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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*.

Keywords: anti-predator behaviour, dilution effect, extinction, mate search, population resilience

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 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 (Kjørboe, 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):

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

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., 2007; Courchamp et al., 2008; Gascoigne and Lipcius, 2004). The former expression can be interpreted as a predation-driven Allee effect invoked by a behavioural response of the population (e.g. herding or mobbing) to a predator with an otherwise linear functional response: the behavioural response is more efficient at higher population densities and reduces the (linear) attack rate α by a factor of $1/(1+N/\beta)$. Note that β scales the maximum per-capita attack rate ($= \alpha\beta$) but also defines the population density at which $F(N)$ declines to 50% of its maximum value, and we call β prey vulnerability in this article. Inserting functional forms for $M(N)$ and $F(N)$ to model (1), our alternative models of population dynamics become:

$$\frac{dN}{dt} = bN \frac{N}{N+\theta} - dN \left(1 + \frac{N}{K} \right) - \frac{\alpha NP}{1+N/\beta} \quad (2a)$$

and

$$\frac{dN}{dt} = bN \frac{N}{N + \theta} - dN \left(1 + \frac{N}{K} \right) - \frac{\lambda NP}{1 + \lambda hN} \quad (2b)$$

We rescale both models to reduce the number of parameters from seven to five. In model (2a), we rescale the state variable as $x = N/K$ and time as $\tau = td$ and define new parameters $\Theta = \theta/K$ (relative strength of mate-finding Allee effect), $B = \beta/K$ (relative prey vulnerability), $g = b/d$ and $\delta = P/d$, to obtain

$$\frac{dx}{d\tau} = gx \frac{x}{x + \Theta} - x(1 + x) - \frac{\alpha x \delta}{1 + x/B} \quad (3a)$$

Rescaling model (2b) analogously, we get

$$\frac{dx}{d\tau} = gx \frac{x}{x + \Theta} - x(1 + x) - \frac{\lambda x \delta}{1 + \lambda Hx} \quad (3b)$$

where $H = hK$ (relative handling time) and the other parameters are as above. The parameters α , B and λ scale the strength of Allee effect due to predation: predation mortality in models (3a) and (3b) increases with increasing α , B and λ . Only the parameter Θ scales the strength of mate-finding Allee effect in these models, and reproductive success declines with increasing Θ . We skip the adjective ‘relative’ when further referring to parameters Θ , B and H .

2.2. Reproduction-predation risk trade-off

Trade-off shapes can strongly influence evolutionary dynamics and endpoints (Bell, 1980; Rueffler et al., 2004; Hoyle et al., 2008). We thus consider a range of trade-off shapes that cover varying costs of reproduction in terms of predation risk, and investigate two trade-offs for model (3a),

$$\alpha = \alpha_{\max} \left(1 - \left(\frac{\Theta}{\Theta_{\max}} \right)^z \right)^{1/z} \quad (4a)$$

and

$$B = B_{\max} \left(1 - \left(\frac{\Theta}{\Theta_{\max}} \right)^z \right)^{1/z}, \quad (4b)$$

and one trade-off for model (3b),

$$\lambda = \lambda_{\max} \left(1 - \left(\frac{\Theta}{\Theta_{\max}} \right)^z \right)^{1/z}. \quad (4c)$$

These three trade-offs can describe a range of situations in which increasing reproductive success of the population (i.e. decreasing Θ) leads to increasing attack rate (α increases, e.g. since individuals become less vigilant or unable to escape), increasing prey vulnerability (B increases, e.g. since individuals devote less time to herding or chasing away predators), or increasing encounter rate (λ increases, e.g. since individuals become more conspicuous). Further on, we refer to model (3a) with trade-off (4a) as the attack rate model, abbreviated as AR, to model (3a) with trade-off (4b) as the prey vulnerability model, abbreviated as PV, and to model (3b) with trade-off (4c) as the encounter rate model, abbreviated as ER.

Maximum predation pressure ($\alpha = \alpha_{\max}$, $B = B_{\max}$ and $\lambda = \lambda_{\max}$) occurs for $\Theta = 0$ when there is no mate-finding Allee effect, and predation ceases ($\alpha = 0$, $B = 0$, and $\lambda = 0$) for $\Theta \geq \Theta_{\max}$ when reproductive activities become so suppressed that predators can no longer exploit the prey. The parameter z quantifies the overall predation risk associated with reproduction. Values of $z < 1$ (convex trade-offs) correspond to ‘cheap’ reproductive activities, for which the predation risk remains low until Θ is relatively small, i.e. until the mate-finding Allee effect is relatively weak due to efficient prey reproductive activities. On the other hand, values of $z > 1$ (concave trade-offs) correspond to ‘costly’ reproduction, for which the predation risk remains

elevated for a wide range of effort associated with reproductive activities, e.g. because courting or gravid individuals are more conspicuous (Fig.1).

2.3. Model analysis

Models (3a) and (3b) can have, in addition to the extinction equilibrium $x_0 = 0$, either no positive equilibrium or a unique positive equilibrium that is stable or two positive equilibria, of which the higher (labelled S) is stable and the lower (U) unstable (see below for exact results). We focus here only on the difference $R = S - U$ and call it population resilience. It can be interpreted as the maximum disturbance after which the population can still return back to the stable equilibrium without going extinct. If there is only a unique positive equilibrium that is stable, we set $U = 0$.

We start with standard viability analysis of models (3a) and (3b) and search for the stable and unstable equilibria and conditions for their existence. In the simplest cases when Θ and/or α or λ are zero or B infinitely large (that is, one or both component Allee effects are absent), the equilibria can be calculated analytically. We use MATLAB (The MathWorks, Inc.) to find the equilibria numerically when both Allee effects are present.

To investigate the role of reproduction-predation risk trade-off, we examine the impact of changes in the strength of mate-finding Allee effect Θ on the population resilience R along the trade-off in the AR, PV and ER models. In addition, we explore relative population resilience along the trade-off for prey with flexible and inflexible reproductive behaviour. In line with the general considerations above, by ‘flexible’ we mean that prey reproductive behaviour can be changed instantly such that there is no mate-finding Allee effect ($\Theta = 0$) in the absence of predators and there is some ($\Theta > 0$) in their presence, while prey with inflexible reproductive behaviour are assumed to keep the same $\Theta > 0$ regardless of predators. For prey with flexible behaviour, we therefore measure the relative population resilience as $\rho_f = (S - U)/(S_0 - U_0)$, where S_0 and U_0 correspond to no predation ($P = 0$) and no mate-finding Allee effect ($\Theta = 0$), i.e. $U_0 = 0$; in fact ρ_f is just a multiple of the population resilience R . For prey with inflexible behaviour, we measure the relative population resilience as $\rho_i = (S - U)/(S_1 -$

U_1), where S_1 and U_1 correspond to no predation and the mate-finding Allee effect remaining at the unchanged strength $\Theta > 0$; ρ_i always equals 1 if there is no predation.

3. Results

3.1. Equilibria of models (3a) and (3b) and their stability

The extinction equilibrium $x_0 = 0$ of model (3a) is locally stable for any mate-finding Allee effect ($\Theta > 0$). It is globally stable, i.e. the population goes extinct regardless of its density, and no other equilibria exist if the mate-finding Allee effect and/or the predation-driven Allee effect are sufficiently strong (i.e. if Θ and/or α are sufficiently large). For no mate-finding Allee effect ($\Theta = 0$), x_0 is locally or globally stable if $\alpha > (g-1)/\delta$ and unstable if $\alpha < (g-1)/\delta$. In the latter case, the population always reaches a unique positive equilibrium (environmental carrying capacity) regardless of its initial density. A complete analysis of the case with no mate-finding Allee effect is given in Appendix (Table A1).

If the extinction equilibrium $x_0 = 0$ is only locally stable, two positive equilibria exist of which the lower is unstable (Allee threshold) and the upper is locally stable (carrying capacity). All else being equal, the two positive equilibria approach one another with increasing Θ and/or α until both merge and the extinction equilibrium becomes globally stable (Fig. 2A). The population resilience R is maximized for no mate-finding Allee effect and no predation ($\Theta = 0$ and $\alpha = 0$; $R = g-1$) and declines as the strength of mate-finding Allee effect Θ and/or the attack rate α increase (Fig. 3A; the thin lines depict isolines along which the resilience is constant). The lower limit of the isolines is the viability limit at which the positive equilibria merge and $R = 0$. For Θ and/or α to the right and above the viability limit, the population cannot persist as deaths exceed births for any population density. We denote the mate-finding Allee effect strength and the attack rate at which the viability limit intersects the respective axes as Θ_{lim} and α_{lim} ($\Theta_{\text{lim}} = 0.172$ and $\alpha_{\text{lim}} = 2.55$ in Fig. 3A). The relative population resilience ρ_i of prey with inflexible reproductive behaviour is maximized in the absence of predation ($\alpha = 0$) and declines with increasing α for any $0 < \Theta < \Theta_{\text{lim}}$ (Fig. 3B).

For high attack rates, $\alpha > (g-1)/\delta$, the dependence of equilibria of model (3a) on the mate-finding Allee effect strength Θ and the prey vulnerability B is qualitatively the same as in Fig. 2A and the corresponding (relative) population resilience plots are analogous to Fig. 3A-B. For low attack rates, $\alpha < (g-1)/\delta$, the results differ qualitatively and high values of B do not affect the equilibria (Fig. 2B). This is because for highly vulnerable prey ($1/B$ close to 0) the predation term in model (3a) reduces to $\alpha\delta x < (g-1)x$, and hence for $\Theta = 0$ the population always attains a unique positive equilibrium (carrying capacity) that is globally stable. In biological terms, the prey cannot go extinct if the mate-finding Allee effect is absent and the attack rate is low enough. Consequently, the viability limit and isolines of the (relative) population resilience in the Θ - B parameter space are much more convex (Fig. 3C-D).

Similar conclusions hold for the existence and stability of the equilibria of model (3b). The extinction equilibrium $x_0 = 0$ is locally or globally stable for any mate-finding Allee effect ($\Theta > 0$). For no mate-finding Allee effect ($\Theta = 0$), $x_0 = 0$ is locally or globally stable for high prey encounter rates $\lambda > (g-1)/\delta$ and unstable for $\lambda < (g-1)/\delta$. A complete analysis for $\Theta = 0$ (see Table A2 in Appendix) implies that if the handling time is sufficiently short, $H < 4\delta/(g-1)^2$, the positive equilibria of model (3b), population resilience and relative population resilience behave similarly as shown in Figs 2A, 3A and 3B, respectively. On the other hand, long handling times, $H > 4\delta/(g-1)^2$, yield results that are qualitatively analogous to Figs 2B, 3C and 3D and the encounter rate λ affects the location of equilibria only when relatively small. This is because the predation-driven Allee effect is not strong enough to drive the population to inevitable extinction even for virtually infinite encounter rates λ , for which the predation term in model (3b) reduces to a constant δ/H .

The isoline plots of (relative) population resilience in Fig. 3 also reveal that the prey population can or cannot always be eliminated by strong predation. Populations that can always be eliminated by strong predation are characterized by plots in which the viability limit intersects the y-axis at some $\alpha_{\text{lim}} < \infty$ (Fig. 3A-B). These populations will be wiped out by predation with $\alpha > \alpha_{\text{lim}}$ irrespective of the strength of mate-finding Allee effect Θ ; we call them *populations with predation limit*. On the other

hand, the viability limit of some populations may not intersect the y-axis (Fig. 3C-D). These populations cannot be wiped out by predation of any strength when the mate-finding Allee effect strength Θ is sufficiently low and we call them *populations without predation limit*. Populations without predation limit appear in the PV model with low attack rates α and in the ER model with long handling times H (Table 3).

3.2. Population resilience under reproduction-predation risk trade-off

How do population resilience and relative population resilience change along the reproduction-predation risk trade-off? And how is the population affected by the shape of the trade-off? We first explain several examples, based on the AR model, in detail before giving the complete results. We have already shown how the population resilience changes with the strength of mate-finding Allee effect and the predation pressure (Fig. 3A). We now overlay different trade-off shapes over the isoline landscape. The curves A, B and C in Fig. 4A are three trade-off curves (4a) that exemplify the main differences in the qualitative outcomes reported in this article.

First, there is a difference between cheap and costly reproduction. For sufficiently ‘cheap’ reproductive activities characterized by a convex trade-off curve ($z < 1$, curve A in Fig. 4A), the resilience R can be maximized at intermediate values of the mate-finding Allee effect strength (curve A in Fig. 4B). Populations with more costly reproductive activities characterized by linear and concave trade-offs ($z \geq 1$, curve B in Fig. 4A) have the resilience always maximized either in the absence of predation ($\Theta = \Theta_{\max}$ and $\alpha = 0$) or in the absence of the mate-finding Allee effect ($\Theta = 0$ and $\alpha = \alpha_{\max}$; as for curve B in Fig. 4B). The exact value of z above which the maximum resilience can no longer occur at an intermediate Θ depends on the curvature of the trade-off relative to the curvature of the isolines; the value will be $z < 1$ because the isolines are always convex.

Second, populations might be always safe or liable to extinction as the strength of mate-finding Allee effect and the predation pressure vary along the trade-off. This is determined by the location of the trade-off relative to the viability limit: populations characterized by trade-off curves A and B persist for any Θ between 0 and $\Theta_{\max}$ and

only go extinct if $\theta > \theta_{\text{lim}}$, while populations characterized by trade-off curve C go extinct for intermediate values of θ between 0 and θ_{max} (curve C in Fig. 4B; the maximum strengths of the two Allee effects due to mate-finding and predation are larger for curve C than for curve B). In extreme cases, the trade-off can be so severe that the population always goes extinct (see below).

Finally, we note that predation ceases and only the mate-finding Allee effect operates for $\theta > \theta_{\text{max}}$. Any two trade-offs thus give the same results for θ above the larger of their θ_{max} values. In addition, if $\theta_{\text{max}} < \theta_{\text{lim}}$, the population resilience declines with increasing θ for $\theta > \theta_{\text{max}}$ until it reaches zero at $\theta = \theta_{\text{lim}}$ (all curves in Fig. 4B).

Now we give the complete results. Results for populations with predation limit can be classified into five qualitatively different scenarios, characterized by the location of the point corresponding to the maximum double Allee effect without any trade-off, i.e. point $[\theta_{\text{max}}, \alpha_{\text{max}}]$ or $[\theta_{\text{max}}, B_{\text{max}}]$ for model (3a) and point $[\theta_{\text{max}}, \lambda_{\text{max}}]$ for model (3b), relative to the viability limit. The five scenarios correspond to the five areas marked as A to E in Fig. 5A. Results for populations without predation limit can be described by only three scenarios (areas A to C in Fig. 5B), which are covered by the former five: parameter combinations from areas A to C in Fig. 5A and Fig. 5B give qualitatively analogous results. We thus present and discuss only the results for populations with predation limit.

In all five scenarios, the population resilience declines with increasing cost of reproduction (i.e. increasing z) for the mate-finding Allee effects satisfying $\theta < \theta_{\text{lim}}$ (Fig. 6). The main distinguishing feature of each scenario is whether and for what values of θ the population cannot persist. The population will survive predation irrespective of the strength of mate-finding Allee effect and the shape of the trade-off only in scenario A (Fig. 6A). In biological terms, this scenario corresponds to prey that can survive predation even when both Allee effects are at maximum strength. In all other scenarios, the population may go extinct; the range of θ that lead to extinction increases with z . In scenario B, the population will not survive predation for intermediate θ and sufficiently costly reproduction (i.e. concave trade-offs with high values of z ; Fig. 6B). This contrasts with the remaining three scenarios in which

intermediate values of Θ are typically ‘the safest’ and the population goes extinct for high, low, and both high and low levels of reproductive activity in scenarios C, D and E, respectively (Fig. 6C-E). In other words, extinction occurs for strong mate-finding Allee effects (high Θ) if their maximum strength is very high (cases C and E) and for weak mate-finding Allee effects (low but positive Θ) if the maximum strength of Allee effect due to predation is very high (cases D and E). In the latter case, the trade-off results in strong Allee effects due to predation. Finally, the population is never viable for sufficiently costly reproduction in scenario E (Fig. 6E).

The relative population resilience ρ_f of prey with flexible reproductive behaviour is a multiple of the population resilience R and can thus be taken from Fig. 6. We observe the same five qualitatively different scenarios for the relative population resilience ρ_i of prey with inflexible reproductive behaviour (Fig. 7), although the value of Θ at which the relative population resilience ρ_i is maximized (or minimized) can be different from that for the (relative) population resilience R (ρ_f) (compare the corresponding panels in Figs. 6 and 7).

4. Discussion

A trade-off between reproduction and predation risk occurs in many animals but its impact on population viability has been little studied. We have focused in this article on the viability of a population that faces, along with this trade-off, two different Allee effects due to reproduction and predation, and examined how various characteristics of the population and shapes of the trade-off affect its resilience to disturbances. We have also compared the results for prey that can or cannot adjust their reproductive activity to the predation level.

4.1. Summary of outcomes and their implications for population management

We have found that the fate of a population, given its demographic rates g and δ , depends on three main factors: the cost of reproduction (that is, the trade-off shape characterized by the parameter z), the maximum strength of mate-finding Allee effect at which predation ceases and the maximum strength of Allee effect due to predation

in the absence of the mate-finding Allee effect (that is, the trade-off location characterized by the parameters $\alpha_{\max}$, $B_{\max}$ or $\lambda_{\max}$, respectively). While the results depend strongly on the reproduction-predation risk trade-off, the flexibility or inflexibility of prey reproductive behaviour as well as the type of Allee effect due to predation (= models AR, PV and ER) do not produce qualitatively different outcomes. We summarize all results jointly in what follows.

Overall, the (relative) population resilience declines with increasing cost of reproduction embodied in the parameter z that represents the strength of reproduction-predation risk trade-off. In some cases, reproduction can be so costly in terms of predation that the population always goes extinct. In other cases, the population goes extinct only over a certain range of mate-finding Allee effects, which may correspond to high, low or intermediate levels of reproductive activity. For example, intermediate levels of reproductive activity might be the only ones that guarantee population survival (e.g., sufficiently convex trade-offs in scenario E in Fig. 6E) or that, on the contrary, lead to population extinction (e.g., sufficiently concave trade-offs in scenario B in Fig. 6B).

Our results on the relative population resilience imply that the impact of predator manipulation (i.e., removal or addition) differs quantitatively but not qualitatively for prey with flexible and inflexible reproductive behaviour. That is, our main results are equally valid if predators exploit hardwired traits associated with reproduction (usually colouration or canalized behaviour) or if they exploit adjustable prey behaviour such as the intensity and duration of mating calls. All else being equal, predator manipulation has the largest effect on populations with high cost of reproduction in terms of predation. This can have either positive or negative consequences depending on the application: conservation biologists have obviously opposing goals to pest managers.

Predator removal is often considered among conservation management strategies because it can increase survivorship in endangered populations (Sinclair et al. 1998). Our modelling results show that removal of predators can be particularly worthwhile for populations with predation limit that can be heavily predated and must suppress

their reproductive behaviour considerably in order to avoid predation (i.e. have relatively high $\alpha_{\max}$ and $\Theta_{\max}$; area E in Fig. 5A). Such populations cannot survive without removal of the predators. On the contrary, pest management might attempt to remove a pest by introducing additional or entirely new predators (Solomon et al. 2000). Here we demonstrate that, within the types of life histories and ecological interactions considered in our models, the most difficult pests fall into the category of populations that are without predation limit and face relatively few difficulties in finding mates when they manage to avoid predation (i.e. have relatively small $\Theta_{\max}$; area A in Fig. 5B). Such pests are impossible to eradicate by adding predators.

Given the disparate results on population viability that depend on quantitative details of the reproduction-predation risk trade-off, it is clear that no general rule of thumb can be put forward and the fate of a population subject to antagonistic mate-finding and predation-driven Allee effects should be evaluated on a case-by-case basis.

4.2. Evidence for the main model ingredients

Although our results show that the shape and location of the reproduction-predation risk trade-off can be the key for survival or extinction of the population, we have found that quantitative data on it are virtually lacking in the literature. In fact, nearly all evidence supporting the existence of such a trade-off is based on ‘binary’ experiments where the prey reproductive activity is observed under the presence or absence of its predators (see the examples in Introduction). This indicates that the relationship is either difficult to measure or that it has so far largely escaped an interest of behavioural ecologists. Nevertheless, many species across various taxa (predominantly insects, but also crabs, fish, frogs or birds) exhibit a trade-off between reproduction and survival from predation, suggesting that the occurrence of the trade-off might be common.

In addition to the presence of a reproduction-predation risk trade-off, the application of our model requires that the species be simultaneously subject to a mate-finding Allee effect and an Allee effect due to predation. Kramer et al. (2009) reviewed the empirical evidence for Allee effects and provided an extensive list of species likely subject to the Allee effect due to predation satiation and an Allee effect due to mate

limitation. The taxa subject to the former include mostly vertebrates such as fishes (salmonids and others) and mammals (elk, caribou or pronghorn) but only a few invertebrates, including the crown-of-thorns starfish *Acanthaster planci* or the rock lobster *Jasus edwardsii*. On the contrary, Allee effects due to mate limitation, including the mate-finding Allee effect, seem to occur mostly in invertebrates with the examples spanning molluscs (queen conch, abalone) and insects (gypsy moth, Glanville fritillary); only a few studies have identified this effect in fishes, mammals and birds.

Our study might appear irrelevant in the light of this heterogeneous body of evidence. However, as Kramer et al. (2009) suggest and we fully agree, expectations and studies of a certain type of the Allee effect can be biased in various species or groups of species (e.g. predation satiation is mostly proposed for herbivorous mammals and mate finding for invertebrates). Studies dealing with ‘less obvious’ Allee effects and multiple Allee effects among all species are lacking. Another reason might be that some combinations of taxa and Allee effects are more amenable to experimental manipulation or field observations than others. For example, insects are good model organisms for the mate-finding Allee effect, while the impact of predation and potential Allee effects driven by it are reasonably easily measured in small populations of large ungulates.

Simultaneous occurrence of both types of Allee effect has been put forth in Berec et al. (2007). The candidate species include the monarch butterfly *Danaus plexippus*, in which individuals in small overwintering groups suffer mating depression in spring and less efficient predator dilution; the social spider *Anelosimus eximius*, where small colonies have a reduced number of eggs per sac and reduced offspring survival to maturation, owing to reduced protection against predators; and the white abalone *Haliotis sorenseni*, in which individuals have reduced fertilization efficiency at small density and where some populations suffer overexploitation equivalent to an Allee effect due to predation. Additional research should reveal how frequent are such examples in other animals.

Potential occurrence of all three mechanisms in a species can also be inferred indirectly from known details on its life history. For example, the golden egg bug

Phyllomorpha laciniata exhibits a component Allee effect in reproduction: females produce twice as many eggs if there are enough conspecifics to lay eggs upon their backs (Garcia-Gonzales and Gomendio, 2003; Katvala and Kaitala, 2003, 2005) and the eggs survive better if carried on backs than if laid on leaves (Garcia-Gonzales and Gomendio, 2003). Major predators of this species are ants, some of which are generalist predators (Hölldobler and Wilson, 1990) and we might expect that they have a saturating functional response. Moreover, individuals that carry eggs are more visible and in a greater risk of predation (Kaitala and Axen, 2000), copulation with an individual carrying eggs increases predation risk for both partners (Kaitala et al., 2003) and the frequency of copulations in the presence of a predator is reduced (Miettinen et al., 2004). Finally, copulation lasts for many hours and pairs are less mobile (Miettinen et al., 2006) and very much susceptible to predation (Kaitala and Axen, 2000). We might therefore conclude that all three mechanisms probably occur in the golden egg bug; however, the available quantitative data are insufficient to apply our model to this species.

On the other hand, other adaptations to increased predation mortality might counteract the decrease in reproductive activities under predation risk. For example, a number of traits related to mating, such as the courtship rate, intensity of colour patterns or female preference for brightly coloured males, decline in response to increased predation risk in the guppy *Poecilia reticulata*. However, guppies from high-predation sites also invest relatively more energy to reproduction, have shorter interbrood intervals and produce more (and smaller) offspring compared to fish from low-predation sites (Magnhagen, 1991, and references therein). Such additional responses to increased predation risk go beyond the reproduction-predation risk trade-off as understood in this article.

4.3. Concluding remarks

As our results suggest, searching for multiple Allee effects and their relationship in plant and animal populations could reveal new and interesting insights and is worth further research both by theoreticians and field workers.

We foresee two distinct ways in which this theory can be extended. First, one could critically assess some of the simplifying assumptions that we made in the model. One restriction of our model is that all predation unrelated to reproductive activities of the population can be included in the mortality parameter d . We also assumed identical male and female life histories to simplify the analyses. Although both assumptions are often reasonable, there are many examples of sex-selective predation (Magnhagen, 1991; Zuk and Kolluru, 1998) and such predation can fundamentally change the predator-prey dynamics (Boukal et al., 2008). Second, one could examine evolutionarily stable reproductive strategies in the present setting to see how individuals benefit from putting energy to reproduction or to predator avoidance, a topic on which we currently work.

Last but not least, we have also highlighted how surprisingly little is known on the processes that, according to our results, drive population dynamics under the reproduction-predation risk trade-off. More data are needed to assess which shapes of the trade-off are most common in nature and how often species are actually caught between two Allee effects caused by reproduction and predation.

Appendix. Analysis of models (3a) and (3b)

Setting the right hand side of equation (3a) to zero always has the trivial solution $x_0 = 0$, corresponding to population extinction. The extinction equilibrium x_0 is locally stable for $\Theta > 0$ as the derivative of the right hand side of equation (3a) with respect to x , evaluated at x_0 , is $-1 - \alpha\delta < 0$ (all model parameters are positive).

To find positive model equilibria for $\Theta > 0$, we solve the equation

$$G(x) = \frac{gx}{x + \Theta} - (1 + x) - \frac{\alpha\delta}{1 + x/B} = 0$$

This leads to solving a third-order polynomial

$$a_3x^3 + a_2x^2 + a_1x + a_0 = 0$$

where

$$a_3 = 1/B$$

$$a_2 = 1 + 1/B + \Theta/B - g/B$$

$$a_1 = 1 + \Theta + \Theta/B + \alpha\delta - g$$

$$a_0 = \Theta + \alpha\delta\Theta$$

Since G is always concave,

$$G''(x) = -\frac{2g\Theta}{(x + \Theta)^3} - \frac{2\alpha\delta/B^2}{(1 + x/B)^3} < 0$$

model (3a) can have at most two different positive equilibria. We used numerical simulations in MATLAB to find out that there is either no positive equilibrium or that they are just two of which the lower is unstable (Allee threshold) and the upper is locally stable (carrying capacity).

The case $\theta = 0$ (no mate-finding Allee effect, only Allee effect due to predation) allows for more detailed analysis. Straightforward yet tedious algebra gives the results summarized in Table A1; the areas I-IV are shown in Fig. A1.

For model (3b) and $\theta > 0$, the analysis follows the same lines as above with analogous results. The results for $\theta = 0$ are summarized in Table A2; the areas I-V are shown in Fig. A2.

For both models (3a) and (3b) and $\theta > 0$, the extinction equilibrium x_0 can also be unique and globally stable if the mate-finding Allee effect and/or the Allee effect due to predation are sufficiently strong; for $\alpha = 0$ or $B = 0$ or $\lambda = 0$, this happens when $\theta >$

$$\theta_{\text{lim}} = (1 - \sqrt{g})^2.$$

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Figure legends

Figure 1: Trade-offs (4a) and (4b) as they vary with the shape parameter z .

Figure 2: Equilibria of model (3a). Stable (solid lines) and unstable (dashed lines) equilibria of model (3a) as they depend on (A) the mate-finding Allee effect strength Θ and the predator attack rate α for $g = 2$, $B = 0.01$ and $\delta = 10$ and on (B) the mate-finding Allee effect strength Θ and the prey vulnerability B for $g = 2$, $\alpha = 0.05$, $\delta = 10$. Lines of equilibria in panel A range from $\alpha = 0$ until 2.4 (step size 0.2; no equilibria beyond $\alpha = 2.55$), and lines of equilibria in panel B start with $B = 0.0001$ and have step size 0.1 (lines for large B approach the leftmost line corresponding to $B \rightarrow \infty$).

Figure 3: Population resilience (panels A and C) and relative population resilience for prey with inflexible reproductive behaviour (panels B and D) for model (3a), plotted as a function of the mate-finding Allee effect strength Θ and the predator attack rate α (panels A and B) and the mate-finding Allee effect strength Θ and the prey vulnerability B (panels C and D). Parameter values: A and B. $g = 2$, $B = 0.01$ and $\delta = 10$, so that $\Theta_{\text{lim}} = 0.17$ and $\alpha_{\text{lim}} = 2.55$. C and D. $g = 2$, $\alpha = 0.05$ and $\delta = 10$, so that $\Theta_{\text{lim}} = 0.17$ and there is no B_{lim} . The thin lines are isolines of the (relative) population resilience, increasing from 0 to $g-1$ with stepsize 0.05 (indicated by thick arrow). These two pairs of panels (A with B and C with D) represent two generic outcomes that all models analyzed in this article produce.

Figure 4: Population resilience under reproduction-predation risk trade-off. Panel A: The population resilience R as a function of Θ and α with examples of three trade-off curves marked A, B and C. Thin black lines = isolines of population resilience, increasing from 0 to $g-1$ with stepsize 0.05 (indicated by thick arrow). Populations cannot persist above the viability limit = the isline connecting the points $[\Theta_{\text{lim}}, 0]$ and $[0, \alpha_{\text{lim}}]$ at which $R = 0$; R is maximized for $\Theta = 0$ and $\alpha = 0$ where $R = g-1$. Panel B: The population resilience R as a function of Θ along the three trade-off curves shown in panel A. Trade-offs A and B yield the same resilience for $\Theta > \Theta_{\text{max}} = 0.08$ and trade-offs A, B and C for $\Theta > \Theta_{\text{max}} = 0.12$. See the main text for details. Parameter

values: $g = 2$, $B = 0.01$, $\delta = 10$; trade-off curves: $\Theta_{\max} = 0.08$, $\alpha_{\max} = 1$, $z = 0.4$ (A), $\Theta_{\max} = 0.08$, $\alpha_{\max} = 1$, $z = 3$ (B), and $\Theta_{\max} = 0.12$, $\alpha_{\max} = 1.8$, $z = 3$ (C).

Figure 5: Parameter regions yielding the five different scenarios for populations with predation limit (A) and the three scenarios for populations without predation limit (B). See also Table 3 and the main text for details.

Figure 6: Examples of the five scenarios of the impact of reproduction-predation risk trade-off between the mate-finding Allee effect strength Θ and the attack rate α on the population resilience R for the AR model. Panels A-E represent examples from the equally marked areas in Fig. 5A. Parameter values: $g = 2$, $B = 0.01$ and $\delta = 10$, so that $\Theta_{\lim} = 0.17$ and $\alpha_{\lim} = 2.55$; A: $\Theta_{\max} = 0.08 < \Theta_{\lim}$ and $\alpha_{\max} = 1 < \alpha_{\lim}$; B: $\Theta_{\max} = 0.08 < \Theta_{\lim}$ and $\alpha_{\max} = 1.8 < \alpha_{\lim}$; C: $\Theta_{\max} = 0.18 > \Theta_{\lim}$ and $\alpha_{\max} = 1 < \alpha_{\lim}$; D: $\Theta_{\max} = 0.08 < \Theta_{\lim}$ and $\alpha_{\max} = 2.6 > \alpha_{\lim}$; E: $\Theta_{\max} = 0.18 > \Theta_{\lim}$ and $\alpha_{\max} = 2.6 > \alpha_{\lim}$.

Figure 7: Examples of the five scenarios of the impact of reproduction-predation risk trade-off between the mate-finding Allee effect strength Θ and the attack rate α on the relative population resilience ρ_i for prey with inflexible reproductive behaviour for the AR model. Legend as in Fig. 6.

Figure A1: Numbers and stability of equilibria of model (3a) in the α - B parameter space for $\Theta = 0$. Areas I–IV explained in Table A1.

Figure A2: Numbers and stability of equilibria of model (3b) in the λ - H parameter space for $\Theta = 0$. Areas I–V explained in Table A2.

Figure 1

Figure 2

A

B

Figure 3

Figure 4

A

B

Figure 5

A

B

Figure 6

Figure 7

Figure A1

Figure A2

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

Table 2: Model parameters and used symbols and abbreviations.

Subject	Symbol	Meaning
Prey	N	population density
	K	population carrying capacity
	x	relative population density N
Predator	P	predator density
	δ	relative predator density P
Prey reproduction	b	birth rate
	g	relative birth rate b
	θ	strength of mate-finding Allee effect
	Θ	relative strength of mate-finding Allee effect θ
Predation	λ	encounter rate (Holling type II functional response)
	α	attack rate (linear functional response)
	h	handling time
	H	relative handling time h
	β	prey vulnerability (= prey density at which attack rate halves due to self-defense)
	B	relative prey vulnerability β
Reproduction-predation risk trade-off	$\lambda_{\max}$	maximum encounter rate λ
	$\alpha_{\max}$	maximum attack rate α
	$B_{\max}$	maximum prey vulnerability B
	$\Theta_{\max}$	reproductive threshold (no predation for $\Theta \geq \Theta_{\max}$)
	z	shape of reproduction-predation risk trade-off
Emergent quantities	$\alpha_{\lim}$	maximum viable attack rate under no mate-finding Allee effect
	$\Theta_{\lim}$	maximum viable mate-finding Allee effect strength under no predation
Equilibria	$S(S_0, S_1)$	stable prey equilibrium
	$U(U_0, U_1)$	unstable prey equilibrium
Population resilience	R	population resilience, $S-U$
	ρ_f	relative population resilience for prey with flexible reproductive behaviour, $(S-U)/(S_0-U_0)$

	ρ_i	relative population resilience for prey with inflexible reproductive behaviour, $(S-U)/(S_1-U_1)$
Abbreviations	AR	attack rate model = model (3a) with trade-off (4a)
	PV	prey vulnerability model = model (3a) with trade-off (4b)
	ER	encounter rate model = model (3b) with trade-off (4c)

Table 3: Two generic cases distinguishing the qualitative shape of the (relative) population resilience surface plots in Fig. 3.

Model	Populations with predation limit (Fig. 3A-B)	Populations without predation limit (Fig. 3C-D)
AR	Always	Never
PV	$\alpha > (g-1)/\delta$	$\alpha < (g-1)/\delta$
ER	$H < 4\delta / (g-1)^2$	$H > 4\delta / (g-1)^2$

Table A1: Analysis of model (3a) for no mate-finding Allee effect ($\Theta = 0$).

Parameters α , g , δ and B are explained in the main text; $\alpha_{\text{lim}}(B) = [B(1+1/B-g/B)^2/4+g-1]/\delta$ and $B_{\text{lim}}(\alpha) = (g-1)^2 / \left[2\alpha\delta - g + 1 + \sqrt{(2\alpha\delta - g + 1)^2 - (g-1)^2} \right]$.

Area	Conditions	Extinction equilibrium x_0	Positive equilibria
I	$\alpha > (g-1)/\delta$ and $\alpha > \alpha_{\text{lim}}(B)$ (alternatively $B > B_{\text{lim}}(\alpha)$)	globally stable	no positive equilibrium
II	$\alpha > (g-1)/\delta$ and $\alpha < \alpha_{\text{lim}}(B)$	locally stable	two equilibria: lower unstable (Allee threshold), upper locally stable (carrying capacity)
III	$\alpha < (g-1)/\delta$ and $B < g-1$	unstable	unique, globally stable equilibrium (carrying capacity)
IV	$\alpha < (g-1)/\delta$ and $B > g-1$	unstable	unique, globally stable equilibrium (carrying capacity) that vanishes at $\alpha = (g-1)/\delta$

Table A2: Analysis of model (3b) for no mate-finding Allee effect ($\Theta = 0$).

Parameters λ , g , δ and H are explained in the main text; $\lambda_{\text{lim}}(H) = 1/(H(1-g) + 2\sqrt{H\delta})$.

Area	Conditions	Extinction equilibrium x_0	Positive equilibria
I	$\lambda > (g-1)/\delta$ and $\lambda > \lambda_{\text{lim}}(H)$	globally stable	no positive equilibrium
II	$\lambda > (g-1)/\delta$ and $\lambda < \lambda_{\text{lim}}(H)$	locally stable	two equilibria: lower unstable (Allee threshold) and upper locally stable (carrying capacity)
III	$\lambda < (g-1)/\delta$ and $1/H < (g-1)^2/(4\delta)$	unstable	unique, globally stable equilibrium (carrying capacity)
IV	$\lambda < (g-1)/\delta$ and $(g-1)^2/(4\delta) < 1/H < (g-1)^2/\delta$	unstable	unique, globally stable equilibrium (carrying capacity)
V	$\lambda < (g-1)/\delta$ and $1/H > (g-1)^2/\delta$	unstable	unique, globally stable equilibrium (carrying capacity) that vanishes at $\lambda = (g-1)/\delta$