

SOME MECHANISTICALLY DERIVED FUNCTIONAL RESPONSES

YANG KUANG

Department of Mathematics and Statistics
Arizona State University, Tempe, AZ 85287-1804

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ABSTRACT. The purpose of this lecture note is to mechanistically formulate Holling type II, Beddington-DeAngelis, and ratio-dependent functional responses.

1. Holling type II functional response. The previous section shows that logistic growth model is a predator-prey model in disguise. However, in logistic growth model, the total resource amount is constant, even though the amount of free nutrient is dynamic. In addition, it is assumed that the nutrient can neither be produced, nor destroyed.

In most models commonly labeled as predator-prey models, the preys or resources are usually allowed to grow and die in highly dynamical ways. The simplistic examples of such ways for growth dynamics include exponential growth for the classical Lotka-Volterra predator-prey model,

$$\frac{dx}{dt} = ax - bxy, \quad \frac{dy}{dt} = cxy - dy, \quad (1.1)$$

the logistic growth for Holling type II predator-prey model (also called Rosenzweig-MacArthur predator-prey model)

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) - \frac{bxy}{a+x}, \quad \frac{dy}{dt} = \frac{cxy}{a+x} - dy. \quad (1.2)$$

The death dynamics is usually dominated by the predation and such terms are frequently expressed in the form of $yp(x)$ and $f(x)$ is called the predator's functional response function, or simply, *functional response*. In the Lotka-Volterra predator-prey model, $p(x) = bx$ while in Holling type II predator-prey model $p(x) = \frac{bx}{a+x}$. This begs the question of how to mechanistically derive $f(x)$. The so-called Gause-type predator-prey model is a more general and also classical form for predator-prey models (Gause 1934, Freedman 1980)

$$\frac{dx}{dt} = xg(x) - yp(x), \quad \frac{dy}{dt} = yq(x) - dy. \quad (1.3)$$

In such form, $q(x)$ is referred as the predator's numerical response function, or simply, numerical response. In most of the existing model, $q(x) = cp(x)$ where c is the conversion or yield constant. Both notions of functional and numerical responses

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are coined by Holling (1959), who studied predation of small mammals on pine sawflies. He found that predation rates increased with increasing prey population density. This resulted from two distinct effects: (1) each predator increased its consumption rate when its prey density is increased, and (2) predator density increases after prey density is increased. Holling considered these effects as two kinds of responses of predator population to prey density: (1) the functional response and (2) the numerical response.

Holling (1959) suggested a model of functional response which is often called “disc equation” because Holling used paper discs to simulate the area examined by predators. It is equivalent to the model of enzyme kinetics developed by Lenor Michaelis and Maude Menten in 1913 (Sharov 1996). This model illustrates the *principal of time budget* in behavioral ecology. It assumes that a predator spends its time on two kinds of activities:

1. Searching for prey
2. Prey handling which includes: chasing, killing, eating and digesting.

Consumption rate of a predator is limited in this model because even if prey are so abundant that no time is needed for search, a predator still needs to spend time on prey handling. Total time T equals to the sum of time spent on searching T_s and time spent on handling T_h .

Assume that a predator captured H_a prey during time T . Handling time should be proportional to the number of prey captured

$$T_h = H_a h$$

where h is time spent on handling of one prey.

We also assume that a predator searches area a (search rate) per unit of time and catch a fixed proportion ρ of all prey in there. Let x be the prey density, then

$$H_a = a\rho x T_s.$$

Hence

$$T_s = \frac{H_a}{a\rho x}.$$

Therefore

$$T = T_s + T_h = \frac{H_a}{a\rho x} + H_a h$$

and hence

$$H_a = \frac{a\rho x T}{1 + a\rho h x}.$$

This gives the functional response of the form of

$$p(x) = \frac{a\rho x}{1 + a\rho h x}.$$

Clearly, at low prey densities, predators spend most of their time on search, whereas at high prey densities, predators spend most of their time on prey handling.

Holling (1959) considered three major types of functional response:

Type I functional response is found in passive predators like spiders. The number of flies caught in the net is proportional to fly density. Prey mortality due to predation is constant (right graph on the previous page).

Type II functional response is most typical and corresponds to the equation above. Search rate is constant. Plateau represents predator saturation. Prey mortality declines with prey density. Predators of this type cause maximum mortality at low prey density. For example, small mammals destroy most of gypsy moth

pupae in sparse populations of gypsy moth. However in high-density defoliating populations, small mammals kill a negligible proportion of pupae.

Type III functional response occurs in predators which increase their search activity with increasing prey density. For example, many predators respond to kairomones (chemicals emitted by prey) and increase their activity. Polyphagous vertebrate predators (e.g., birds) can switch to the most abundant prey species by learning to recognize it visually. Mortality first increases with prey increasing density, and then declines. If predator density is constant (e.g., birds, small mammals) then they can regulate prey density only if they have a type III functional response because this is the only type of functional response for which prey mortality can increase with increasing prey density. However, regulating effect of predators is limited to the interval of prey density where mortality increases. If prey density exceeds the upper limit of this interval, then mortality due to predation starts declining, and predation will cause a positive feed-back. As a result, the number of prey will get out of control. They will grow in numbers until some other factors (diseases of food shortage) will stop their reproduction. This phenomenon is known as “escape from natural enemies” discovered first by Takahashi.

Numerical Response means that predators become more abundant as prey density increases. Reproduction rate of predators naturally depends on their predation rate. The more prey consumed, the more energy the predator can allocate for reproduction. Mortality rate also reduces with increased prey consumption. The simplest model of predator’s numerical response is based on the assumption that reproduction rate of predators is proportional to the number of prey consumed. This is like conversion of prey into new predators.

2. Beddington-DeAngelis type functional response. Many predators compete for prey. This can result in time wasted in interfering each other’s effort of capturing and consuming prey. This consideration suggests that we may extend the principal of time budget to include predator interference time T_i . Let y be the predator density. It is plausible to think this interference time is proportional to the predator density y and the amount of prey captured H_a , but inversely proportional to the prey density. Hence

$$T_i = byH_a/x.$$

Therefore

$$T = T_s + T_h + T_i = \frac{H_a}{a\rho x} + H_a h + \frac{byH_a}{x}$$

and hence

$$H_a = \frac{a\rho x T}{1 + a\rho h x + ab\rho y}.$$

This gives the functional response of the form of

$$p(x, y) = \frac{a\rho x}{1 + a\rho h x + ab\rho y}. \quad (2.1)$$

The above functional response is called the Beddington-DeAngelis type functional response (Beddington 1975, DeAngelis et al. 1975). Predator-prey models employing such form of functional response are called Beddington-DeAngelis type predator-prey models. Some important Beddington-DeAngelis type predator-prey models are systematically studied by Hwang (2003, 2004). It is known that such models behave more or less like the classical Holling type II predator-prey models.

When $a\rho hx \gg 1$ and $ab\rho y \gg 1$, then the above expression of $p(x, y)$ can be approximated by

$$p(x, y) = \frac{a\rho x}{a\rho hx + ab\rho y}. \quad (2.2)$$

This type of functional response is referred as (pure) **ratio-dependent** functional response. Predator-prey models employing such form of functional response are called ratio-dependent type predator-prey models. This may be appropriate in situations where the predator-prey interaction takes place in an ever decreasing environment (patch size) while the predators are capable of searching a very large area in a unit of time such as eagles, tigers, wolves and whales. Ratio-dependent models are well-known for its ability to exhibit the often observed deterministic mutual extinctions of both prey and predator that often characterize the extinction of many predator and prey species (Kuang and Beretta 1998, Kuang 1999, Jost et al. 1999).

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REFERENCES

- [1] Beddington J. R. (1975). Mutual interference between parasites or predators and its effect on searching efficiency, *J. Animal Ecol.*, **44**, 331-340.
- [2] Jost, C. O. Arino, R. Arditi, (1999). About deterministic extinction in ratio-dependent predator-prey models, *Bull. Math. Biol.*, **61**, 19-32.
- [3] DeAngelis D. L., R. A. Goldstein and R. V. O'Neill (1975). A model for trophic interaction, *Ecology*, **56**, 881-892.
- [4] Freedman, H. I. (1980). *Deterministic Mathematical Models in Population Ecology*, Marcel Dekker, New York.
- [5] Gause, G. F. (1934). *The struggle for existence*, Williams & Wilkins, Baltimore, Maryland, USA.
- [6] Holling, C.S. (1959). The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Canad. Entomol.* **91**, 293-320.
- [7] Holling, C.S. (1959). Some characteristics of simple types of predation and parasitism. *Canad. Entomol.* **91**, 385-398.
- [8] Hwang, T.-W. (2003). Global analysis of the predator-prey system with Beddington- DeAngelis functional response, *J. of Math. Anal. Appl.*, **281**, 395-401.
- [9] Hwang, T.-W. (2004). Uniqueness of limit cycles of the predator-prey system with Beddington- DeAngelis functional response, *J. of Math. Anal. Appl.* **290**, 113-122.
- [10] Kuang, Y. (1999). Rich dynamics of Gause-type ratio-dependent predator-prey system, *The Fields Institute Communications*, **21**, 325-337.
- [11] Kuang, Y. and E. Beretta (1998). Global qualitative analysis of a ratio-dependent predator-prey system, *J. Math. Biol.*, **36**, 389-406.
- [12] Kuang, Y., Huisman J. and Elser J.J. (2004). Stoichiometric plant- herbivore models and their interpretation, *Math. Biosc. and Eng.*, **1**, 215-222.
- [13] Leadbeater, B. S. C. (2006). The 'Droop equation- Michael Droop and the legacy of the 'cell-quota model of phytoplankton growth. *Protist*, **157**, 345-358.
- [14] Lotka A. J. (1925). *Elements of physical biology*. Williams and Wilkins, Baltimore. Reprinted as *Elements of mathematical biology*, Dover, New York.
- [15] Kooijman, S.A.L.M. (2000). *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge Univ. Press, Cambridge, UK.
- [16] Rosenzweig, M.L. (1971) Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science*, **171**, 385-387.
- [17] Volterra, V. (1926) Fluctuations in the abundance of a species considered mathematically. *Nature*, **118**, 558-60.