

REVIEWS AND  
SYNTHESES

## Allee effects in biological invasions

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## Abstract

Understanding the dynamics of small populations is obviously important for declining or rare species but is also particularly important for invading species. The Allee effect, where fitness is reduced when conspecific density is low, can dramatically affect the dynamics of biological invasions. Here, we summarize the literature of Allee effects in biological invasions, revealing an extensive theory of the consequences of the Allee effect in invading species and some empirical support for the theory. Allee effects cause longer lag times, slower spread and decreased establishment likelihood of invasive species. Expected spatial ranges, distributions and patterns of species may be altered when an Allee effect is present. We examine how the theory can and has been used to detect Allee effects in invasive species and we discuss how the presence of an Allee effect and its successful or unsuccessful detection may affect management of invasives. The Allee effect has been shown to change optimal control decisions, costs of control and the estimation of the risk posed by potentially invasive species. Numerous ways in which the Allee effect can influence the efficacy of biological control are discussed.

## Keywords

Allee effects, biological invasions, depensation, invasive species, positive density-dependence, spread rate.

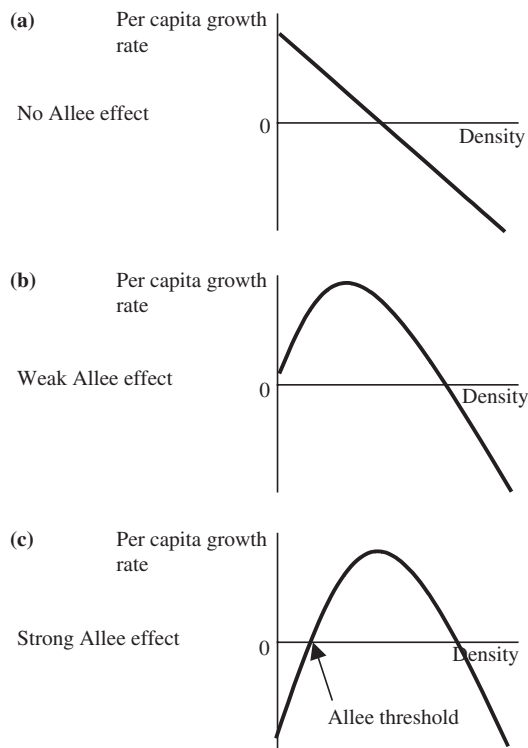
*Ecology Letters* (2005) 8: 895–908

## INTRODUCTION

Allee effects have become much studied in recent years, largely because of their potential role in extinctions of already endangered, rare or dramatically declining species (Fowler & Baker 1991; Stephens & Sutherland 1999; Barnett 2001). Less well recognized is the fact that Allee effects are also important in the dynamics of invasive species. Low density at the edge or in the initial population of an invader provides an opportunity for Allee effects to substantially alter invasion dynamics. As this review will illustrate, theoretical studies predict that Allee effects in an invader can cause longer lag times, slower spread and decreased probability of establishment. These may lead to underestimation of the invasion risk posed by some species. Under some circumstances, Allee effects can cause different spatial distributions including a halt to range expansion and the presence of an Allee effect in an invasive species may affect optimal control strategies and costs. In turn, invasive species, often introduced at low density or at low density at the edges of their ranges, provide an opportunity to learn about the consequences,

especially spatial consequences, of Allee effects and to test theoretical predictions.

An Allee effect, named after the ecologist Warder C. Allee (Allee 1931, 1938, 1958), is defined as ‘a positive relationship between any component of fitness of a species and either numbers or density of conspecifics’ (Stephens *et al.* 1999) meaning that an individual of a species that is subject to an Allee effect will suffer a decrease in some aspect of its fitness when conspecific density is low. Stephens *et al.* (1999) distinguish between ‘component’ and ‘demographic’ Allee effects. When a population experiences a ‘component’ Allee effect, some component of individual fitness has a positive relationship with density, i.e. is reduced at low density. In some cases this leads to a ‘demographic’ Allee effect where the overall fitness has a positive relationship with density that results in per capita growth rate of the species being reduced at low density. A demographic Allee effect can be either ‘weak’ or ‘strong’ (Wang & Kot 2001; Deredec & Courchamp 2003). Populations subject to a ‘strong’ Allee effect experience negative per capita growth rates when density falls below a critical threshold (Fig. 1). Under deterministic dynamics a



**Figure 1** Definition of the demographic Allee effect. The positive relationship between per-capita growth rate and density when density is low defines an Allee effect as in both (b) and (c). When per-capita growth rate is negative below a threshold density, this is a strong or critical Allee effect as in (c).

population that does not exceed this threshold will become extinct. Many studies consider only 'strong' Allee effects but the examples in Allee's original work show clearly that the definition should also include 'weak' Allee effects (Allee 1931, 1938, 1958; Fowler & Baker 1991; Stephens *et al.* 1999; Wang & Kot 2001; Wang *et al.* 2002). Populations with 'weak' Allee dynamics experience lower per capita growth rates at low densities but never experience negative per-capita growth rates and therefore have no critical threshold to exceed (Fig. 1). We shall also refer to 'weak' Allee effects as 'non-critical' Allee effects and 'strong' Allee effects as 'critical' Allee effects. Other terms that have been used to describe Allee effects include 'positive density-dependence', 'inverse density-dependence' and 'disoperation'. In the fisheries literature, the Allee effect is known as 'depensation' (because it is the opposite of compensation; more often known as (negative) density-dependence usually caused by competition). Strong Allee effects are termed 'critical depensation' and weak Allee effects 'non-critical depensation' (Clark 1990). Occasionally the term depensation is used to refer to population

phenomena that do not arise from changes in individual fitness and therefore are not Allee effects (Stephens *et al.* 1999).

Many mechanisms can give rise to Allee effects. The most prevalent is that of mate shortage in sexually reproducing species (Dennis 1989; Boukal & Berec 2002). Early work refers to Allee effects as the absence of cooperation (sometimes called disoperation), or simply asociality in sexually reproducing species (Odum & Allee 1954; Philip 1957; Bradford & Philip 1970a,b). Other mechanisms include sex ratio changes, asynchrony in reproductive timing of potential mates, sexual selection, more effective predator avoidance in large groups, obligate cooperation and many others. Reviews of mechanisms can be found in (Dennis 1989; Fowler & Baker 1991; Courchamp *et al.* 1999; Stephens & Sutherland 1999). Allee effects have been shown to be present in all major taxonomic groups of animals (Allee 1958; Fowler & Baker 1991; Myers *et al.* 1995; Liermann & Hilborn 1997; Gascoigne & Lipcius 2004a) and seem to also be common in plants (Groom 1998). Given the pervasiveness of the Allee effect, it seems likely that it is experienced by many populations of invasive species.

Many investigators have explored the consequences and the different ways of incorporating Allee effects into population models. Most of these are non-spatial single species models and have been reviewed by Boukal & Berec (2002). Additionally, there are numerous theoretical studies in which Allee effects have been incorporated into spatial population models which, taken together, reveal an extensive theory regarding the consequences of Allee effects in biological invasions (Table 1). Recent empirical studies demonstrating the presence of Allee effects in invasive species may provide the first tests of the theory. The aims of this review are (i) to summarize the literature in order to catalogue the theoretical consequences of Allee effects on invasion dynamics, (ii) to summarize the empirical work and models of specific systems to determine how well the theory is supported and to demonstrate the different ways in which Allee effects can be detected, and (iii) to explore the implications of Allee effects in invasive species for control, prediction and prevention of biological invasions.

## MODELLING ALLEE EFFECTS IN INVASIONS

We examine work that has explored the population level consequences of an Allee effect that are relevant to invasion biology. Allee effects have been added to many different kinds of population models (Table 1). The simplest, non-spatial, single species population model in continuous time takes the form of eqn 1 where  $n$  is the population size or density and  $f(n)$  is the per capita growth function,

**Table 1** Ecological consequences of Allee effects on dynamics of invasive species

Consequence	Model type	Type of Allee effect	References
Non-spatial consequences			
Species must be introduced at higher than critical threshold for invasion to succeed	Deterministic	Critical	Volterra (1938) and Odum & Allee (1954)
Probability of establishment declines sharply at critical density	Stochastic	Critical	Dennis (1989, 2002)
No establishment possible if Allee effect is too strong	Deterministic	Critical	Lewis & Kareiva (1993), Kot <i>et al.</i> (1996), Amarasekare (1998a), Wang <i>et al.</i> (1999), Ferdy & Molofsky (2002) and Hui & Li (2003)
Spatial consequences			
Rate of spread slower	Deterministic or stochastic	Critical or non-critical	Lewis & Kareiva (1993), Kot <i>et al.</i> (1996), Wang & Kot (2001), Wang <i>et al.</i> (2002) and Hadjivagousti & Ichtiaroglou (2004)
Range pinning	Deterministic or stochastic with discrete (patchy) space	Critical	Fath (1998), Keitt <i>et al.</i> (2001) and Hadjivagousti & Ichtiaroglou (2004)
Accelerating invasions converted to finite speed invasions	Deterministic, integrodifference with fat-tailed dispersal kernels	Critical or non-critical	Kot <i>et al.</i> (1996) and Wang <i>et al.</i> (2002)
Different levels of occupancy of patches and segregation of competing species	Discrete patches	Critical	Gruntfest <i>et al.</i> (1997), Amarasekare (1998b) and Gyllenberg <i>et al.</i> (1999)
Patchy invasion in continuous landscape	Stochastic models with continuous space or lattice models	Critical	Petrovskii <i>et al.</i> (2002), Soboleva <i>et al.</i> (2003) and Hui & Li (2004)
Initial population must occupy area larger than critical spatial threshold	Deterministic	Critical	Bradford & Philip (1970a), Lewis & Kareiva (1993), Kot <i>et al.</i> (1996), Etienne <i>et al.</i> (2002) and Soboleva <i>et al.</i> (2003)

$$\frac{dn}{dt} = nf(n). \quad (1)$$

It is the shape of the function  $f(n)$  at small  $n$  that determines whether or not there is an Allee effect. If there is no Allee effect,  $f(n)$  has a negative slope at small densities ( $f'(0) < 0$ ). If there is an Allee effect,  $f(n)$  has a positive slope at small population sizes ( $f'(0) > 0$ ) (Fig. 1). Many forms of  $f(n)$  that meet this criterion are possible (for a review see Boukal & Berec 2002). In addition, if  $f(n)$  is negative for small  $n$  and positive for larger  $n$ , then the Allee effect has a threshold (found by evaluating  $n$  when  $f(n) = 0$ ) and the Allee effect is 'critical' or 'strong'. If  $f(n)$  is positive for small  $n$ , the Allee effect is 'non-critical' or 'weak' (Fig. 1).

When modelling invasions, space becomes important. In ecology, the most common analytical models in which space is represented explicitly are reaction–diffusion (RD) models and integrodifference equations (IDE) (for a review see Hastings *et al.* 2005). The RD model is a partial differential equation of the form,

$$\frac{\partial n(x, t)}{\partial t} = n(x, t)f(n(x, t)) + D\frac{\partial^2 n(x, t)}{\partial x^2}, \quad (2)$$

where  $n$  is the density of the populations,  $t$  is time and is continuous (generations are overlapping),  $f(n)$  is the per capita growth function and  $D$  is the diffusion constant.

Integrodifference models are an alternate means of describing spatial dynamics when time  $t$ , is discrete (generations do not overlap). If  $k(x, y)$  is the dispersal

kernel; the probability that an individual moves from spatial location  $x$  to  $y$  in a given time step and  $f(n)$  is the per capita growth function then the dynamics are given by

$$n_{t+1}(x) = \int_{-\infty}^{\infty} n_t f(n_t(y)) k(x, y) dy. \quad (3)$$

As in the non-spatial model (eqn 1), it is the shape of  $f(n)$  in both RD and IDE models that determines whether or not the population is subject to an Allee effect.

The models we have discussed describe space as continuous. Yet, in many cases, such as insects on host plants, or on clumps of plants as in meadows, space may be more accurately described as discrete patches. Discrete space versions of continuous time (RD) models or discrete time (IDE) models have a long history in ecology, and when studying Allee dynamics may in fact behave differently. When space is discrete, a patch with a population level below the Allee threshold can be next to a patch with a population level above the Allee threshold; when space is continuous, the population level would need to vary smoothly and pass through the Allee threshold. We will consider the important consequences of this below while discussing range pinning.

Metapopulations are another description of spatial dynamics in which space is represented as a collection of discrete connected populations or patches, but with stochasticity assumed to operate at the spatial scale of the patch. This has further important consequences for understanding the impact of Allee effects. In the simplest version of a metapopulation model, each patch is either occupied or not occupied and there is global connectivity between patches; an individual can move from any patch to any other patch. In the classic Levins model, the proportion of occupied patches is modelled using the same mathematical form as eqn 1 and if the per occupied patch rate of growth has a positive slope at low levels of occupancy, then there is a metapopulation-level Allee effect (Amarasekare 1998a). Biologically this means that the rate at which new patches become occupied is disproportionately reduced when the level of occupancy of other patches is low. If the Allee effect is critical, there is a critical number of patches that need to be occupied in order for the metapopulation to persist.

An extension to the metapopulation model is to consider a collection of subpopulations in which each patch has its own local non-spatial dynamics (eqn 1). This is sometimes called a 'structured' metapopulation (Hastings 1991). An Allee effect is added to a structured metapopulation by modifying the local dynamics for individual patches. It has been shown that adding an Allee effect to local dynamics leads to an Allee effect at the metapopulation level (Courchamp *et al.* 2000; Zhou & Wang 2004). In structured metapopulations, an Allee effect provides a deterministic

way of including patch extinction and a closer parallel between structured metapopulation models and a Levins-type metapopulation model.

Allee effects can also be incorporated mechanistically into models. For instance if two sexes of a species are modelled separately, the mate-finding mechanism can be limited by (low) density and lead directly to an Allee effect. Allee effects can also be included mechanistically in spatially explicit simulation models (e.g. Berec *et al.* 2001; South & Kenward 2001; Taylor *et al.* 2004) and in spatially implicit models derived from spatially explicit models (Berec *et al.* 2001; Taylor *et al.* 2004).

Whenever population size is described by a continuous variable, Allee effects can be useful mathematically because they circumvent mathematical problems that lead to non-biological effects. Deterministic, continuous-time models implicitly assume that dynamics are the same for finite populations and for infinitesimally small populations and this can lead to non-biological effects; for example in epidemic models, epidemics will re-emerge from infinitesimally small population sizes. Adding a small critical Allee effect is a practical way to eliminate this problem because populations will decline to extinction at low densities and do not stay infinitesimally small for long enough for the epidemic to re-emerge (Cruickshank *et al.* 1999).

## THEORETICAL CONSEQUENCES OF ALLEE EFFECTS IN INVASIONS

### Invasion thresholds in deterministic models

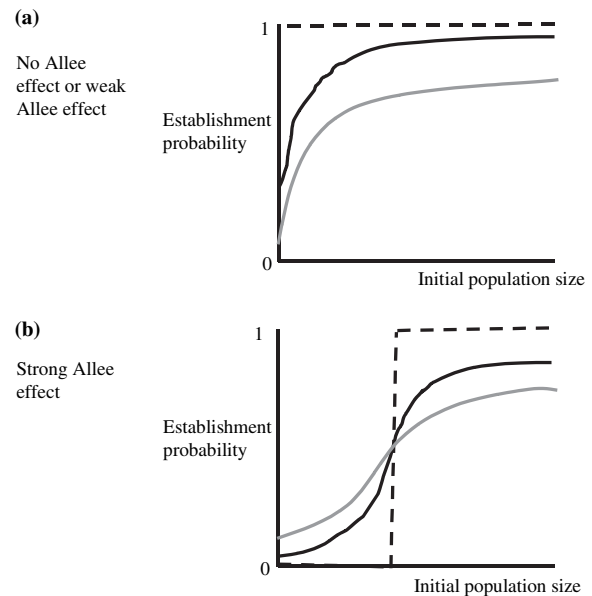
The most general consequence of an Allee effect is the creation of a critical density threshold. In the simplest models, a population without an Allee effect or with a weak Allee effect will grow from any initial density until it reaches the only stable equilibrium point, its carrying capacity. Models with a strong demographic Allee effect have a zero stable equilibrium point, and a positive unstable equilibrium that acts as a threshold. If the population exceeds this density, the population will grow until it reaches carrying capacity (i.e. invades or becomes established in the context of invasive species). If the initial density is lower than the unstable equilibrium/threshold, the population declines to extinction (i.e. fails to establish). This result is found in the simplest population models (Volterra 1938; Odum & Allee 1954) and has been generalized to a variety of metapopulation models where the threshold is an occupancy level (Lande 1987; Amarasekare 1998a; Ovaskainen & Hanski 2001; Harding & McNamara 2002), and to structured metapopulation models where the Allee effect operates on the within-patch dynamics (Zhou & Wang 2004). In models where the population is structured (e.g. by space, age,

stage or sex), thresholds are hypersurfaces (Schreiber 2004). Hence there is no single threshold density. For instance, when sexes are modelled separately and a mate finding mechanism leads to an Allee effect, there are interrelated thresholds for both males and females (Berec *et al.* 2001).

Invasions, of course, are spatial processes and including space and dispersal in the models changes the predicted value of the critical initial density. The effect of dispersal (diffusion) in one-dimensional RD models is to dilute the population at any given location thereby reducing density and resulting in higher initial densities necessary to overcome the Allee effect than in the corresponding non-spatial models (in which diffusion is zero) (Bradford & Philip 1970b). Two dimensional RD models predict critical densities even higher than found in one-dimensional models (Bradford & Philip 1970a; Soboleva *et al.* 2003). Increasing dispersal rates in a spatial model is likely to increase the critical initial density (Berec *et al.* 2001), although here the effects of boundary conditions are likely to be very important; if suitable habitat is finite, conditions for persistence will depend dramatically on whether individuals remain in or leave the suitable habitat. Adding either advection (density independent) that might be caused by physical forcing (e.g. wind or ocean currents) or density-dependent migration to a one-dimensional RD model reduces the Allee threshold above, which the invasion will succeed. Advection and migration interact to alter the threshold; depending on the assumptions this interaction can either enhance or inhibit invasion (Petrovskii & Li 2003).

### Invasion thresholds in stochastic models

Stochastic models are used to represent both variable environments (environmental stochasticity) and variable vital rates between individuals in the population (demographic stochasticity). In a stochastic model, no exact threshold between extinction and establishment exists; instead the threshold becomes probabilistic. Measuring the probability of extinction can be problematic because the outcome of all stochastic population models is eventual extinction. Either additional constraints, for example, time limits within which the population either persists or becomes extinct, have to be introduced or another metric must be used. For instance, many studies report the mean time to extinction. More useful for the study of invasions is the 'first passage probability', the probability that a population will reach level  $a$  before reaching level  $b$ . If  $a$  is small and  $b$  large then this is an effective measure of extinction likelihood; if the levels are reversed it becomes a measure of establishment likelihood (Fig. 2). This metric can be calculated from simulation or analytically (Dennis 2002; Drake 2004).



**Figure 2** Schematic representation of effect of stochasticity on probability of establishment: dashed line is deterministic dynamics, black solid line is stochastic dynamics with low levels of stochasticity and grey solid line is stochastic dynamics with high levels of stochasticity. (a) Stochasticity always reduces establishment probability when no or weak Allee effect. (b) Stochasticity reduces establishment probability for large population sizes but increases establishment probability for small population sizes when strong Allee effect. There is an inflection point at the threshold population size.

Under non-Allee dynamics, stochasticity reduces the probability of establishment for small initial populations. Demographic stochasticity has been shown to create a type of threshold below, which most populations tend to extinction. This has been dubbed a 'type of Allee effect' (Lande 1998) but it is not a true (biological) Allee effect according to the definition used here because there is no decrease in individual fitness (Stephens *et al.* 1999). By incorporation of Allee effect into a stochastic differential equation, Dennis (1989, 2002) has shown that a true critical Allee effect will produce an inflection point in the first passage probability as function of population size at the point where the unstable equilibrium (critical density) would be in the underlying deterministic dynamics. Without an Allee effect and with only demographic stochasticity, the first passage probability is a concave-down saturating function of population size (Fig. 2).

In interaction with critical Allee effects, both demographic and environmental stochasticity tend to increase the probability of establishment for a population smaller than the Allee threshold and decrease the probability of establishment for a population larger than the Allee threshold (Fig. 2) (Dennis 1989, 2002; Grevstad 1999;

Liebhold & Bascompte 2003) and this effect is exaggerated as the degree of stochasticity increases (Liebhold & Bascompte 2003). Even if the population experiences only a non-critical Allee effect, we should expect that the addition of stochasticity will reduce the probability of establishment for small populations more than if there was no Allee effect (Liebhold & Bascompte 2003). The probability of establishment is further reduced as the strength of Allee effect increases and this is more dramatic when stochasticity is low; increasing the Allee density threshold causes a greater reduction in mean time to extinction (or in probability of establishment) for populations in stable environments than in variable environments (Brassil 2001; Zhou & Wang 2004).

### Invasion thresholds in spatial models

Allee effects not only lead to thresholds in initial population numbers or densities but also in initial area occupied. This result is a special case of a hypersurface threshold in a structured (spatially structured in this case) population (Schreiber 2004). A threshold has been demonstrated analytically, for critical Allee effects, in RD models in both one and two dimensions (Bradford & Philip 1970b; Lewis & Kareiva 1993; Soboleva *et al.* 2003), in integrodifference models (Kot *et al.* 1996), and is supported by results from a simulation model of fruit flies (Etienne *et al.* 2002). The result implies also that invasions might not succeed if there is insufficient habitat, i.e. if the area available is smaller than the spatial threshold (Bradford & Philip 1970b). An analytical calculation of the size of the spatial threshold as a function of initial population density, diffusion rate and strength of the Allee effect shows that the size of the threshold is larger if the calculation is carried out in two dimensions (assuming a circular initial invasion and symmetrical subsequent spread in all directions) than if the calculation is in one dimension (Soboleva *et al.* 2003). If the assumption of symmetrical spread is dropped, the spatial threshold is reduced, leading to the conclusion that an invader will typically not spread symmetrically even in an isotropic habitat (Soboleva *et al.* 2003).

Allee effects also raise the proportion of good habitat necessary for persistence in metapopulation models with fragmented habitat. This threshold exists in models without an Allee effect but is increased by the addition of Allee dynamics (Lande 1987; Amarasekare 1998a). In a spatially structured metapopulation, a metric called 'metapopulation capacity' is calculated from the size of individual patches and their connectivities. Analogous to the proportion of good habitat in the simpler models, metapopulation capacity has to exceed a threshold for persistence and, again, the addition of an Allee effect raises the threshold (Amarasekare 1998a; Ovaskainen & Hanski 2001).

### Invasion speeds with Allee effects

Even when an invasion exceeds initial density and spatial thresholds the existence of an Allee effect can affect the rate of spread. Invasion speed decreases as the Allee effect increases in strength and this is shown in many types of model (Lewis & Kareiva 1993; Kot *et al.* 1996; Hadjiavgousti & Ichtiaroglou 2004). Both non-critical and critical Allee effects can depress invasion speeds. The same mathematical expression for invasion speed, derived from solving a RD model, is used to predict speeds for species with a critical Allee effect and for species with a non-critical Allee effect that is sufficiently strong (Lewis & Kareiva 1993; Wang & Kot 2001). The expression for the speed of an invasion with a very weak non-critical Allee effect is the same as that for an invasion with no Allee effect (Wang & Kot 2001). This result holds also for integrodifference models with several different dispersal kernels (Wang *et al.* 2002).

When examined in two dimensions, the shape of the invasion front affects the rate of spread. Invasions with more corrugated fronts increase their range more rapidly than invasions with planar boundaries (Lewis & Kareiva 1993). Allee effects may also slow down the initial rate of spread of an invader (Lewis & Kareiva 1993) leading to the potential to underestimate later spread rates if the Allee effect is undetected (Hastings 1996).

The impact of an Allee effect on rate of spread depends on the shape of the dispersal kernel. Rate of spread is often sensitive to whether the kernel is, or is not, 'fat-tailed' (i.e. not exponentially bounded) (Kot *et al.* 1996; Schofield 2002; Wang *et al.* 2002). Some fat-tailed dispersal kernels lead to continually accelerating spread (Kot *et al.* 1996) and, in some cases, adding an Allee effect converts the continually accelerating invasion into a finite-speed invasion (Kot *et al.* 1996; Wang *et al.* 2002). Both critical and sufficiently strong non-critical Allee effects can produce this result (Wang *et al.* 2002). Other fat-tailed kernels compete with Allee effects as possible alternate explanations for dynamics in which spread accelerates initially and then settles to constant speed (Kot *et al.* 1996; Wang *et al.* 2002).

### Range pinning

Allee effects may also provide an explanation for lack of range expansion of a species even when suitable habitat patches are nearby (Keitt *et al.* 2001). This consequence, referred to as both 'range-pinning' and 'propagation failure', shows up only in a patchy landscapes, i.e. when space is represented as discrete patches, the Allee effect operates on local within patch dynamics, and there is dispersal between patches (Fath 1998; Keitt *et al.* 2001; Hadjiavgousti & Ichtiaroglou 2004). Allee effects can cause range pinning in discrete space even when stochastic effects are not included.

Allee effects do not cause range pinning in a homogeneous continuous landscape (Keitt *et al.* 2001) because in continuous space models, range pinning or zero invasion speed results only from a single, exact, unchanging set of parameter values and is therefore realistically infeasible, although this result can be altered by finite boundary conditions. When space is described as continuous the part of the habitat that has population levels exactly at the Allee threshold is at an unstable equilibrium of the spatially independent model and will either have population levels increase or decrease, leading to either an increase or decrease in range size. In contrast, with discrete space, neighbouring patches can have levels on opposite sides of the Allee threshold.

For species with overlapping generations (continuous time), individual patches are either completely invaded (density reaches carrying capacity) or not at all invaded (density is zero) (Fath 1998; Keitt *et al.* 2001). For species with non-overlapping generations, it is also possible to generate patterns where the initially invaded patch has a final density close to carrying capacity and the density of neighbouring patches declines exponentially with distance from the initial patch (Hadjivagousti & Ichtiaroglou 2004). Whether range pinning will occur depends on the dispersal rate and the strength of the Allee effect in local patches. Critical Allee effects with high-density thresholds and low dispersal lead to range pinning whereas critical Allee effects with high dispersal lead to range contraction. Critical Allee effects with low density thresholds and low dispersal also exhibit range pinning but with low density thresholds and high dispersal predict range expansion (Fath 1998; Keitt *et al.* 2001). Additionally, in metapopulation models, the finally predicted occupancy is reduced by the inclusion of an Allee effect (Lande 1987; Ovaskainen & Hanski 2001). In a specific model of African wild dogs, both the number of occupied patches and the number of individuals within patch were reduced by the inclusion of an Allee effect in the local dynamics (Courchamp *et al.* 2000).

### Production of spatial heterogeneity

Several theoretical studies suggest that final spatial distributions resulting from dynamics that include an Allee effect will be spatially heterogeneous without the need for underlying differences in habitat. In models of two habitat patches, local Allee dynamics and low migration between the patches, asymmetric stable states exist where one patch has much higher density than the other (Gruntfest *et al.* 1997; Amarasekare 1998b; Gyllenberg *et al.* 1999; Ferdy & Molofsky 2002). This result is only possible under Allee dynamics and is affected by competition between patches (Gyllenberg *et al.* 1999), by whether environment (mortality) is stable or fluctuating (Gruntfest *et al.* 1997), and by

whether dispersal is density-dependent or independent (Amarasekare 1998b). If migration is density-dependent it is possible for one patch to have densities lower than the Allee threshold thus creating source–sink dynamics (Amarasekare 1998b).

Allee effects can also cause the formation of irregular spatial clusters. Asymmetrical solutions of RD models with an Allee effect are possible and may be more likely outcomes than circular symmetrical solutions (Soboleva *et al.* 2003). In a lattice model, an Allee effect causes aggregations of individuals including ‘circumscription’ patterns in which aggregations are tied together by local interactions forming static borders. (Hui & Li 2004). Similarly in a predator–prey model an Allee effect lead to a patchy distribution of an invader. In this system if either the predator or the Allee effect is removed the invasion is not patchy (Petrovskii *et al.* 2002). In a simulation models of fruit flies, spatial heterogeneity in either initial densities or in resource distribution was found necessary for persistence and an Allee effect prevented rapid homogenization of patches leading to more stable dynamics (Etienne *et al.* 2002).

An Allee effect can promote heterogeneity between competitors. Two competitors in a single patch that both have Allee effects can coexist at different densities (Gyllenberg *et al.* 1999) but as the strength of the Allee effect increases, coexistence becomes less likely and eventually becomes impossible (Ferdy & Molofsky 2002). In two patches with two competitors an Allee effect can promote segregation of species between the patches and when competition is asymmetric can therefore promote coexistence (i.e. save the weak competitor) through segregation. Also high migration can destabilize dynamics but this can be mitigated by the Allee effect (Ferdy & Molofsky 2002). A disease that exists in two strains that are reproductively incompatible provides a mechanism for an Allee effect and leads to founder control, the first strain to invade tends to competitively exclude the other, in a continuous spatial model but spatially irregular (patchy) coexistence is possible if space is modelled as discrete (Keeling *et al.* 2003).

### Persistence and coexistence

In the presence of a critical Allee effect that is too strong, an invasion will fail regardless of initial density (Lewis & Kareiva 1993; Kot *et al.* 1996; Amarasekare 1998a; Wang *et al.* 1999; Ferdy & Molofsky 2002; Hui & Li 2004). However, adding an Allee effect to a single-species model tends to stabilize the dynamics in the following two ways. First, the parameter range under which a stable equilibrium is predicted is increased by adding an Allee effect (Scheuring 1999). Second, the dynamical complexity of the system is

reduced from chaotic to fluctuating to a single stable equilibrium as the strength of the Allee effect is increased (Fowler & Ruxton 2002). The latter has been shown to be true also in a metapopulation model (Hui & Li 2003). However, it should be noted that under chaotic population dynamics, the addition of an Allee effect can cause extinction of the population when chaotic fluctuations drive the population below its critical threshold (Schreiber 2003).

A different result is found when examining co-existence in two-species competitive models. Adding an Allee effect tends to destabilize co-existence of the two species. Sets of parameter values that predict stable co-existence in a model without Allee effects give rise to extinction of one or both species in the model with added Allee effects (Wang *et al.* 1999). More generally, increasing the strength of the Allee effect gradually reduces the range of initial conditions that lead to stable co-existence until eventually co-existence becomes unstable (Ferdy & Molofsky 2002).

### Evolutionary consequences

We expect that an Allee effect in an invasive species would provide selective pressure for adaptations that could overcome or mitigate the Allee effect. For instance, a reduction in reproductive function at low density might provide selective pressure for an increase in self-fertilization or asexual reproduction. Likewise if long distance dispersal causes initial density to drop and the Allee effect then causes extinction, this could provide selective pressure for evolution of different dispersal mechanisms. When a species tries to occupy a novel, harsh (sink) environments, an Allee effect lowers the probability of adaptation to the habitat but increases the positive effect of immigration on the probability of adaptation. High immigration has a more substantial effect with an Allee effect than without (Holt *et al.* 2004).

### Effects on biodiversity and invasibility

Allee effects may also influence invasibility of communities. In models of species packing along a resource gradient without Allee effects any number of species in a community can be stable. However, an Allee effect imposes a cost to rarity and leads to a finite number of species or range of packing distances. The Allee effect gives a range of community densities that are stable to invasion and a packing distance limit below, which a new species cannot invade. Increasing the strength of the Allee effects results in a substantial decrease in species diversity (Hopf & Hopf 1985).

### DETECTING ALLEE EFFECTS IN INVASIVES

Most empirical studies of Allee effects focus on rare or endangered species because of the obvious conservation

consequences. However, the potential consequences of Allee effects for invasive species, as documented in this review, are beginning to drive attempts to detect Allee effects in invasives. Allee effects have been detected in invasive plants, for example, pale swallow-wort (*Vincetoxicum rossicum*) (Cappuccino 2004) and smooth cordgrass (*Spartina alterniflora*) (Davis *et al.* 2004a,b); in pest insect species pine sawyers (*Monochamus alternatus*) (Yoshimura *et al.* 1999) and gypsy moths (*Lymantria dispar*) (Liebhold & Bascompte 2003); in the introduced house finch (*Carpodacus mexicanus*) (Veit & Lewis 1996) and other avian species (Green 1997); in pathogens such as *Wolbachia* (Turelli & Hoffmann 1991) and the karnal bunt wheat pathogen (*Tilletia indica*) (Garrett & Bowden 2002); and in the aquatic invasive zebra mussel (*Dreissena polymorpha*) (Johnson & Padilla 1996; Leung *et al.* 2004).

### Detecting a demographic Allee effect resulting from a component Allee effect

Typically, empirical work can show that some component of fitness is reduced when the density of conspecifics is low, thereby detecting a component Allee effect (Stephens & Sutherland 1999). To show that a component Allee effect leads to a demographic Allee effect generally requires a model of the species as in the following examples.

Field studies document that pollen limitation leads to reduced seed production of *Spartina alterniflora* in low density regions of an invasive population (Davis *et al.* 2004a,b). A model of this population shows that this component Allee effect leads to a non-critical demographic Allee effect (Taylor *et al.* 2004) and slows down the invasion consistent with theory (Wang & Kot 2001; Wang *et al.* 2002). This grass is unusual for a wind-pollinated plant in that the ratio of pollen dispersal distance to seed dispersal distance is low giving rise to an Allee effect that is reminiscent of the finding of the importance of the ratio of mate finding to natal dispersal distance (South & Kenward 2001).

A microbial infection, *Wolbachia*, in fruit flies induces cytoplasmic incompatibility in which uninfected females are incompatible with infected males (Turelli & Hoffmann 1991, 1995) leading to a critical Allee effect; the proportion of infected individuals needs to exceed a threshold before *Wolbachia* can spread. Models show that the threshold level is sensitive to the vertical transmission rate (Schofield 2002; Keeling *et al.* 2003) and that the spread rate is sensitive to the dispersal kernel (Schofield 2002). A non-spatial model with two strains of the infection that are incompatible with each other demonstrates founder control; the established strain always competitively excludes the invading strain (Keeling *et al.* 2003). A discrete spatial model allows patchy coexistence of the two strains arising from enhancement of



small heterogeneities in the initial random configuration (Keeling *et al.* 2003).

The insect pine sawyer introduces and spreads pine wilt disease (indirectly through a nematode). The disease weakens and eventually kills pine trees. The insect needs dead or weakened trees for oviposition. This feedback interaction leads to a positive relationship between density and reproductive success, i.e. to an Allee effect in the insect population. (Yoshimura *et al.* 1999). A model of this system was used to explore the relationship between the threshold and the eradication rate (Yoshimura *et al.* 1999).

Another plant pathogen, *Tilletia indica*, that causes the disease Karnal bunt in wheat, has four mating types and individuals of two different types must infect the same wheat floret in order to reproduce sexually and produce a new infection (Garrett & Bowden 2002). This causes an Allee effect. A model of this system shows that the Allee effect leads to a reduction in the probability of the establishment of new foci of infection and a reduction in the spread rate that depends on environmental conditions (Garrett & Bowden 2002).

### Detecting a demographic Allee effect directly

Another approach is to attempt to detect Allee effects by examining the dynamics of a single or multiple populations. Meta-analysis, the simultaneous analysis of data from many populations, provides a useful tool for estimating demographic parameters including existence and strength of Allee effects. Among non-invasive species, estimates of spawner abundance and recruitment for 128 fish stocks provide an extensive database for the potential detection of Allee effects using a meta-analysis. Myers *et al.* (1995) fit both a model with no Allee effect and a model with a free parameter representing the Allee effect to these data. They significantly (at the 0.05 level) detected an Allee effect in only three of the 128 stocks even though their power analysis shows that the power to detect an Allee effect is  $>0.95$  in 26 of the stocks. They conclude that Allee effects are a rare phenomenon among fish populations. However, Shelton & Healey (1999) show that a different way of calculating power would yield much lower power estimates and that the power estimates are highly dependent on the strength of the Allee effect. Also, Liermann & Hilborn (1997) show that the free parameter in the model used by Myers *et al.* (1995) does not independently represent the strength of the Allee effect as this depends also on other parameters in the model. Liermann & Hilborn (1997) reparameterize the model so the Allee effect parameter is more biologically meaningful. They use a Bayes hierarchical approach on the same data to determine the distribution of, and therefore the uncertainty in, the estimate of the Allee parameter for each fish stock and between stocks. They

conclude that a large degree of uncertainty exists and that the possibility of Allee effects cannot be ruled out.

For invasive species, meta-analysis can be used to detect the presence of critical Allee effects if the fates of multiple introductions of the same or related species have been recorded. The difficulty is distinguishing between Allee effects and stochasticity. Hopper & Roush (1993) reasoned that if environmental stochasticity was the most important factor then the number of releases would best explain the variation in establishment success, but if critical Allee effects were more important, the size of individual releases would be a better predictor of successful establishment. They discovered that the latter was true in a meta-analysis of parasitoid introductions that were deliberately released for biological control of pest insects. Similarly, Green (1997) found that numbers released was the best predictor of success in the establishment of bird species introduced to New Zealand.

As already noted, Dennis (1989, 2002) shows that a critical Allee effect in stochastic dynamics leads to an inflection point in the first passage probability as a function of initial population size. He suggests the presence or absence of an inflection point as competing statistical hypotheses could be tested by fitting a flexible parametric distribution to data of establishment success. This approach is used by Leung *et al.* (2004) who fit a Weibull distribution to success/failure data from multiple introductions of the zebra mussel. They find that there is significant support for the presence of an inflection point and therefore for the presence of a critical Allee effect in this species (Leung *et al.* 2004).

For a single invasion, population models can be fit directly to data that has recorded the extent of the invasion over time. As shown in this review, models with an Allee effect often predict qualitatively different dynamics than models without an Allee effect. In their study of the spread of the house finch across eastern North America, Veit & Lewis (1996) found that a model with an Allee effect gave a much better fit to the data and more similar qualitative dynamics than did a model without an Allee effect (Veit & Lewis 1996). Liebhold & Bascompte (2003) fit a stochastic model that included an Allee effect to data on the spread of the Gypsy moth. This approach gives an estimate for both the Allee threshold and the level of stochasticity in the population (Liebhold & Bascompte 2003).

The distribution of a species may imply the existence of an Allee effect. Habitat-selection theory shows that comparison of densities between two habitat types leads to a hiatus (no data points) at low densities assuming animals distribute themselves so that expected fitness is same in each. This approach is used to detect and measure an Allee effect in small mammals (Morris 2002). It has also

been suggested that a prey species with an Allee effect is likely to invade in a patchy manner (Petrovskii *et al.* 2002).

## IMPLICATION OF ALLEE EFFECTS FOR MANAGEMENT OF INVASIVES

### Non-biological control when Allee effects are present

It is likely that management of invasive populations with Allee effects should be different from those without Allee effects and that failure to detect an Allee effect could lead to management errors. Removing a constant proportion per year (or other unit of time) from a population with a critical Allee effect increases the density threshold needed for establishment. This is true for any level of removal, which could either be for the purposes of eradication or harvesting. Harvesting a population with a non-critical Allee effect introduces a threshold only if the harvesting is above a certain level and further increasing the harvesting level increases the threshold level (Dennis 1989; Clark 1990). In order to eradicate an invasive species, it is only necessary to reduce the population below the threshold caused by the combination of an Allee effect and stochasticity (Liebhold & Bascompte 2003). In this work, the predicted eradication of Gypsy moths requires much less effort in the presence of both an Allee effect and environmental stochasticity. The interaction with stochasticity means that even a non-critical Allee effect can reduce the effort needed for eradication (Liebhold & Bascompte 2003). Similarly, in their model of pest insects with an Allee effect, Yoshimura *et al.* (1999) found that increasing levels of eradication raised the invasion threshold. For the invasive grass, *Spartina alterniflora*, the optimal strategy for control (whether to prioritize removal of high or low density regions of the population) is predicted to be different because of an Allee effect; although this result depends on the choice of goals of the control programme (Taylor & Hastings 2004).

### Biological control when Allee effects are present

Biological control agents that are deliberately introduced to control an invasive species may be more likely to succeed if the invasive host has an Allee limit. This is only true if the biocontrol agent does not itself have an Allee limit or if its limit is lower than that of the host (Deredec & Courchamp 2003). The degree of specialization of the biocontrol agent may also determine effectiveness because there is an interaction between specialization of the predator and Allee dynamics of the pest. Generalist predators can slow or stop the spread of any pest but specialist predators can only affect pest populations that are subject to Allee effects; slowing the spread of pests with non-critical Allee effects and stopping the spread of pests with critical Allee

effects (Fagan *et al.* 2002). If a parasitic biocontrol agent can become established, the presence of an Allee effect in the host species can stabilize the equilibrium point; potentially increasing the establishment probability of the agent (Scheuring 1999).

The number of individuals released can affect the success of a biocontrol agent if an Allee effect is experienced by the biocontrol agent and not the host species. Biocontrol collapses occur if the agent is released in numbers smaller than the threshold density (Courchamp *et al.* 1999; Barnett 2001). In a meta-analysis of parasitoid species introduced as biocontrol agents, Hopper & Roush (1993) found that the number of individuals released (per release) explains most of variation in establishment. They further found that the critical number needed per release is sensitive to the net reproductive rate, the mate detection distance and the dispersal distances of the agent (Hopper & Roush 1993). The interaction of Allee effects and stochasticity on biocontrol establishment is explored by Grevstad (1999). She predicts that when an Allee effect is combined with environmental stochasticity, small populations actually have a larger probability of establishment than a population that has an Allee effect but is not subject to stochastic forces. Similarly large populations with an Allee effect have a smaller probability of establishment when subjected to stochastic forces (Grevstad 1999). This work also explores the strategy of releasing biocontrol agents given a fixed total number that can be released. At one extreme, with an Allee effect and no stochasticity, the best strategy is a small number of large releases. At the other extreme, without an Allee effect but with stochasticity, the best strategy is a large number of small releases. When both an Allee effect and environmental stochasticity are present, the best strategy is intermediate between the two extremes.

### Biological control: inducing an Allee effect in a pest population

Another strategy for control is to induce an Allee in a pest population. Introducing a predator as a biocontrol agent can induce an Allee effect under certain conditions. An Allee effect will be induced if predation is the main driver of prey dynamics, the prey have few refugia from predation and the predator has a linear or saturating (type I or II) functional response without a sigmoid (type III) aggregative response or vice versa (Gascoigne & Lipcius 2004b). By an alternate mechanism, introducing a parasite may induce an Allee effect because the number of parasites per prey may be much higher when prey densities are low (Fowler & Baker 1991) and this may have a disproportionate effect on the growth rate of the population at low densities (Borowicz & Juliano 1986). A biocontrol agent might have higher success if the conditions under which it is like to induce an Allee

effect are met and understanding these conditions could be key to good selection of biocontrol agents.

Another strategy for inducing an Allee effect in insects is to disrupt fertilization by the sterile male release strategy (Dennis 1989; Lewis & van den Driessche 1993; Krafur 1998; Courchamp *et al.* 1999; Fagan *et al.* 2002). Models of sterile insect release show that it introduces a density threshold into the population and the size of the threshold depends on the number or density of sterile insects released (Lewis & van den Driessche 1993). For control of pest mammals a control technique called immunocontraception is being explored. In this technique, sterilization is induced in individuals via a deliberately modified and introduced virus or other pathogenic agent. As the infection spreads through the population, more animals become sterile and the population eventually start to decline because of the induced Allee effect (McCallum 1996; Courchamp & Cornell 2000; Hood *et al.* 2000).

## CONCLUDING REMARKS

We wish to emphasize both that invasions provide unique opportunities to study Allee effects and that the understanding and prediction of invasions, both qualitatively and quantitatively, will require including Allee effects in the description. Allee effects draw attention to important fundamental aspects of modelling spatial dynamics of invasive species. The underlying biology will determine the impact of the Allee effect and hence conclusions are dependent on the modelling framework chosen. For instance, whether space is described as discrete or continuous appears to have a large effect on whether an invasion will stop at a particular spatial extent through the dynamics of range pinning. Thus consideration of Allee dynamics may shed light on fundamental issues of translation of invasion processes to and from their description in simple models.

Invasions are useful systems for the study and detection of Allee effects. Many of the dynamics predicted by Allee effects are easier to detect in an expanding, rather than a declining or stationary, population. When spatial data exist, documenting the spread of an invasive species, this can be used to try to detect spatial patterns and dynamics potentially generated by Allee effects. Finally, the study of invasions might reveal the extent to which Allee effects are important in different taxa and the mechanisms that successful invasive species use to overcome Allee effects.

Allee effects are important in invasion biology as well as in conservation of rare and endangered species and thus should not be left out of the study of invasive species. The dynamics of invasive species when population size is small can affect many aspects of their dynamics including the probability of successful invasion, the rate of spread and even the final range and distribution of the invasive species.

An undetected Allee effect can cause the miscalculation of the risks of invasive species. On the one hand, an undetected Allee effect might cause the overestimation of the invasion probability for small introductions (Green 1997; Dennis 2002; Drake 2004; Leung *et al.* 2004). On the other hand, the spread rate or apparent impact of an invading population when it is small initially may not be a good predictor of its eventual spread rate, if an Allee effect is present but unaccounted for, and this may lead to underestimation of its potential impact (Hastings 1996).

It is important to consider Allee effects when planning control of invasive species because population dynamics with and without Allee effects can be so dissimilar. Threshold densities caused by critical Allee effects may make the eradication of some invasives easier. Again, miscalculation of Allee thresholds can lead to mistakes in the estimation of control costs and effort needed. Allee dynamics can greatly influence the success of biocontrol agents that are introduced to act as predators or parasites on a target pest species. Both agent and target species can be subject to Allee effects and it is necessary to understand the relative strengths of Allee effects in each to be able to accurately predict outcomes.

How pervasive are Allee effects in invasive species? This remains an open question and suggests a direction for future research. Empirical evidence for Allee effects in invasive species is still fairly rare although the number of examples has increased in recent years. Existing methods to detect Allee effects could be applied to some invasions and alternate methods for detection will need to be developed for others. Demonstration of Allee effects in invasives would allow further testing of the collection of theoretical results described in this review. If Allee effects are present in invasive species then ignorance of the Allee effects might lead to bad management decisions. Hence, the influence of Allee effects on control strategies and costs, for example, on the choice between eradication and containment of invasions also warrants further investigation. Another potentially productive area for research is exploring the influence of Allee effects on the efficacy of biological control. It is possible that Allee effects are more important in biocontrol than has been recognized to date. Benefits of future research in this area would include a better understanding of the dynamics of biocontrol when Allee effects are present in the target pest species, the biocontrol agents, or both. Additionally, the role of Allee effects potentially induced by biological control needs to be further explored.

## ACKNOWLEDGEMENTS

We thank two anonymous referees for thoughtful comments that greatly improved this manuscript. This work was

supported by National Science Foundation Biocomplexity Grant no. DEB0083583 (P.I. Alan Hastings) and National Science Foundation Biological Invasions IGERT, NSF-DGE no. 0114432.

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Editor, Jonathan Sherratt

Manuscript received 28 December 2004

First decision made 16 February 2005

Second decision made 21 April 2005

Manuscript accepted 11 May 2005