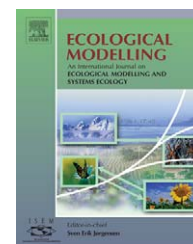


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Modelling predation in functional response

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ABSTRACT

Functional response is important in understanding the dynamics of predator–prey systems—it is essentially the interpretation of a bio-assay system in which individual predators have access to fixed numbers of prey for a given period of time. The classical approach to the problem has entailed the use of mechanistic models to interpret the data, but more recently several papers have argued that the use of simple logistic regression is both more consistent with the nature of the data and allows for the stochastic variation inherent in the system. Nevertheless, both the classical approach and this newer interpretation focus only on the modelling of means, and ignore the variability of the data. Another overlooked difficulty is that many published data sets display over-dispersion which itself may be a function of prey density. In this paper we present some models which, as well as modelling the mean response, also account for the over-dispersion. The beta-binomial is a common model for admitting extra-variation, and here we develop some variants that allow a dependency on prey density. We also develop some new models based on stochastic counting processes. These models are compared and contrasted on a strict likelihood basis. It is found that beta-binomial models provide a markedly better fit to the data than do simple binomial models. The best-fitting counting process model is almost as good (in likelihood terms) as the best-fitting beta-binomial model. We argue that the counting process models offer richer insights into the predation process than do the other more ‘descriptive’ models.

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1. Introduction

“The number of prey that an individual predator kills (or the number of hosts a parasitoid attacks) is a function of prey density and is known as the functional response”. The above definition is due to Juliano (2001) and although he attributes the phrase ‘functional response’ to Holling (1959a), the term was originally coined by Solomon (1949). The principle of the functional response assay is straightforward: the experimental set-up is essentially a bio-assay system in which individual predators are given access to fixed numbers of prey for a given period in a (usually) small arena according to some exper-

imental design. The design itself usually comprises several ‘treatment’ (or prey) levels arranged in a geometric series, which possibly owes more to classical bio-assay (cf. Finney, 1971) than to specific experimental concerns. The majority of assays utilise simple arenas in which either leaf discs (or discs of an inert material) are used for the assay. The outcome of such experiments in terms of the number of prey predated (or hosts parasitized) plotted against the initial number available gives a basic response curve that can be described by some form of regression; this is the basic idea of functional response. Functional response is the essential starting point for quantitative studies of predator–prey (or parasitoid–prey)

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interactions. The Juliano reference (op. cit.) and Section 2.4 of the recent book by Hassell (2000) give excellent accounts of functional response from an ecological standpoint, Juliano, in particular, giving some details of the current methods of fitting non-linear models to data. Mills and Getz (1996) give a useful account of general host–parasitoid models in the historical context of biological control, in which functional response is a key component.

In another paper Holling (1959b) developed a simple model called the ‘disc equation’ in which he derived the expected number of prey eaten as a non-linear function of initial prey number and available time. He used two parameters: a , the instantaneous ‘attack rate’, and T_h , the ‘handling time’; a is, in fact, the product of the rate of searching and the probability of finding a prey. The equation takes the form:

$$n = \frac{aNT}{1 + aT_h N} \quad (1)$$

where n is the number of prey eaten, N the initial number of prey and T is the total duration of the assay—the model assumes sampling with replacement. Hassell and others (Rogers, 1972; Rogers and Hassell, 1974; Beddington et al., 1976; Hassell et al., 1977) developed this into a formal framework, and, in particular, derived a corresponding equation for sampling without replacement. Rogers (1972) is attributed with developing this ‘without replacement’ analogue known as the ‘random predator equation’, in which n is the solution of the equation:

$$n = N\{1 - \exp[-a(T - T_h n)]\}, \quad (2)$$

where the negative exponential function accounts for the declining numbers of prey due to sampling without replacement. However, as Juliano (2001) pointed out, many authors continued to use the ‘with replacement’ equation even when their data were collected without replacement. Notice that Eq. (1) represents the solution of a linearised version of (2) where the exponential function is replaced by $1 - a(T - T_h n)$.

Another complication arises from arguments about the shape of the response curve. Holling (1959a) distinguished between the function (1) – essentially concave increasing in N – and a sigmoid function in which there is an initial delay. Hassell et al. (1977) formalised this by making the parameter a in (1) a function of the initial number of prey N . Juliano (2001) provides a very clear description of the various models, suggesting in his equation 10.2 the very general form $a = (d + bN)/(1 + cN)$, and then de-constructing it in Table 10.1 via some examples. Many of the arguments relate to ecological theory and need not concern us here; nevertheless, they appear to have complicated the mathematics and confused successive generations of ecologists. Functional response for parasitoid–host interactions involves similar arguments – its mechanistic justification also starting with Holling’s disc equation – but uses the complement of non-encounter (hosts are not eliminated in the parasitization process, so can be visited more than once) to determine the number of hosts parasitized.

To statisticians three features of all this are immediately apparent: one is the essentially mathematical argument which seems to focus exclusively on estimation of parameters such as ‘handling time’, and the derivation of a mean response function to describe experimental data. This precludes any discussion of the statistical nature of the data, particularly their variability. Second, nearly all the responses are predicated on Holling’s (1959b) equation (1) and its derivatives in which the binomial-like nature of the data is ignored—estimation was usually by simple least squares, though, increasingly, non-linear least squares is being advocated (Morales-Ramos et al., 1996; Juliano, 2001). And finally, even though Holling hinted at a process, his handling time has nearly always been taken as deterministic.

More recently the second of these points has been addressed in papers by Trexler et al. (1988) and Casas and Hulliger (1994) who have questioned some of the detailed arguments and pointed to the natural use of a binomial model as the basis for estimation. Fernando and Hassell (1980) also noted this but preferred to adhere to least squares estimation rather than maximum likelihood as advocated by the later critics. The Holling equation (1) does have an asymptote, T/T_h , as $N \rightarrow \infty$, and Casas and Hulliger commented that the estimation of such an asymptote is not straightforward when the natural or ‘canonical’ binomial model is used. Both Trexler et al. (1988) and Casas and Hulliger (1994) used the data of Hassell et al. (1977), stressing the variability of the response and its effective stochastic nature. Casas and Hulliger (1994) also commented on the over-dispersion of the data, i.e. the fact that the variance at a given design point is greater than would be expected from a binomial model (see, for example, Collett, 2002). Indeed, one of the driving forces behind this paper was the need to find a suitable methodology for modelling the variance associated with functional response in large-scale stochastic models of predator–prey systems in biological control (Skirvin et al., 2002).

Exceptions to the deterministic rule are in two papers by Curry and co-authors. In the first, Curry and DeMichelle (1977) draw an analogy between predator–prey interactions and queuing systems. The authors treat the inter-arrival time as the prelude to digesting the prey which then effectively takes the service time. The authors demonstrate that the expected number of prey captured is identical to the Holling disc equation. In a second paper, Curry and Feldman (1979) turn their attention to the model with depletion, and demonstrate that the stochastic model deviates from the classical deterministic model proposed by Rogers (1972). This work is rarely referenced.

In this paper we take the original data of Hassell et al. (1977) as presented in Casas and Hulliger (1994) and analyse them using several different models. In our view, simply modelling means is not sufficient—the variance also needs to be modelled. Lindsey (1999) lists several classes of model with over-dispersion for binomial-like data, but notes that these are essentially descriptive. Nevertheless, we illustrate how these data can be well-modelled using models based on the beta-binomial distribution. In an earlier paper (Faddy and Fenlon, 1999), we showed how, using stochastic birth-process modelling, it is possible to model over-dispersion in binomial-like

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