very quickly. To allow this possibility, Getz revolutionized the predator's equation. He discarded its additivity and included the effect of the predation in an expanded version of a logistic equation:

$$dP/dt = \rho P\{1 - [\zeta(\chi + V + \eta P)/kV]\}$$

where ζ is the value of V at which $dP/dt = 0$.

In the lab and the field, the oscillations of predator and victim are asymmetrical – populations grow slowly and decline precipitously. But most simple models result in symmetrical waves – populations take just as long to decline as they did to grow. Without adding to the number of coefficients, the Getz model frees predatory interactions from such unrealistic wave forms. It also pays more attention to the biological functions that determine the dynamics.

Predation models may result in an additional dynamical behavior called **chaos**. Chaotic equilibria, belying their name, are fully deterministic. But trajectories around them are so dependent on initial conditions and so variable from oscillation to oscillation that they resemble those dominated by stochastic influences.

Isocline analysis constitutes a parallel approach to modeling predation with explicit equations. Instead of specific equations, it combines properties of the interaction and inequalities of the interaction into robust models that apply to whole classes of equations. The first such model used the definition of predation, and the assumptions that (1) the underlying, unspecified equations are autonomous and continuous; (2) victims compete directly with each other; (3) predators do not; (4) predators are limited only by their victim supply; (5) victims have a positive K value; (6) predators reproduce successfully if $J < V$, where $J \geq 0$. This assumption set leads by deduction to a graph of the shapes and relationships of its zero isoclines. (The zero isocline of x in a dynamic system is the set of points (x, y) at which $dx/dt = 0$. For y 's zero isocline, $dy/dt = 0$.)

Isocline analysis can combine with linearized stability analysis – analysis based on properties of the isoclines in the neighborhood of their equilibria. The combination predicts many of the properties of predatory systems: An equilibrium will be stable if victims compete with each other in its neighborhood. It will be unstable if they are mutualistic. Thus, the better a predator at reproducing on a short supply of victims, the more likely the equilibrium will be unstable. Equilibria will often be oscillatory, but strong competition among victims eliminates the oscillations. The same interactions amongst predators have similar but weaker effects. Intraspecific interactions of the two species are not additive; instead, there are thresholds of mutualism which confer instability no matter how strong the competition in the other species. Finally, optimal use of habitats that differ in their predation coefficients can serve to stabilize the interaction (the victim-refuge model). If patches vary in victim density and predators aggregate where victims are dense, the effect on victims is like a partial refuge; such aggregative predator responses allow very low victim densities to be stable, and contribute greatly to the success of biological control.

Isocline analysis predicts the period of a predation interaction:

$$T = 4\pi / (4\alpha\gamma - \alpha^2 k_1^2)^{0.5}$$

where k_1 is the slope of the victim isocline in the neighborhood of the equilibrium, and

$$\alpha = \partial(dV/dt) / \partial P$$

$$\gamma = \partial(dP/dt) / \partial V$$

This formula succeeds if – as in laboratory systems – enough data can be obtained to estimate the isoclines and the partial derivatives.

Prudent predator concept The idea that predators moderate their individual predation rates to avoid causing the extinction of their victims.

In its extreme form, the concept requires rates that predators maximize the production rate of their victims. Given an additive model of predation, this rate is achieved when predators maintain their victims at that population generating the point of inflection of the victim's sigmoid growth curve.

But the evolutionary interests of individual predators usually clash with those of its population. If natural selection forces predators to become increasingly proficient as individuals, evolution will reduce populations of victims until the predators (and perhaps their victims) become extinct. In such circumstances, the evolution of prudent predators would require group selection. That weak force and the more potent evolutionary opposition of their victims separates such predators from extinction.

Prudent predation or an approximation of it can evolve when the fitness of the individual predator benefits from moderate predation. For example, the *Myxoma* virus evolved a profoundly reduced lethality to European rabbits in Australia: lethal strains of *Myxoma* kill so quickly that they have relatively few successful offspring. Predators, like giant California limpets, *Lottia gigantea*, that control, as individuals, at least a subpopulation of their victims for a considerable length of time can also evolve moderate predation rates. *Lottia* establish territories from which they exclude other grazers and within which

they allow algae to flourish. Smaller, wandering limpet species rapidly denude the rocks tended by *Lottia* after it is experimentally removed.

Predator satiation, swamping Reduction of the per capita loss rate to predators because of a large ratio of victim to predator individuals.

Swamping occurs because each individual predator can pursue, kill and digest victims at a limited rate. Swamping sometimes causes an increase in the net per capita growth rate of victims (V) in the presence of larger victim populations:

$$\partial \ln V / \partial V > 0$$

That is equivalent to intraspecific victim mutualism, which, paradoxically, can destabilize predatory dynamics. Periodical cicadas have evolved life cycles lasting 13 or 17 years because these prime numbers allow large synchronized cohorts to swamp generalized vertebrate insectivores.

Predator-victim coevolution Predators and victims are engaged in a co-evolutionary game of counter-adaptation. This leads to the development of features with anti-predator effects such as poisons, thorns, tissues difficult to digest, camouflage, speed, hard shells, exquisite sensory organs, special life-cycles and other life history adjustments. Predators play the game the same way, often with some of the same features. Sometimes this game may lead to a revolution in adaptation as when durophagous predators evolved in the Paleozoic. Their victims soon evolved thick armor or highly ornamented shells difficult for a predator to crush. Otherwise they disappeared or found themselves — like brittle stars, a primitive kind of starfish — restricted to refugia.

Theories of the coevolutionary game suggest that in most instances neither predator nor victim outdistances the other. One possible outcome sees both at a coevolutionary steady state. At such a state, any further improvement of a species abilities to succeed in the interaction would severely reduce its ability to fulfill some other function. Natural selection would thus produce stasis in both predator and victim because of the compromises that every species must reach when facing tradeoffs.

Another outcome suggests that the coevolution never stops. Relative rates of predator and victim improvement are balanced but exceed zero. Since neither species ever makes a net improvement in its position relative to the other, this outcome has been called the Red Queen hypothesis (because in her races it took all the running you could do merely to stay in the same place). But the Red Queen hypothesis depends on special characteristics of species, *i.e.*, features independent of all others, and with an infinite supply of genetic variability.

Some predators and victims seem to fulfill the Red Queen's assumptions. Their coevolutionary game is gene matching. Predators (such as Hessian flies) cannot succeed unless they have the right gene to counter the genetic defense of their victim (wheat). There is no evidence that such genes play any other role in either species. Moreover, once the victim's defense is countered, both species should abandon the alleles and move on to others. And once abandoned, the alleles become available for future re-use, thus supplying each species with effectively infinite variation.

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