Kinetics of Functional Response

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Suppose we have a large number of predators interacting with a large number of prey. We could build an individual-based model for the behavior of the predators, and then find overall relationships such as the total consumption rate versus prey abundance. This is how functional response curves were originally developed (Holling 1965, Real 1977).

Symbols we need are defined in the following table.

Symbol	Definition	Units
A	prey density or concentration	prey/m^2 or prey/m^3
C	consumption rate of prey per predator	prey/time or prey/time (λ P_S)
λ	capture rate	prey/time (A/S)
P_S	probability that a predator is searching	unitless
P_H	probability that a predator is handling food	unitless
q	learning coefficient; q-1 is the number of prey that must be encountered per unit time to evoke searching behavior by the predator	unitless
s	search parameter, or time to focus on the prey type	t A^{q-1}/m^2 or t A^{q-1}/m^3
S	time to search a unit of area or unit of volume	t/m^2 or t/m^3
V_{max}	maximum consumption rate	captured prey/time

At any given time, assume that a particular predator is either searching for prey or handling prey, so $P_S + P_H = 1$ or $P_H = 1 - P_S$.

Assume that predators search for prey only if prey abundance is sufficiently high (or equivalently, that predators seek patches that offer enough prey to be worthwhile). So the time to search a unit of area or volume is

[1] $$S = \frac{s}{A^{q-1}}$$

As the abundance of prey goes up, the predator searches faster, so the time required to search a unit area or unit volume (S) decreases.

Then the capture rate is

[2] $$\lambda = \frac{A}{S} = \frac{A}{s/A^{q-1}} = \frac{A^q}{s}$$

Now consider the rate of change of P_S. Over a tiny time increment dt, P_S can decrease if a prey item is caught by a predator (λ P_S dt), or increase if a predator finishes eating a prey item (V_{max} P_H dt which is the same as V_{max} (1 - P_S) dt) and resumes searching. Writing out the equation,

[3] $$P_S(t+dt) = P_S(t) - \lambda P_S(t)dt + V_{\max}(1 - P_S(t))dt$$

The three terms on the right side are P_S at the beginning of the small time increment, the decrement due to some predators catching a prey item, and the increment due to some predators completing consumption and resuming the search. Rewrite [3] as a differential equation

[4] $$\frac{dP_S}{dt} = -\lambda P_S + V_{\max}(1 - P_S)$$

Now assume that behavior is much faster than population dynamics, so it is interesting to consider equation [4] at equilibrium. The equilibrium P_S is

[5] $$P_S = \frac{V_{\max}}{\lambda + V_{\max}}$$

If P_S is not changing, then the capture rate has to match the rate of handling prey. The consumption rate $C = \lambda P_S$, so $P_S = C/\lambda$. Plug this expression and equation [2] for λ into [5] to get

[6] $$\frac{s}{A^q} C = \frac{V_{\max}}{\dfrac{A^q}{s} + V_{\max}}$$

Clean up the algebra by multiplying both sides of [6] by A^q/s to find

[7] $$C = \frac{V_{\max} A^q}{A^q + sV_{\max}}$$

Equation [7] is a type II (asymptotic, Michaelis-Menten) functional response if $q=1$, i.e. the predator starts eating the prey on first encounter. If $q \geq 2$, then equation [7] is a type III (Hill equation) functional response. This applies to a predator that will not begin (or risk) feeding until there have been several encounters with prey. Real (1977) describes many ecological situations that are likely to cause $q \geq 2$.

References

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