Modulation of predator–prey interactions by the Allee effect

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ABSTRACT

An Allee effect arising from density-dependent mating success can have significant impacts at the ecosystem level when considered in the context of predator–prey interactions. These are captured by a mathematical model for the exchange of biomass between a structured predator population (continuous weight distribution) and a resource. Because the predator's mating success affects the amount of resources required for the production of offsprings and their future growth into mature organisms, it influences the flux of biomass between trophic levels. Under simple assumptions, the equations can be reduced to an equivalent unstructured predator–prey model in which the Allee effect modulates the predation rate: the mating probability multiplies the rate of predator growth as well as the rate of resource depletion. Implications of the Allee effect for the bifurcation structure and equilibrium densities are examined. The model is compared to a modified version in which the Allee effect instead modulates the assimilation efficiency, hence the mating probability does not appear in the dynamical equation for the resource density. Both models exhibit qualitatively similar dynamics. However, compared to the model in which the Allee effect modulates predation, the model in which the Allee effect modulates assimilation efficiency predicts (i) unrealistically inefficient resource assimilation when predator density is low, (ii) a higher risk of catastrophic extinction resulting from a change in the parameter controlling the strength of the Allee effect, and (iii) no possibility of an increase in population size when the density dependence is enhanced.

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1. Introduction

The positive feedback between per capita growth rate and population density is known as the demographic Allee effect (Stephens et al., 1999). It arises in animal populations when the mating success depends on the probability of encountering mates (Dennis, 1989; McCarthy, 1997; Courchamp et al., 1999; Stephens and Sutherland, 1999) and is associated with animal extinctions when there is a critical density below which the population cannot increase. Allee effects can be incorporated into single-species population models simply by multiplying the reproduction function by the probability of successful mating (Boukal and Berec, 2002). The resulting density dependence has significant implications for population dynamics; in simple deterministic models it has been shown to drive abrupt population collapse (e.g. Dennis, 1989; McCarthy, 1997), induce chaotic transient fluctuations (Schreiber, 2003), and stabilize asymptotic dynamics (Scheuring, 1999). The theoretical framework finds applications in ecological conservation (Stephens et al., 1999) and pest control (Boukal and Berec, 2009).

Multi-trophic systems also experience the consequences of Allee effects (e.g., de Roos and Persson, 2002; de Roos et al., 2003;

Webb, 2003). The consumption of resources will likely be influenced by an Allee effect in the consumer population, and it may be relevant to account for this effect in predator–prey models to correctly represent the transfer of biomass between trophic levels. For example, to simulate the dynamics of krill in social aggregations, we need to capture both the benefit of density-dependent mating and the cost of resource depletion within aggregations (Verdy, 2008; Verdy and Flierl, 2008).

Classical models of interacting species have been adapted to include Allee effects, including models of host–parasitoid (Deredec and Courchamp, 2006) and predator–prey interactions (Courchamp et al., 2000; Kent et al., 2003; Zhou et al., 2005; Boukal et al., 2007; Hadjiavgousti and Ichtiaroglou, 2008). In most cases, the population with Allee effect is the one occupying the lowest trophic level, i.e. the prey or host. The Allee effect can then be included as in single-species models. An Allee effect in the predator, however, is not as straightforward to implement because it modulates the interspecific interaction through life cycle processes not represented in simple models. The intuitive approach is to include a density-dependent function in the predator's growth term, but to assume no explicit effect on the prey (Bazykin, 1998; Zhou et al., 2005). This implies a break in the symmetry between the functions describing depletion of the resource (in the prey equation) and uptake by the consumer (in the predator equation), hence the mass budget is not properly closed. This limitation can be particularly important when modeling systems in which

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biomass is the measured quantity, as is typically the case in studies of small aquatic populations such as plankton communities.

In this paper, it is argued that the Allee effect modulates the predation rate, such that the mating probability multiplies the rate at which resources are taken up as well as the rate at which they are converted into consumer biomass. We derive a set of predator–prey equations from a more complex physiologically-structured model for a predator with density-dependent mating success (Section 2). The approach is similar to the one used by de Roos et al. (2008) to transform a continuous size-structured model into a discrete-stage predator–prey (biomass) model. The structured model explicitly represents the consumer's life cycle and the utilization of resources for reproduction and growth; it provides a quantitative framework, based on biomass, that can be used for studying ecological dynamics resulting from the interplay of life history and consumer-resource interactions.

We examine the stability of asymptotic solutions in this model, both analytically (Section 3) and numerically (Section 4). To highlight the importance of including the Allee effect term in the equation for the prey as well as the equation for the predator, we compare the bifurcation structure in our model with that occurring (i) in models without Allee effect and (ii) in models where the Allee effect does not modulate the resource uptake. It is found that both versions of the model with an Allee effect are qualitatively similar from a dynamical point of view; for example, both support multiple equilibria and bifurcations that can trigger the catastrophic collapse of the predator population. However, significant quantitative differences exist with regards to the parameter values for which these bifurcations occur, as well as the sensitivity of bifurcations to the parameters. We also examine the sensitivity of equilibrium densities (Section 5), and find that enhancing the density dependence can lead to an increase in the steady-state predator population, a counter-intuitive result that does not occur unless the Allee effect modulates the resource uptake. The exchange of biomass between prey and predator populations is discussed in Section 6.

In the model derivation below, we adopt the view that consumption of resources is driven mainly by processes through which predator biomass is generated, namely reproduction and growth.

2. Stage-structured model formulation

A dynamical model describes the interaction between a predator and a prey (or, more generally, of a consumer and a resource). We begin with a model for a population continuously distributed in weight space, whose life cycle consists of juvenile and mature stages. This is converted into biomass equations and coupled to an equation for the prey biomass. We then formulate an equivalent unstructured predator–prey model by assuming a single stage for the predator population.

2.1. Set-up

Dynamics of the predator population are described by a partial differential equation adapted from the McKendrick–vonFoerster equation for a population with weight-structure. There is a continuous weight distribution, with $n = n(w, t)$ the number density per unit weight. Growth is a function of the resource density, P. This yields the model

$$\frac{\partial n}{\partial t} + \frac{\partial}{\partial w} G(w, P)n = -\mu n \tag{1}$$

with boundary condition (representing the flux of newborns)

$$G(w_B, P)n(w_B, t) = \int B(w, P)\Pi(n)n(w, t)\,\mathrm{d}w \tag{2}$$

where w_B is the weight at birth, G is the growth function, B is the density-dependent reproduction function, Π is the mating probability, and μ is the mortality rate. We assume that birth and recruitment are limited by the availability of resources, and that reproduction is a function of adult density; a constant mortality rate is assumed. We impose $n(\infty, t) = 0$.

The growth function, G, gives the rate at which weight increases; it can depend on the current weight and generally increases with the amount of resources available. The reproduction function gives the rate at which newborns are produced; it can also depend on the (parents) weight and the resource density. These functions are decomposed into weight-dependent and resource-dependent parts,

$$G(w, P) = g(w)f(P) \tag{3}$$

$$B(w, P) = b(w)f(P) \tag{4}$$

The resource is allowed to vary in time (we will write a dynamical equation for P), hence the advection rate in (1) is time-dependent. We can remove this time dependence by scaling time by $f(P)$. Let t^* denote scaled time; then

$$\frac{\partial n}{\partial t^*} + \frac{\partial}{\partial w} g(w)n = -\frac{\mu}{f(P)}n \tag{5}$$

This can be rewritten as

$$\frac{\partial \tilde{n}}{\partial t^*} + \frac{\partial \tilde{n}}{\partial \xi} = -\frac{\mu}{f(P)}\tilde{n} \tag{6}$$

by introducing the changes of variables

$$\tilde{n} = gn \tag{7}$$

$$\xi(w) = \int_0^w g^{-1}\,\mathrm{d}w' \tag{8}$$

Eq. (6) can be solved using the method of characteristics:

$$\tilde{n}(\xi, t^*) = \tilde{n}(\xi_B, t^* - \tau)e^{-\int_{t^*-\tau}^{t^*} \mu f(P)^{-1}\,\mathrm{d}t'} \tag{9}$$

where $\xi_B = \xi(w_B)$ and $\tau = \xi(w) - \xi(w_B)$.

The solution, in scaled time, can then be expressed as

$$n(w, t^*) = \frac{g(w_B)}{g(w)}n(w_B, t^* - \tau)e^{-\int_{t^*-\tau}^{t^*} \mathrm{d}f(P)^{-1}\,\mathrm{d}t'} \tag{10}$$

Now that we have the basic framework laid-out, we will examine the specific case of a population with an Allee effect and a two-stage life cycle.

2.2. Two-stage life cycle

We consider a simple life cycle for the predator population, consisting of juvenile and adult stages. The life cycle is represented schematically in Fig. 1: birth of new individuals supplies the juvenile stage, during which organisms develop; juvenile individuals growth until they reach w_A, at which point they become mature and begin to reproduce.

The number of juveniles and adults is given by

$$N_J = \int_{w_B}^{w_A} n\,\mathrm{d}w \tag{11}$$

$$N_A = \int_{w_A}^{\infty} n\,\mathrm{d}w \tag{12}$$

Juveniles allocate all their resources to growth, and adults allocate all their resources to reproduction, such that

$$g(w) = \begin{cases} g_0 w & \text{if } w < w_A \\ 0 & \text{if } w \geq w_A \end{cases} \tag{13}$$