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A predator–prey model with generic birth and death rates for the predator

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ABSTRACT

We propose and study a predator–prey model in which the predator has a Holling type II functional response and generic per capita birth and death rates. Given that prey consumption provides the energy for predator activity, and that the predator functional response represents the prey consumption rate per predator, we assume that the per capita birth and death rates for the predator are, respectively, increasing and decreasing functions of the predator functional response. These functions are monotonic, but not necessarily strictly monotonic, for all values of the argument. In particular, we allow the possibility that the predator birth rate is zero for all sufficiently small values of the predator functional response, reflecting the idea that a certain level of energy intake is needed before a predator can reproduce. Our analysis reveals that the model exhibits the behaviours typically found in predator–prey models – extinction of the predator population, convergence to a periodic orbit, or convergence to a co-existence fixed point. For a specific example, in which the predator birth and death rates are constant for all sufficiently small or large values of the predator functional response, we corroborate our analysis with numerical simulations. In the unlikely case where these birth and death rates equal the same constant for all sufficiently large values of the predator functional response, the model is capable of structurally unstable behaviour, with a small change in the initial conditions leading to a more pronounced change in the long-term dynamics.

1. Introduction

The first continuous-time predator–prey model was the Lotka–Volterra model [1, p. 63]. It was proposed in the 1920s by Volterra [2], and independently in a different context by Lotka [3], and was subsequently named after them. It is simple to state. Indeed, if we let $N = N(t)$ and $P = P(t)$ represent, respectively, the number or density of prey and predators at time $t \geqslant 0$, then the model is:

$$\left.\begin{array}{l} \left.\begin{array}{l} \frac{dN}{dt} = rN - aNP, \\ \frac{dP}{dt} = \chi aNP - dP, \end{array}\right\} t > 0, \\ N(0) \geqslant 0, \quad P(0) \geqslant 0, \end{array}\right\} \qquad (1)$$

where r, a, χ, and d are positive constants. The terms $rN, -aNP, \chi aNP$, and $-dP$ can be justified by making, respectively, assumptions (A1), (A2), (A3), and (A4), as follows:

(A1) the average prey per capita growth rate in the absence of predation is a constant r;
(A2) the average prey consumption rate per predator, also called the functional response of the predator or predator functional response, increases linearly in the prey population N, specifically as aN;
(A3) the average predator reproduction rate, per predator, is proportional, with constant of proportionality χ, to the average prey consumption rate per predator or predator functional response;
(A4) the average per predator death rate is a constant d.

Model (1) can be justified in other ways [4, p. 127], but our term by term approach is perhaps the most useful in facilitating discussion of its weaknesses. Clearly assumptions (A1) and (A2) are too simple to be realistic. From (A1), the prey population would grow without bound in the absence of the predator, which obviously could not happen in the real world. A reasonable replacement for assumption (A1), and one which is often made [5, pp. 94–102], is:

(B1) in the absence of predation, the prey population satisfies logistic growth, that is, $dN/dt = rN(1 - N/K)$ for positive constants r, K.

From assumption (A2), the predator functional response grows without bound in the prey population N. In other words, individual

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predators have an unlimited ability to catch and consume prey. However, in reality, this ability will be limited, since it will take time for a predator to capture, consume, and digest every particular food item. Therefore, whilst it may be sensible to assume that the predator functional response is an increasing function of the prey population N, it should not grow without bound in N but rather saturate for N large. The simplest function which satisfies these criteria is called the Holling type II functional response and has the form $aN/(1+bN)$ for positive constants a, b. The Holling type II functional response is perhaps the most widely used predator functional response [6]. Accordingly, we replace assumption (A2) by:

(B2) the predator functional response is an increasing yet saturating function of the prey population N, specifically taking the form $aN/(1+bN)$ for positive constants a, b, known as Holling type II.

Collecting assumptions (B1), (B2), (A3), and (A4), we arrive at the Rosenzweig–MacArthur model [5, p. 95]:

$$\left.\begin{array}{l}\left.\begin{array}{ll}\frac{dN}{dt} & = rN\left(1-\frac{N}{K}\right)-\frac{aNP}{1+bN}, \\ \frac{dP}{dt} & = \frac{\chi aNP}{1+bN}-dP,\end{array}\right\} t>0, \\ N(0) \geqslant 0, \quad P(0) \geqslant 0.\end{array}\right\} \tag{2}$$

The Rosenzweig–MacArthur model is certainly more realistic than the Lotka–Volterra model, and has been gainfully employed in many real-world applications [5, p. 46 and chapter 14]. Nevertheless, its underlying assumptions are open to improvement, and in particular we now address assumptions (A3) and (A4).

Given that prey consumption fuels the activity of the predator, it is sensible to suppose, as in assumption (A3), that the average predator reproduction rate, per predator, is increasing in the predator functional response. However, assumption (A3) claims more specifically that the per predator reproduction rate increases *linearly* in the predator functional response. How realistic is this? There is empirical evidence, for some arthropod predator species, that the birth rate per adult female (egg-laying rate) *can* increase linearly in the predator functional response (rate of prey consumption), across a range of small to intermediate levels of the predator functional response [7, Figs. 10 and 13(c)]. Therefore, assuming that the proportion of the predator population composed of females capable of reproduction is a (time-invariant) constant ζ, and that the predator functional response F remains at small to intermediate levels, then in some circumstances the total reproduction rate for predators can be approximated by $(\zeta P)(eF) = P(\zeta eF)$, where e is a positive constant, so that the predator reproduction rate per predator is ζeF, which increases linearly in the predator functional response F. In summary, a case can be made for assumption (A3) in some circumstances.

There are circumstances, however, in which assumption (A3) is not so readily supportable. A certain level of energy intake is needed before a predator can reproduce, so for all sufficiently small values for the predator functional response, predator reproduction will be zero rather than linearly increasing in the predator functional response. Indeed, the complete cessation of breeding in predator populations, during times of low prey density, has been observed for various real world predator–prey systems [8, Table 1]. In addition, there is experimental evidence, for at least two arthropod predator species, showing that the reproduction rate of an adult female can reach a plateau level if its prey consumption rate becomes sufficiently high [7, Figs. 13(a) and 13(b)]. In any event, there will always be a limit to the rate at which an individual predator can reproduce. Hence it seems reasonable to assume that the reproduction rate of a female predator that is capable of reproduction, if represented solely as a function of the predator functional response F, can always be bounded above by cF for some constant $c>0$. Our remarks suggest that an improvement on assumption (A3) can be made as follows:

(B3) the predator reproduces sexually; the proportion of predators composed of females capable of reproduction is a constant $\zeta > 0$; the average reproduction rate, per reproducing female, is a function B of the predator functional response F such that
(i) $B(0) = 0$,
(ii) for $F \geqslant 0$, we have $0 \leqslant B(F) \leqslant cF$ for some constant $c > 0$, and we also have $dB/dF \geqslant 0$,
(iii) $dB/dF > 0$ either for $F \in [F_1, \infty)$ where F_1 is a non-negative constant, or for $F \in [F_1, F_2]$ where F_1 and F_2 are constants with $0 \leqslant F_1 < F_2$.

Finally, assumption (A4) is clearly not sensible, since it claims that the per predator death rate is independent of the predator functional response. In reality, a predator will need to consume prey at some minimal rate to avoid death by starvation or by the consequences of weakness brought on by excessive hunger. As its prey consumption rate increases from a small to intermediate value, we might expect a predator to be healthier, and therefore less likely to die in the near future. But provided the predator has a sufficiently high prey consumption rate, then further increases to this rate may have little impact on its short-term chance of death. In view of our observations, we propose an alternative to assumption (A4):

(B4) the average per predator death rate is a function D of the predator functional response F; for $F \geqslant 0$, we have $0 < d_m \leqslant D(F) \leqslant d_M$ where d_m, d_M are constants; for $F \geqslant 0$, we have $dD/dF \leqslant 0$.

Collecting assumptions (B1) to (B4) yields a model that has not, to our knowledge, previously been studied. Our objective in this paper will be to study it. Although our model is new, we are not the first to consider breeding and mortality assumptions for predators that are more realistic than those stated, respectively, in assumptions (A3) and (A4). For example, Kokko and Ruxton have studied a discrete-time predator–prey model in which: (i) adult predators and adult prey make optimal breeding decisions which allow them to vary their brood size; (ii) the survival rate of a parent decreases if it has more offspring to raise; and (iii) the survival rate of offspring decreases with the number of siblings [8]. Kokko and Ruxton found by numerical simulation that the dynamics of their model are complex – breeding suppression in either the predator or the prey can be either stabilising (reducing the variability of the dynamics) or destabilising. Nakazawa et al. have considered a continuous-time resource-consumer model, where the resource and consumer could represent, respectively, prey and predator populations [9]. Their model is based on these assumptions: (i) the consumer (predator) switches from reproductive to non-reproductive behaviour when the resource (prey) becomes less abundant; and (ii) non-reproducing consumers (predators) have lower mortality than reproducing ones, to represent the idea that there is a survival cost associated with reproduction. From numerical simulations of their model, Nakazawa et al. show (amongst other results) that resource-dependent reproductive adjustment can stabilise the dynamics. Note also that we have performed an analysis of a continuous-time predator–prey model with variable per predator death rate in [10].

We outline the format for the rest of this paper. In Section 2, we state our new model explicitly and comment on the positivity, boundedness, existence, and uniqueness of solutions to it. In Section 3, we find the fixed points of the model. The local stability of these fixed points is investigated in Section 4. In Section 5,