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Caught between two Allee effects: Trade-off between reproduction and predation risk

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ABSTRACT

Reproductive activities are often associated with conspicuous morphology or behaviour that could be exploited by predators. Individuals can therefore face a trade-off between reproduction and predation risk. Here we use simple models to explore population-dynamical consequences of such a trade-off for populations subject to a mate-finding Allee effect and an Allee effect due to predation. We present our results in the light of populations that belong to endangered species or pests and study their viability and resilience. We distinguish several qualitative scenarios characterized by the shape and strength of the trade-off and, in particular, identify conditions for which the populations survive or go extinct. Reproduction can be so costly that the population always goes extinct. In other cases, the population goes extinct only over a certain range of low, intermediate or high levels of reproductive activities. Moreover, we show that predator removal (e.g. in an attempt to save an endangered prey species) has the least effect on populations with low cost of reproduction in terms of predation and, conversely, predator addition (e.g. to eradicate a pest) is most effective for populations with high predation cost of reproduction. Our results indicate that a detailed knowledge of the trade-off can be crucial in applications: for some trade-off shapes, only intermediate levels of reproductive activities might guarantee population survival, while they can lead to extinction for others. We therefore suggest that the fate of populations subject to the two antagonistic Allee effects should be evaluated on a case-by-case basis. Although the literature offers no quantitative data on possible trade-off shapes in any taxa, indirect evidence suggests that the trade-off and both Allee effects can occur simultaneously, e.g. in the golden egg bug *Phyllomorpha laciniata*.

1. Introduction

Various trade-offs affect individual life history decisions and in turn influence dynamics of populations. One such trade-off links reproduction and predation risk. Many species have evolved anti-predator behaviour during which they stop mating and perform an escape manoeuvre (e.g. Svensson et al., 2004, 2007). Higher levels and/or prolonged periods of spatial movement (Anholt and Werner, 1995; Kotiaho et al., 1998) or sexual signalling (Zuk and Kolluru, 1998) during mate search help find a mate or choose a better one but can also attract predators. For example, neotropical bats can exploit frog calls (Ryan et al., 1982; Tuttle and Ryan, 1981), parasitic flies can target calling male field crickets (Lewkiewicz and Zuk, 2004) and skuas can respond to male petrel calls (Mougeot and Bretagnolle, 2000). Predation risk may also be high during copulation (Trochine et al., 2005), pregnancy, spawning and breeding period when the individuals are often less motile or easier to detect. For example, gravid females of the copepod *Eudiaptomus gracilis* become an easier prey as the brood looks like a conspicuous dark spot inside the body (Svensson, 1997) and gravid females of other copepods can be eaten by fish because of reduced manoeuvrability (Winfield and Townsend, 1983).

Both reproductive success and probability of avoiding predation, involved in the reproduction-predation risk trade-off, may be positively related to population size or density and therefore subject to a component Allee effect (Courchamp et al., 1999, 2008; Stephens and Sutherland, 1999). Allee effects are mostly studied as single mechanisms of positive density dependence, but multiple Allee effects can be common and the ways in which two or more component Allee effects interact can be complex (Berec et al., 2007).

Various mechanisms can lead to component Allee effects in reproduction (Table 1). In particular, individuals in small or sparse populations can face a mate-finding Allee effect and have reduced

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Table 1
Effects of population density on various activities related to reproduction; all of them can be accompanied by an elevated predation risk.

Reproductive activity	Effect of population density on reproductive success
1. Mate search	Positive – probability of finding a mate increases with population density
2. Intra- and intersexual conflict and mate choice	Negative – intra- and intersexual competition increases with increasing population density and may decrease individual fitness Positive – chance of finding a more suitable mate increases with population density (wider choice of mates)
3. Fertilization	Dependent on species' features
4. Fecundity	Dependent on species' features, it might be positive in some cases: for example, multiple matings or presence of conspecifics induce higher egg production in females of some species, or higher egg or offspring survival
5. Parental care	Negative – if parents compete with others for limited resources Positive – among cooperative breeders or when group living enhances resources

reproductive success due to their inability to find a (suitable) mate during their receptive period. The mechanisms include male–female encounters in motile animals, encounters between pollen grains and egg cells in plants, and encounters between male and female gametes in many sessile or semi-sessile marine invertebrates (Gascoigne et al., 2009). Evidence for Allee effects affecting reproduction in general and for mate-finding Allee effects in particular is quite widespread; observations of the latter span a wide spectrum of taxa from sheep ticks (Rohlf, 1969) to polar bears (Molnár et al., 2008) among terrestrial animals and from copepods (Kiørboe, 2006) to queen conch (Stoner and Ray-Culp, 2000) among marine species. Other mechanisms by which larger population size or density may enhance reproduction success include sperm limitation, physiological stimulation of reproduction and female choice (Gascoigne et al., 2009).

Likewise, individuals in small or sparse populations may be more susceptible to predation due to reduced ability to avoid or escape predators thanks to passive or active defence. Prey can actively defend themselves through predator mobbing (Krebs and Davies, 1993), more vigilant scanning for predators (Mooring et al., 2004) or confusion effect when schooling (Nottestad and Axelsen, 1999). Passive defence (the dilution effect) is characterized by per-capita predation probability declining with increasing prey density and corresponds to a type II functional response (Gascoigne and Lipcius, 2004). For example, woodland caribou face higher predation risk in smaller groups as predators usually kill one animal per group per attack irrespective of the group size (Wittmer et al., 2005).

In this article, we explore the dynamics of a population that faces a trade-off between two Allee effects: one due to reproduction and the other due to predation. Our study is motivated by situations in which the population belongs to an endangered species, and we identify properties of its predators and trade-offs that might put the population under extinction risk. Alternatively, our model describes a pest species that needs to be controlled or eradicated. To quantify the extinction risk and eradication potential we use population resilience, defined as the maximum disturbance the population in a stable state may sustain to avoid extinction (Beisner et al., 2003), and relative population resilience, by which we mean a relative change in the resilience of the population after a predator removal/addition. When measuring relative resilience, we also distinguish prey with flexible and inflexible reproductive behaviour. We assume that flexible reproductive behaviour (determining strength of the mate-finding Allee effect) can be instantly changed after predator removal or addition, whereas inflexible behaviour cannot respond to predator presence or absence. They represent extreme but useful approximations of real reproductive behaviour, which can involve both morphological and behavioural traits. Most morphological traits such as bright colouration of males in many birds and many types of behaviour such as lekking displays of various birds and flies (Andersson, 1994) are 'hardwired' characteristics that individuals cannot change and therefore correspond to the inflexible behaviour. On the other hand, quite a number of behavioural traits such as mating calls in some orthopteroid insects are plastic. They can be adjusted to the perceived predation risk (Zuk and Kolluru, 1998) and we represent them by the flexible behaviour in our model.

We ask the following questions: When do the two component Allee effects lead to extinction of the population and how do they affect its extinction risk or eradication potential? How are the results affected by the shape of the reproduction-predation risk trade-off? And finally, are the results for prey with flexible and inflexible reproductive behaviour different?

2. Methods

We use several simplifying assumptions on the life histories and population densities of males and females in this paper: identical mortalities, balanced sex ratio at birth and equal initial densities. This allows us to follow changes of the total population density N in time without discerning between males and females (Boukal and Berec, 2009):

$$\frac{dN}{dt} = bNM(N) - dN\left(1+\frac{N}{K}\right) - F(N)P \tag{1}$$

That is, we assume that negative density dependence affects only the prey mortality rate but not its birth rate and that predators do not interfere with each other and do not respond numerically to changes in abundance of the focal population; b is the per capita birth rate, d is the intrinsic mortality at low densities, K scales the environmental carrying capacity, $M(N)$ represents a mate-finding Allee effect or reduction of the reproductive rate bN due to difficulties in finding mates at low densities, $F(N)$ is a predator functional response, and P represents a constant predator population density. The parameters are summarized together with other symbols in Table 2.

2.1. Allee effects in reproduction and due to predation

Mate-finding Allee effects are commonly quantified through positive density dependence in the female mating rate (Boukal and Berec, 2002; Courchamp et al., 2008; Dennis, 1989). The simplest and at the same time most widely used models of positively density-dependent mating rates include the exponential function $M(N)=1-\exp(-N/\theta)$ and the hyperbolic function $M(N)=N/(N+\theta)$, in which θ quantifies the strength of mate-finding Allee effect (Dennis, 1989). We use the hyperbolic function in model (1) as it allows for some analytical calculations. Any of these functions can likewise be used as a (phenomenological) model of other Allee effects in reproduction beyond mate finding (Courchamp et al., 2008).

Predation-driven Allee effects arise for type II functional responses. We use two alternative descriptions, $F(N)=\alpha N/(1+N/\beta)$ and $F(N)=\lambda N/(1+\lambda hN)$. The latter form is the standard formulation due to Holling (1959), in which λ scales the predator–prey encounter rate and h is the handling time of one prey individual, and represents an Allee effect due to predator dilution (Berec et al.,