

Emergence of functional responses from interactions of individuals

Donald L. DeAngelis, Shu Ju, and J. Nathaniel Holland

Introduction

Ratio-dependent functional responses are regarded by many ecologists to be relatively uncommon in nature, or at least lacking in a solid mechanistic basis. Our objective was to show that such responses can be given a mechanistic basis, and to show that such responses might actually occur more commonly than thought and can be appropriate for some broad classes of consumer-resource systems, such as wading birds feeding in a wetland.

The prey-dependent Holling Type II functional response, F , can be written as

$$F = \frac{caN}{I + caN} \quad (1)$$

where a = rate at which an individual forager encounters prey by sweeping out an area (area or volume per unit time per unit forager); c = prey capture rate per encounter with prey; h = handling time of individual prey by a forager (units of time); and N = density of prey (number per unit area or volume). In all the many variations on this basic model, the functional response depends only on prey density, and all are derived by considering the instant by instant movement of a consumer through a field of resources.

Key words: consumer-resource model, host-parasitoid model, ratio-dependent model

Methods

Another class of models, that of arthropod parasitoid-host models, has long focused on an alternative conceptualization. It differs primarily in being discrete rather than continuous in time, because in many cases reproduction of hosts and parasitoids occurs periodically rather than continuously, and generations do not overlap. It is convenient to take the length of a generation as the time step. During the interval following one reproduction period to the next, a new cohort of hosts, represented as a value, N_t , at time t , decays due to parasitism, up to the next time step, $t+T$. The loss rate of

hosts during that time period can be described using the Holling Type 2 response

$$\frac{dN(t)}{dt} = -\frac{aN(t)P_t}{I + ahN_t}, \quad (2)$$

(simplified by letting $c = 1$). Here, $N(t)$ represents the instantaneous density of non-parasitized hosts during the interval t to $t+T$, and P_t is the number density of the adult parasitoids, which can be considered constant during the interval. The host density in the denominator is also considered constant here, as is frequently done, because parasitized hosts are assumed to still be alive and can be 'handled' by further parasitoids, although they are removed from the population as far as reproduction is concerned.

Results and discussion

Note that the coefficient of $N(t)$ on the right-hand side of (2) is $aP_t/(I + ahN_t)$, and thus is assumed constant through the time period t to $t+T$. When Eq. (2) is integrated over time, and subtracted from the initial number of hosts, it yields the number of parasitized hosts:

$$\begin{aligned} N_{\text{parasitized}} &\equiv N_t - N(T) = N_t \left(1 - e^{-\frac{aTP_t}{I + ahN_t}} \right) \\ &= \frac{N_t}{P_t} \left(1 - e^{-\frac{aTP_t}{I + ahN_t}} \right) P_t \end{aligned} \quad (3)$$

where the factor multiplied by P_t constitutes the functional response (see GUTIERREZ 1996). If $1 \ll ahN_t$, this reduces to an effectively ratio-dependent form

$$N_{\text{parasitized}} = \frac{N_t}{P_t} \left(1 - e^{-\frac{TP_t}{hN_t}} \right) P_t \quad (4)$$

which was originally derived by THOMPSON (1939). Note that in the limit of small N_t this approaches a resource-dependent response, and in the limit of small P_t it approaches a consumer-dependent response, but always remains strictly ratio-dependent.

Is this approximation valid in many situations? HOLLAND & DEANGELIS (2002) and DEANGELIS & HOLLAND (2006) showed that the approximation may be a good one for the case of flower pollination/seed parasitism of the senita moth on the senita cactus, using a model that has some similarity to that above, but where the time step is a day and the pollination/parasitism takes place during nights. Each night the cacti put out a new set of flowers, many of which are pollinated, and a subset of these also parasitized. Following the general idea of the host-parasitoid model above, HOLLAND & DEANGELIS (2002) modeled a consumer foraging during the night for a period T to obtain an expression analogous to Eq. (1). They then argued that the response for the senita moth-senita cactus system should be approximately ratio-dependent. Their argument was that the moths are very good at finding the host flowers, so rather than spending time searching, they simply move among flowers. However, each moth has only a few eggs to oviposit; therefore, a moth will likely be 'saturated' by available flowers, and Eq. (2) will hold. Alternatively, if the moths could not recognize flowers from a distance but had to search the area in a time-consuming way, then the response would have the form of the NICHOLSON & BAILEY (1935) function

$$N_{\text{parasitized}} = \left(\frac{N_t}{P_t} \right) (1 - e^{-aTP_t}) P_t \quad (5)$$

This is easily explained; if the moth search is limited by the area it can cover, then no matter what the density of flowers is, the fraction removed will be the same. DEANGELIS & HOLLAND (2006) confirmed this with individual-based simulations of moths and flowers.

The next question is whether the same considerations apply to a much broader class of consumer-resource interactions; that is, are there other situations that are analogous to the well-known parasitoid-host system? In fact, they could potentially apply to consumers that exploit prey, not by continually moving through space to search for prey, but by moving from site to site where prey might be and staying at each site for a period of time to stalk prey. Wading birds such as herons seem to do this. Consider the following assumptions: (1) a population of consumers moves among sites during the day, spending time at each site; any given consumer is assumed ignorant of whether a site has already been visited by other consumers and depleted of prey; (2) the number of sites at which prey may be found expands or contracts in proportion to the size of the prey population, that is, on a time scale of weeks or months. This is not an unreasonable assumption. FORTIN et al. (2005) showed that the number of subpopulations within a population expands as $N^{3/4}$. We can imagine that, if the population of prey fish

increases, then the number of sites at which wading birds might be able to catch them should increase, if not directly in proportion, at least closely. We assume then that the forager population moves among sites whose number is related to the resource population's size. The forager's are aware of what sites are likely to be occupied, but not of which sites have been temporarily depleted by foragers visiting earlier in the day.

If the number of sites available during a day is S_t , we can represent the number of depleted sites on that day as

$$S_{\text{depleted}} = S_t \left(1 - e^{-\frac{aTP_t}{1+ahS_t}} \right) \quad (6)$$

The above only represents what happens in a single day, but it provides the starting point to develop a continuous-time model of plant and pollinator/parasite populations over longer times. In Eq. (4), S_{depleted} should be proportional both to the daily food intake of the wading birds, and hence related to their biomass gain, and to the loss of fish from the population, and hence to their biomass loss. We can write for the fish biomass, N_t and wading bird biomass P_t changes on day t . If fish biomass is related to the number of sites as $N_t = GS_t$, and a is the fraction of fish biomass converted into wading bird biomass, then we have

$$N_{t+\Delta t} = N_t + r \left(1 - \frac{N_t}{K} \right) N_t \Delta t - \left(1 - e^{-\frac{aTP_t}{1+ahN_t/G}} \right) N_t \Delta t \quad (7a)$$

$$P_{t+\Delta t} = P_t + \gamma \left(1 - e^{-\frac{aTP_t}{1+ahN_t/G}} \right) N_t \Delta t - m_{\text{bird}} P_t \Delta t \quad (7b)$$

where m_{bird} is the wading bird biomass loss rates. We can replace N_t by $N(t)$ and P_t by $P(t)$ because these are now considered to be continuous variables on a longer time scale in which a day is just an increment. We can now write these as continuous time equations,

$$\frac{dN(t)}{dt} = r \left(1 - \frac{N(t)}{K} \right) N(t) - \left(1 - e^{-\frac{aTP(t)}{1+ahN(t)/G}} \right) \frac{N(t)}{P(t)} P(t) \quad (8a)$$

$$\frac{dP(t)}{dt} = \gamma \left(1 - e^{-\frac{aTP(t)}{1+ahN(t)/G}} \right) \left(\frac{N(t)}{P(t)} \right) N(t) - mP(t) \quad (8b)$$

The functional response,

$$\left(1 - e^{-\frac{aTP(t)}{1+ahN(t)/G}} \right) \left(\frac{N(t)}{P(t)} \right) \quad (9)$$

is not ratio-dependent. We can now examine conditions under which $ahN(t) \ll 1$. This will occur when the wading birds tend to stay in one place for a long period of time and move infrequently. It is quite plausible that this is often the case.

It appears that a number of conditions favor the emergence of ratio-dependence in the functional response:

- Some sort of possible overlap of several predators on a given prey (individual, or site with individuals) occurs, so 'sharing' of prey among predators is essential.
- There is a scaling up from the foraging period to a longer time scale.
- Thus, there is a shorter time scale over which encounters occur but the populations do not effectively change, and a longer time scale over which populations change.

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Authors' addresses: D.L. DeAngelis, Florida Integrated Science Center, U.S. Geological Survey, Department of Biology, University of Miami, Coral Gables, FL 33124. E-mail: ddeangelis@bio.miami.edu
 Shu Ju, Department of Biology, University of Miami, Coral Gables, FL 33124.
 J. Nathaniel Holland, Department of Ecology and Evolutionary Biology, MS-170, Rice University, Houston, TX 77005.