Original Research Article

Protective parenting may have population-level consequences

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ABSTRACT

In many animal species, recruitment is facilitated by adults' efforts to protect offspring from predation. Theoretical studies of this phenomenon have usually focused on resolving the conflict between an individual's self-preservation and its attempts to successfully reproduce. While the decision to protect is made at the level of a single individual, the aggregation of these decisions may affect population density and structure. This idea motivates the development of a functional response for predators that is compatible with the protective behaviour of prey. We use this functional response to study the long-term behaviour of a protective prey population under different levels of predation. We find that contribution of protective effort may promote or inhibit population density depending on the riskiness associated with interference. Moreover, our results suggest that, in environments characterised by intense predation, a protection-driven Allee effect allows sufficiently large populations to persist. We interpret these results in the context of different strategies for newborn defence.

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1. Introduction

In many animal species, the survival of offspring depends on parental care which includes protection from predators. More generally, in cooperatively breeding species, an alloparent may intervene to prevent predators killing young members of the population (Clutton-Brock, 2006). Observed instances of group defence (i.e., mobbing) may be thought of as a combination of parental and alloparental protection. Parents that are successful in defending their offspring benefit from increases in personal fitness. Alloparents that ensure the survival of their own kin may likewise benefit from increased inclusive fitness. Other alloparents are compensated directly through 'delayed reciprocity', the acquisition of parental experience or continuing access to the benefits of group living (Riedman, 1982; Kokko et al., 2001).

Although parental protection has been observed in several species of insects (Tallamy, 1984; Tallamy and Wood, 1986), studies of the phenomenon have largely focused on vertebrates. For example, adults in many bird and fish species attempt to deter predators from attacking their broods (Brunton, 1986; Dale et al., 1996; Perrone et al., 1979). Maternal defence is particularly widespread in mammal populations (reviewed in Smith, 1987),

with a depth of study devoted to ungulates (Hamlin and Schweitzer, 1979; Coté et al., 1997). Moreover, mobbing occurs in populations of ungulates, birds and fish, thereby, providing numerous examples of adults protecting offspring that are not their own (Marion and Sexton, 1979; Hoogland and Sherman, 1976; Dominey, 1983). However, provision of alloparental protection may instead come from individual 'helpers' as has been observed, for instance, in populations of mountain goats and African wild dogs (Coté et al., 1997; McNutt, 1996).

The gains made by an adult (e.g, in fitness) are balanced by the additional risk incurred in engaging with a dangerous predator. Particularly overt tactics heighten this risk but are more likely to be successful (Andersson et al., 1980; Brunton, 1986). The effort made by an individual parent may be influenced by the parent's personal risk of predation, the reproductive value of the offspring and the harm that the offspring would suffer in the absence of the parent (Dale et al., 1996). In addition, an alloparent may be motivated by the threat of expulsion from its group (Kokko et al., 2002). Differences in the relative influences of these factors may account for variations in effort among individuals of the same species.

While each individual optimises its own contribution, these choices may have consequences for the population. The benefit accrued to the population in increased recruitment is, at least partially, offset by heightened adult mortality rates. These competing factors are mediated by the predators' consumption rate or functional response of adult and newborn prey. In an

unstructured population, the benefits associated with group defence are often represented as a unimodal Holling Type IV response (Taylor, 1984; Sabelis, 1985). However, such a functional response may not accurately represent protection that is inherently stage-dependent. Though predation models containing two prey stages have been reasonably well studied (Hastings, 1983; Pavlová and Berec, 2011; McNair, 1987), the consequences of including protective behaviour remain, to the best of our knowledge, unexplored.

The broad aims of this article are: (i) to assess if protection of newborns is a positive influence on the survival of a population and (ii) to understand how the answer to this question depends on the level of risk assumed by adults as well as the intensity of predation. To these ends, we utilise a simple two-stage continuous-time model of the dynamics of a prey population. This model is introduced in Section 2. In Section 2.1, we develop an explicitly stage-dependent functional response that can represent protective behaviour. Once this has been accomplished, we explore the effects of protection on population density, in the context of weak predation (Section 3.1) and strong predation (Section 3.2). The paper concludes with Section 4, a discussion of implications and extensions of this work.

2. Mathematical model

We consider the densities of two overlapping generations of a single prey species, adults $A = A(t)$ and newborns $B = B(t)$. This population is assumed to be arranged into groups which may be familial units or larger communities. We do not explicitly divide reproductive and non-reproductive adults. Therefore, in this context, an adult is characterised both by reproductive activity and its ability to protect newborns. Conversely, a newborn does not reproduce and may benefit from predation protection. The aging process is governed by a maturation rate m which is related to the average length of the newborn period (Hastings, 1983). Variation in the population is modelled using a pair of ordinary differential equations of the form

$$\frac{dA}{dt} = mB - d_A A^2 - P\kappa_A(A, B), \tag{2.1}$$

$$\frac{dB}{dt} = rA - d_B B^2 - mB - P\kappa_B(A, B), \tag{2.2}$$

where time t will be measured in days. The constant $r > 0$ is a birth-rate coefficient and the parameters d_A and d_B represent resource-limitation effects at high densities of A and B respectively. The corresponding quadratic terms ensure the suppression of indefinite growth of either stage, in the absence of predators. For simplicity, inter-stage competition for resources is not considered. We also note that predator population dynamics are not included. Instead, predation is represented by the product of the constant density of a predator population $P \geq 0$ and stage-dependent functional responses. These functional responses, denoted $\kappa_A = \kappa_A(A, B)$ and $\kappa_B = \kappa_B(A, B)$, apply to interactions in which predators are solitary and prey occur in groups. The forms of the responses will be derived in Section 2.1. However, certain assumptions about predator–prey interactions will be invoked implicitly in the derivation. We outline these assumptions in the remainder of this section.

The first assumption is that the time spent switching from a newborn target to an interfering adult as well as the time spent handling newborn prey prior to the adult's intervention are both effectively zero. Secondly, we assume that time spent interacting with an adult prey individual is unaffected by how the interaction arose, i.e. whether it was planned or the result of the adult's interference. Thirdly, we assume that a single attack cannot lead to

more than one kill. As we assume that predators do not hunt in groups, this simply means that the handling time of adult prey must be larger than the escape times of prey. An important consequence of this assumption is that the intervention of adults always allows a newborn to escape.

The final assumption is related to prey behaviour rather than the composition of a predator's hunting time. We suppose that a newborn can survive the loss of a protector, with other adults prepared to provide care and help in preventing any subsequent predator attacks. In cooperatively breeding species, the fulfillment of this condition is unlikely to present an issue. However, if alloparental care does not occur, the functional response for newborns may underestimate predation losses by neglecting these indirect mortality effects (Andersson et al., 1980).

2.1. Derivation of functional responses κ_A and κ_B

Following the time-utilisation approach of Holling (1959) and Beddington (1975), we study a small period of time in the life of an average predator. We denote this period ΔT and split it into three parts, time spent searching for food, time spent interacting with adults and time spent interacting with newborns. In this context, an interaction includes the killing, eating and digesting of prey. Strictly speaking, time spent interacting with any other species that constitute part of the predator's diet should also be included but for simplicity, we neglect this detail. We denote the number of individual adults and newborns killed during ΔT as ξ_A and ξ_B, respectively.

In order to generate a description of protective behaviour, we first introduce the random variables ξ_A^n and ξ_B^n which are the number of pre-meditated or "natural" attacks on A and B respectively (i.e. those that occur due to the predator's hunt). We will also utilise functions denoted by $g = g(\xi_B^n, A)$ and $f = f(\xi_B^n - g(\xi_B^n, A))$. The function g determines the number of newborn kills from the number of attacks on newborns and the number of adult individuals. The quantity $\xi_B^n - g(\xi_B^n, A)$ therefore represents the number of attacks on newborns that are thwarted by members of the adult population and f determines the number of adult deaths that occur as a result of this interference. The numbers of kills during the time interval can then be expressed as

$$\xi_A := \xi_A^n + f(\xi_B^n - g(\xi_B^n, A)), \tag{2.3}$$

$$\xi_B := g(\xi_B^n, A). \tag{2.4}$$

The predator's consumption rate of a stage is equal to the expected number of kills of that stage during a particular time interval divided by the (constant) length of the interval, i.e.,

$$\kappa_A := \frac{\mathbb{E}[\xi_A]}{\Delta T}, \tag{2.5}$$

$$\kappa_B := \frac{\mathbb{E}[\xi_B]}{\Delta T}. \tag{2.6}$$

We express the length of the period ΔT in terms of expected time spent by the predator engaged in each activity, i.e.

$$\Delta T = \mathbb{E}[\Delta T_s] + h_A \mathbb{E}[\xi_A] + h_B \mathbb{E}[\xi_B], \tag{2.7}$$

where the random variable ΔT_s is time spent searching for food and $h_A > 0$ and $h_B > 0$ can be interpreted as expected handling times. From Eqs. (2.3) and (2.4), it follows that

$$\mathbb{E}[\xi_A] = \mathbb{E}[\xi_A^n] + \mathbb{E}[f(\xi_B^n - g(\xi_B^n, A))], \tag{2.8}$$

$$\mathbb{E}[\xi_B] = \mathbb{E}[g(\xi_B^n, A)]. \tag{2.9}$$