

Short communication

Emergence of ratio-dependent and predator-dependent functional responses for pollination mutualism and seed parasitism

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Abstract

Prey (N) dependence [$g(N)$], predator (P) dependence [$g(P)$ or $g(N,P)$], and ratio dependence [$f(P/N)$] are often seen as contrasting forms of the predator's functional response describing predator consumption rates on prey resources in predator–prey and parasitoid–host interactions. Analogously, prey-, predator-, and ratio-dependent functional responses are apparently alternative functional responses for other types of consumer–resource interactions. These include, for example, the fraction of flowers pollinated or seeds parasitized in pollination (pre-dispersal) seed-parasitism mutualisms, such as those between fig wasps and fig trees or yucca moths and yucca plants. Here we examine the appropriate functional responses for how the fraction of flowers pollinated and seeds parasitized vary with the density of pollinators (predator dependence) or the ratio of pollinator and flower densities (ratio dependence). We show that both types of functional responses can emerge from minor, but biologically important variations on a single model. An individual-based model was first used to describe plant–pollinator interactions. Conditional upon whether the number of flowers visited by the pollinator was limited by factors other than search time (e.g., by the number of eggs it had to lay, if it was also a seed parasite), and on whether the pollinator could directly find flowers on a plant, or had to search, the simulation results lead to either a predator-dependent or a ratio-dependent functional response. An analytic model was then used to show mathematically how these two cases can arise.

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1. Introduction

A functional response for a consumer–resource system was originally proposed to represent how

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consumer (P) rate of resource consumption (amount of resource consumed per unit time) changes with the size or density of the resource population (N) (Solomon, 1949). Today there are three common ways of biologically and mathematically expressing such functional responses for consumer–resource systems: (1) prey dependence [$g(N)$], (2) predator dependence [$g(P)$ or $g(N,P)$], and (3) ratio dependence [$g(P/N)$] (Gutierrez, 1996; Abrams and Ginzburg, 2000). For prey dependence, the consumption rate of the resource per unit consumer (that is, the consumer's functional response), varies with resource density alone. For predator dependence, the consumption rate of the resource depends on the consumer density or the consumer and resource densities. For ratio dependence, the consumer's functional response depends only on the ratio of consumer and resource densities. Much debate occurs over which functional response is most appropriate (Berryman, 1992; Ginzburg and Akçakaya, 1992; Arditi and Saiah, 1992; Gutierrez, 1992; Gleeson, 1994; Sarnelle, 1994; Abrams, 1994; Berryman et al., 1995; Akçakaya et al., 1995; Abrams, 1997), with no clear consensus among ecologists (Abrams and Ginzburg, 2000; Jost, 2000). Although the ratio-dependent functional response has been in the literature for many decades (Thompson, 1939; Leslie, 1948), it is particularly controversial to many ecologists, to a large degree because no clear mechanistic derivation has been presented, as has been done in the case of other functional responses. Our intention here is not to review or resolve this debate, but to explore how such different functional responses may apply to other, less well recognized consumer–resource systems, mutualisms in particular (Holland et al., in press).

In the same way that predator–prey systems give rise to assumptions of different forms of functional responses, other types of consumer–resource interactions lead to alternative models of prey, predator, and/or ratio dependence. Among these systems are plant–insect interactions in which insects are pollinators, seed parasites, or both. Pollinators both exploit resources from flowers and pollinate them (so are usually classified as mutualists). Insect seed parasites oviposit on flowers or fruits such that their larvae consume the seeds. What is characteristic about both cases is that the consumer (mutualist or parasite) utilizes resources from the reproductive structures of plants, but usually does not physically remove these

structures from the population of apparent resources. Therefore, many insects may spend time in handling the same individual structures. Insect parasitoids also have this same characteristic, although they search out and oviposit on host insects, rather than plant hosts.

For these cases, “functional response” is defined to mean the fraction of flowers pollinated, or seeds or insects parasitized. In the well-known Nicholson–Bailey parasitoid model this fraction has the form of a predator-dependent response; $(1 - e^{-sPT})$ (Nicholson and Bailey, 1935), where P is the parasitoid density and s (search rate) and T (time spent searching) are constants. Thompson (1939) was first to derive an alternative parasitoid model on the basis of probability theory, describing the fraction of prey, of density N , parasitized by a searching parasitoid of density P , as ratio-dependent; $(1 - e^{-sPT/N})$, where the functional response depends on P/N rather than P (see Gutierrez, 1996; p. 66). This apparent dichotomy is analogous to that between the prey- and ratio-dependent responses for predator–prey interactions. Because ratio dependence was not originally derived mechanistically, it may be difficult to see the biological connection between the two responses.

Here we show that both of these functional responses may emerge from mechanistic models differing only in one assumption. To demonstrate this, we use two individual-based models describing insect pollination of flowers. (A model of seed or insect parasitism would be similar.) We then interpret the results of these models from a single analytic model that can produce either a ratio-dependent or predator-dependent (i.e., pollinator-dependent) function.

2. Materials and methods

2.1. Individual-based model

Individual-based models (IBMs) simulate populations or systems of populations as being composed of discrete agents that represent individuals or groups of individuals, with sets of traits that may vary among individuals. Each agent has a unique history of interactions with its environment and other agents. IBMs may be useful in developing a better understanding of functional responses, as they can capture

the variation among individuals that is relevant to the questions being addressed. Here IBMs are used to simulate a number of individual insects pollinating individual flowers of a plant or patch of plants over some time period. An example is senita cactus flowers, which bloom for only one night, being pollinated and oviposited on by senita moths during the course of that night (Holland and DeAngelis, 2002).

2.2. Model 1

We performed simulations with different numbers of flowers, $F = 100, 200, 300,$ or 400 during the night, subjected to visits from insect pollinators present in the area in different numbers, $M = 5, 10, 15, \dots,$ or 150 . Each pollinator was simulated independently, and allowed to spend some randomly chosen fraction of the night (from 0 to 1) around the plant. The pollinator was simulated to visit and pollinate flowers on the plant. The steps in this simulation were as follows. For each pollinator:

- The fraction of the night (10 h) that the pollinator was in the vicinity of the plant was chosen from a uniform random distribution between 0 and 1.
- Using the rate of flowers per hour visited (assumed the same for all pollinators), a particular realization of flowers visited (and pollinated) was chosen using a Poisson distribution in time.
- Which specific flowers were visited by the pollinator was chosen randomly. Visits to each individual flower were recorded. It was possible for more than

one insect to visit the same flower, but multiple visits to one flower counted as one pollination.

- No explicit assumption was made on ‘handling’ time needed to pollinate a flower, as it is likely to be small. Nonetheless, the number of visits of pollinators to flowers was assumed small (mean of two visits per hour). This small rate may be reasonable for pollinator/seed predators, because their visits to plants are also associated with ovipositing a limited number of eggs.

The number of flowers pollinated was recorded for each of the $30 \times 4 = 120$ cases simulated. Because this was a Monte Carlo simulation, stochastic variation was incorporated.

Using least squares, we fit to the number of flowers pollinated at the end of the night, both a predator-dependent function,

$$P_1(T) = F(1 - e^{-\alpha_1 M}) \quad (1)$$

and a ratio-dependent function,

$$P_2(T) = F(1 - e^{-\alpha_2 M/F}) \quad (2)$$

with one fitting parameter for each model; α_1 and α_2 , respectively. The terms within the parentheses of (1) and (2) are the functional responses; that is, fraction of flowers pollinated.

For model 1 the ratio-dependent response was the best fit (Fig. 1). The parameter values and the least square values for the entire set of four simulations for each of the two cases (predator versus prey dependence) were: $\alpha_1 = 0.032$ (LS = 52,371) (predator dependence) and $\alpha_2 = 10.4$ (LS = 9000) (ratio depen-

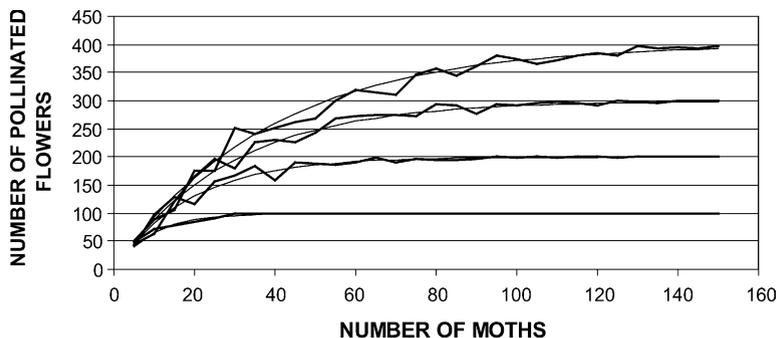


Fig. 1. Least square fits of ratio-dependent functional response to data generated by individual-based model 1 of flowers pollinated by insects on a single plant or cluster of plants. Four different numbers of flowers were used: 100, 200, 300, and 400. The parameter value and least square value are: $\alpha_2 = 10.4$ (LS = 9000).

dence). Note that these statistics are cumulative variance explained among the four simulations for each of the two cases.

2.3. Model 2

Model 2 was identical to model 1 with one exception; the effective surface area of the model plant or patch of plants was divided into a large number of spatial cells, only some of which were flowers. In model 1 we assumed that pollinators were able to detect flowers from a distance and land directly on flowers, although the flowers visited were chosen at random. In model 2, we simulated the pollinators landing on spatial cells on the plant or plants at random, some of which had flowers and some of which did not. Thus the pollinator was simulated as searching. Visits to each spatial cell were recorded and the number of flowers pollinated was calculated based on the number spatial cells that were flowers and had at least one visit.

All simulations had 1000 spatial cells, but each had 100, 200, 300, or 400 flowers (F), as well as 5, 10, 15, 20, . . . , or 150 pollinators (M). The number of flowers pollinated was recorded for each of the $30 \times 4 = 120$ cases simulated. As in model 1, a least squares fit of the number of flowers pollinated by the end of the night was made for both functional responses of Eqs. (1) and (2). In this case, however, the predator-dependent response was the best fit (Fig. 2). Parameter values and the least square values were: $\alpha_1 = 0.018$ (LS = 6180) (predator dependence) and $\alpha_2 = 6.2$ (LS = 61,400) (ratio dependence). As with model 1, parameter and LS values are

cumulative for all four simulations of each of the two alternative cases.

2.4. Analytic model

Why did two different functional responses, ratio-dependent and predator-dependent, emerge from the pollination model that had only a ‘minor’ difference in using flowers or spatial cells as the basic units that insects visited? A mathematical model that has possible relevance can be derived starting with a traditional prey-dependent functional response that describes the second-by-second dynamics of insect flower pollination or oviposition during a given night. In particular, consider a standard Holling type 2 (prey-dependent) functional response, which incorporates both handling time and search time to describe pollination or oviposition of flowers over the time period of a night:

$$\frac{dF}{dt} = -\frac{aMF}{1 + ahF} \quad (3)$$

where M is the mean density of insects (number per unit area) that are in the vicinity of a given plant during the night, F the density of unpollinated flowers, a the rate coefficient at which flowers are found by searching pollinators, and h time spent handling each flower. The right hand side represents the rate at which flowers are pollinated or removed from the population of unpollinated flowers (a similar equation could represent rate of oviposition). Eq. (3) can be derived from first principles (e.g., Case, 2000). The insects move through an area as they search and encounter flowers, spending some time on each flower before they resume their search. In

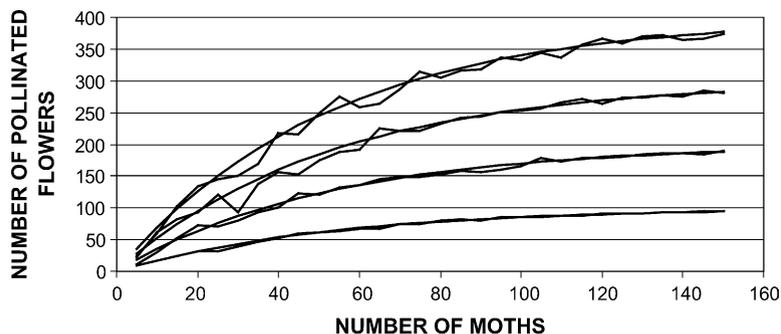


Fig. 2. Least square fits of predator-dependent functional response to data generated by individual-based model 2 of flowers pollinated by insects on a single plant or cluster of plants. Four different numbers of flowers were used: 100, 200, 300, and 400. The parameter value and least square value are: $\alpha_1 = 0.018$ (LS = 6180).

this model of one night, insect number, M , is assumed to remain constant.

Eq. (3), however, is not a good representation of the decrease of unpollinated flowers, because in reality, although the number of unpollinated flowers is reduced through time, the total number of flowers is not, and previously pollinated flowers can be visited multiple times by pollinators. Thus, F in the denominator of (3) should be constant through time. To show this mathematically we use a new variable for unpollinated flowers, U , and rewrite Eq. (3) as,

$$\frac{dU}{dt} = -\frac{aMU}{1 + ahF} \quad (4)$$

Note that the coefficient of U on the right-hand side of (4) is $aM/(1 + ahF)$, and thus is assumed constant through the night. When Eq. (4) is integrated over the second-by-second dynamics of a night and subtracted from the initial number of flowers, it yields the number of pollinated flowers,

$$P(T) = F - U(T) = F(1 - e^{-aTM/(1+ahF)}) \quad (5)$$

where $T=1$ represents one night. The terms within the parentheses represent the functional response. An equation of the form of (5) was derived by Hassell (1978); Eq. (A1.21) and similarly in Arditi and Saiah (1992); their Eq. (7). Those authors noted that in the two limiting cases of $1 \gg ahF$ and $1 \ll ahF$, $P(T)$ reduces to forms $P_1(T)$ and $P_2(T)$, respectively. The exponent approaches $-TM/hF$ (ratio-dependence) in the case that $1 \ll ahF$, and $-aTM$ (predator-dependence) in the case that $1 \gg ahF$.

In our IBM simulations (model 1 and model 2) we made no assumptions concerning handling time, so the above analytic model might not seem initially applicable. But the IBMs do make implicit assumptions. The assumption made in model 1 that some mean number of flowers was visited by an individual pollinator during a night in model 1 may be operationally equivalent to assuming a handling time limiting visits, even though the actual time spent visiting an individual flower was nonexistent in the model. This limitation on flowers visited is reasonable to assume in the case of pollinator/parasites, which may have only a limited number of eggs to oviposit, and so would stop pollinating after a few visits. This limitation in visits to flowers, although not explicitly linked to handling time, could be equivalent to a dominance of effective handling time in Eq.

(3) and a ratio-dependent response. In model 2, the fact that there was no handling time, and that the pollinator was modeled as searching for flowers, led to the predator-dependent functional response.

3. Discussion and conclusion

Functional responses of Eqs. (1) and (2) resemble previous models of responses in the literature, the probability-based parasitoid model of Thompson (1939) and the predator-dependent parasitoid model of Nicholson and Bailey (1935). What we have done, however, is to show mechanistically the similar origin of both the predator-dependent and ratio-dependent forms of the functional response. Our explanation is somewhat similar to that suggested by Hassell (1978) and Arditi and Saiah (1992). However, for those authors the ratio dependence arises in Eq. (5) from the occurrence of a large prey handling time by the predators. We suggest that other factors in the behavior and level of perception of the pollinator can lead to ratio dependence. In particular, pollinators that visit relatively few flowers (due to limited number of eggs to lay) and are able to find the flowers on a plant or cluster of plants directly without much searching, may create a ratio-dependent response for the fraction of those flowers pollinated. Our simulation data also suggests that it may be difficult to tell predator-dependent and ratio-dependent responses apart in empirical data (even the simulation output are not easily distinguished by eye), so that sophisticated statistical techniques may be needed.

Our application was to a mutualism, in particular pollination mutualism, but essentially the same applies to pre-dispersal seed parasitism. This is a general result that should hold for most consumer–resource interactions in which the consumer does not immediately decrease the chance that the resources will be “handled” by other searching consumers. These cases of consumer–resource interactions will likely often be found embedded within interspecific mutualisms. As more attention is given to consumer–resource interactions within mutualism (Holland et al., in press), the appropriate types of functional responses for mutualism will be more fully investigated. With our present level of knowledge, both ratio- and predator-dependent functional responses should be considered equally

valid for such consumer resource interactions embedded within mutualism. More generally, we repeat Jost's (2000) conclusion that it may be that which form of functional response is best or most appropriate depends on the biology of the particular consumer–resource interactions being investigated. In evolutionary time, it is certainly feasible for natural selection to favor species traits that influence one or both of search and handling times.

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