Derivation of Holling's Disk Equation[1]

Ethology and Behavioral Ecology

This equation was originally empirically derived by having students pick up disks of sandpaper. Thus its name. It can also be derived from a set of reasonable assumptions about foraging and that is what we will do, following Stephens and Krebs[1]

For rate maximization (R) models:

eq. 1. Rate = R = Net Energy Intake / Time

Foraging time is assumed to be composed of search time per prey item, T_S and handling time per prey item, T_H

Thus:

eq. 2 $R = E_F \ / \ (T_H + T_S) = (E - \text{cost}) \ / \ (T_H + T_S)$

Where E_F is the net energy intake and E is the total energy intake. Now, the number of prey encountered, N, is

eq. 3 $N = T_S * \lambda$

where λ is the rate at which prey are encountered (prey or patches / time).

Now, since encounters with prey (N) are assumed to be linearly related to search time (eq. 3), then both net energy intake, E_F, and handling time, T_H, should be expressible as linear functions of search time, T_S. The reason for this is that the total energy, E, should be:

eq. 4a $E = N * \bar{e}$

where $\bar{e}$ is the average energy per prey item or patch. This is a linear equation. By substitution using equation #3:

eq. 4b $E = T_S * \lambda * \bar{e}$

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[1] For additional information on other forms of this equation, see *Foraging Theory* by D. W. Stephens and J. R. Krebs 1986 or later, Princeton University Press. The original (hard to find) is: Holling, CS. 1959. Some characteristics of simple types of predation and parasitism. Can. Entom. 91:385-398.

Likewise, the handling time, T_H , would be given as:

eq. 5a $$T_H = N * \bar{h}$$

and once again, by substitution using eq. 3:

eq. 5b $$T_H = T_S * \lambda * \bar{h}$$

where $\bar{h}$ is the average handling time per prey item.

Finally, there is the matter of the cost of obtaining prey (C). Most inclusively it will include both costs involved in searching (C_S) and handing (C_H)

eq. 6a $$C = C_S + C_H = s_S * T_S + s_H * T_H$$

where s_S and s_H are the rates of accruing costs.

We commonly make the assumption that handling costs are small enough to ignore **(this is certainly not always true as you can easily imagine**). Nevertheless, using the simplifying assumption that $s_H = 0$:

eq. 6b $$C = s_S * T_S$$

We can now substitute eqs. 4b, 5b and 6b into eq. 2:

eq. 7a $$R = (T_S * \lambda * \bar{e} - s_S * T_S) / (T_S * \lambda * \bar{h} + T_S)$$

and factoring:

eq. 7b $$R = T_S *(\lambda * \bar{e} - s_S) / T_S (\lambda * \bar{h} + 1)$$

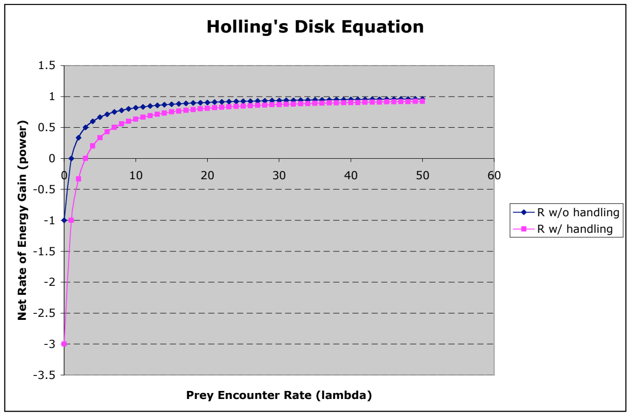
After simplifying we obtain:

eq. 8a $$R = \frac{\lambda * \bar{e} - s_s}{1 + \lambda * \bar{h}}$$

Eq. 8a is known as Holling's Disk equation. It is a fundamental equation in rate maximizing optimalization models. **The equation has a very different appearance if handling costs are high**.

eq. 8b $$R = \frac{\lambda * \bar{e} - s_s}{1 + \lambda * \bar{h}} - \frac{s_H \lambda * \bar{h}}{1 + \lambda * \bar{h}} = \frac{\lambda * \bar{e} - s_s - s_H \lambda * \bar{h}}{1 + \lambda * \bar{h}}$$

Also notice that it is not linear but instead predicts that for given mean handling times, prey energy values, and search costs per prey that the rate that energy is taken in (R) approaches an asymptote. Why must that be the case?



Symbols

λ	rate at which prey are encountered when searching (prey/time)
$\bar{e}$	mean energy per prey item (or patch) (J per prey or patch)
C	cost of obtaining prey (J)
C_H	handling cost (J)
C_S	search cost (J)
E	total energy intake (J)
E_F	net energy intake (J)
$\bar{h}$	mean handling time (time/prey)
N	number of prey encountered
R	rate of net energy gain, a power term (W or J/time)
s_H	handling cost rate – the power requirements for handling prey -- cost per unit time of handling a prey, sometimes assumed to be zero. (W or J/time)
s_S	search cost rate – the power requirements of searching for prey -- cost per unit time of searching for prey. (W or J/time)
T_S	search time per prey item
T_H	handling time per prey item