What Is the Allee Effect?

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Oikos, Vol. 87, No. 1. (Oct., 1999), pp. 185-190.

FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

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W. C. Allee brought attention to the possibility of a positive relationship between aspects of fitness and population size over fifty years ago. This phenomenon, frequently termed the Allee effect, has been the focus of increased interest over the past two decades in the light of concerns over conservation and the problems of rarity. Use of the term suffers from the absence of a clear definition however, with the result that Allee effects are frequently thought to involve only a narrow range of phenomena and are often overlooked altogether. We propose a definition for the effect and attempt to resolve the major issues underlying the confusion surrounding this term.

It is recognised that individuals of many species may benefit from the presence of conspecifics (Fig. 1), a concept broadly referred to as the Allee effect after the pioneering work of W. C. Allee (Allee 1931, 1938, Allee et al. 1949). Unfortunately, however, the concept suffers from widespread confusion and misuse. It has been interpreted solely as the difficulty in finding mates at low densities (Myers et al. 1995, Amarasekare 1998), is explained variously as a reduction in fitness at low population size (McCarthy 1997, Fischer and Matthies 1998) or at low population density (Gruntfest et al. 1997, Kindvall et al. 1998, Kuussaari et al. 1998, Wells et al. 1998), and has even been erroneously defined as negative density dependence (Levitan et al. 1992). Other authors have demonstrated decreases in aspects of survival or breeding output at low numbers or densities, but have not termed these Allee effects (Carbone et al. 1997, Green 1997, Macedo and Bianchi 1997, Storer et al. 1997).

We believe that inconsistent use of the term results from the absence of a single clear definition. In this article we aim: (1) to investigate the origins of the term and to develop a much-needed definition; (2) to explore the distinction between the component Allee effect, of particular interest to behaviourists, and the demo-graphic Allee effect, of overriding concern to conservationists; and (3) to clarify two of the central areas of confusion within the definition –those regarding issues of scale and demographic stochasticity.

In order to clarify the meaning and use of the term Allee effect, we focus attention on a limited number of examples of mechanisms of this effect. For those unfamiliar with the range of mechanisms which may lead to Allee effects, these have been reviewed more extensively elsewhere (Dennis 1989, Fowler and Baker 1991, Stephens and Sutherland in press). In brief, these benefits of conspecific presence may include one or more of: predator dilution or saturation; antipredator vigilance or aggression; cooperative predation or resource defence; social thermoregulation; collective modification or amelioration of the environment; increased availability of mates; increased pollination or fertilisation success; conspecific enhancement of reproduction; and reduction of inbreeding, genetic drift, or loss of integrity by hybridisation.

Origins of the term

Allee was initially stimulated by an example only loosely linked to the current interpretation of the Allee effect: he showed that goldfish grew faster in water which had previously contained other goldfish, than in water that had not (Allee 1931). Further experiments with a range of species showed that larger group size or some degree of crowding may stimulate reproduction, prolong survival in adverse conditions (through resistance to desiccation or by social thermoregulation) and enhance protection from toxic reagents (Allee 1931, 1938). Allee saw these phenomena as 'automatic cooperation', believing that the beneficial effects of numbers of animals present in a population represented a funda-

mental biological principle (Allee 1938). By 1953 E. P. Odum was referring to 'Allee's principle' as the concept that "undercrowding (or lack of aggregation) may be limiting" (Odum 1953: 154). Perhaps inevitably, we discovered that similar observations had been made previously by Darwin who noted that, "in many cases, a large stock of individuals of the same species, relatively to the number of its enemies, is absolutely necessary for its preservation" (Darwin 1872: 86). Reduction in fitness or population growth at low abundance has received considerable attention in conservation genetics, under such guises as the '50/500 rule' (Soulé and Wilcox 1980), and is also widely debated in fisheries science, where it is usually referred to as depensation (Myers et al. 1995, Liermann and Hilborn 1997). Depensation is principally a population level phenomenon, which may or may not arise from changes in individual fitness, and thus need not be directly analogous to the Allee effect.

Definition

Although the Allee effect is reasonably well known, the concept has a range of meanings, not all of which are acknowledged by contemporary use. Allee did not provide a definition but he clearly considered "certain aspects of survival values" (Allee et al. 1949: 396) rather than total fitness and we thus define the Allee
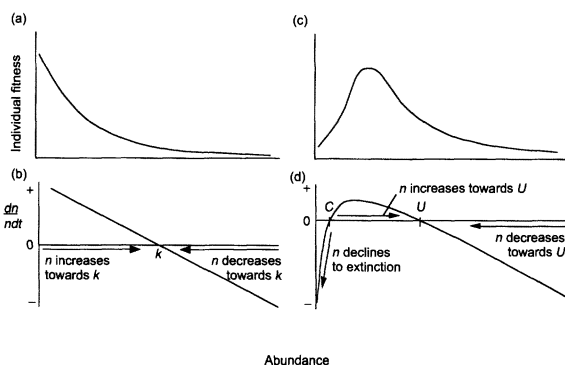

Fig. 1. Negative density dependence and the Allee effect. (a) As populations grow there will often be reductions in the fitness of individuals, for example from increasing competition and depletion of resources, resulting in decreased natality and survival. (b) Population growth rate will decline linearly with increasing abundance, as illustrated by the logistic equation, giving a single, stable equilibrium (k). (c) For many species however, there are benefits associated with the presence of conspecifics. At low numbers or densities, the benefits from the addition of each successive individual outweigh the costs, such that there is a net gain in individual fitness, and fitness is highest at intermediate numbers or densities. (d) In this case, population growth rate may also be low at low levels of abundance, as shown by the adjusted logistic equation. If growth becomes negative at low numbers, two equilibria will result: a lower, unstable equilibrium (C) and an upper, stable equilibrium (U).
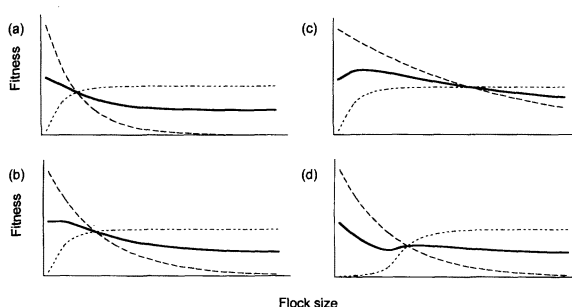

Fig. 2. Component Allee effects and demographic Allee effects. A mechanism such as vigilance among a group may give rise to a component Allee effect (short dashes). Whether this results in a demographic Allee effect will depend on the strength of negative density dependent effects (long dashes), such as interference and depletion. Overall fitness (solid line) is shown for (a) strong, (b) intermediate, and (c) weak negative density dependence. (d) A sigmoid component Allee effect may lead to demographic Allee effects at intermediate population sizes.

effect as: a positive relationship between any component of individual fitness and either numbers or density of conspecifics.

In the spirit of Allee's original observations, this definition requires that some measurable component of the fitness of an organism (e.g. probability of dying or reproducing) is higher in a large population. Whether all components of mean fitness combine to produce an overall increase or decrease with increasing abundance will depend on the relative strength of negative density dependence. We suggest that it is therefore important to differentiate between *component Allee effects* (Allee effects manifested by a component of fitness) and *demographic Allee effects* (Allee effects which manifest at the level of total fitness). As an illustration, larger bird flocks are (up to a point) more likely to detect predators early, thus reducing their mortality rate (Kenward 1978). There are also likely to be negative effects of increasing numbers, such as interference and depletion of food resources, and a variety of relationships between these components of fitness and flock size are possible (Fig. 2). Although the positive effect of increasing flock size on vigilance is consistent, only where negative density dependent effects are weak is there a positive relationship between total fitness and number at any stage. Thus, component Allee effects are seen in all Figs 2a–d, whilst demographic Allee effects are seen only in Figs 2c and d. The overall relationship between fitness and abundance may be seen as the cumulative effects of all component Allee effects and all negative density dependent effects, or as Allee himself termed it, all terms of cooperation and disoperation (Odum and Allee 1954).

In practice, distinguishing between component Allee effects and demographic Allee effects may enable Allee effects to be described with greater certainty in the field. The instability of the lower equilibrium (see Fig. 1d)

means that natural populations subject to a demographic Allee effect are unlikely to persist in the range of population sizes where that effect is manifest. It has been observed that empirical data on Allee effects are sparse (Dennis 1989, Kuussaari et al. 1998). Establishing whether an observed component Allee effect will lead to a demographic Allee effect is further complicated by the effects of environmental variability on the strength of negative density dependence, and by a potential lag between component and demographic Allee effects. For example, in colonial breeding birds, higher fledging success due to increased colony size could be negated due to greater over-winter mortality of young, perhaps as a result of increased competition for food and hence decreased fat reserves before winter. The component Allee effect of increased fledging success would not be translated into a demographic Allee effect, due to the seasonal nature of negative density dependence. Thus it is interesting to note that whilst theoreticians are principally concerned with demographic Allee effects, empiricists, by the very nature of their work, are usually constrained to the quantification of component Allee effects. In practice, the importance of identifying component Allee effects is usually that their existence indicates the potential for the existence of a demographic Allee effect, which is far less easily demonstrated.

Number, density and issues of scale

Widespread confusion over the use of the term Allee effect surrounds the contrast between Allee effects that result from low population sizes and those that result from low population densities. Allee himself did not confront this issue directly but clearly his examples included effects of both number, for example, improved social thermoregulation in larger litters of mice, *Mus* sp., and of density, for example, increased per capita reproduction among higher densities of flour beetles, *Tribolium confusum* (Allee 1938). However, for the majority of mechanisms which lead to Allee effects, the distinction between number and density is complex, depending largely on the spatial resolution at which the system is studied. To the field ecologist, working within a fixed study area, any drop in number will be inseparable from a corresponding reduction in density. Local density may be a more useful measure but still may be difficult to interpret.

A useful thought experiment to distinguish between number and density as the basis for a given mechanism is to consider isolated, closed systems, and then compare the consequences of a change in density with those of a concomitant increase in number and area. This approach may be used to distinguish a mechanism such as maintenance of balanced sex ratios that is dependent on numbers of individuals present, from a mechanism
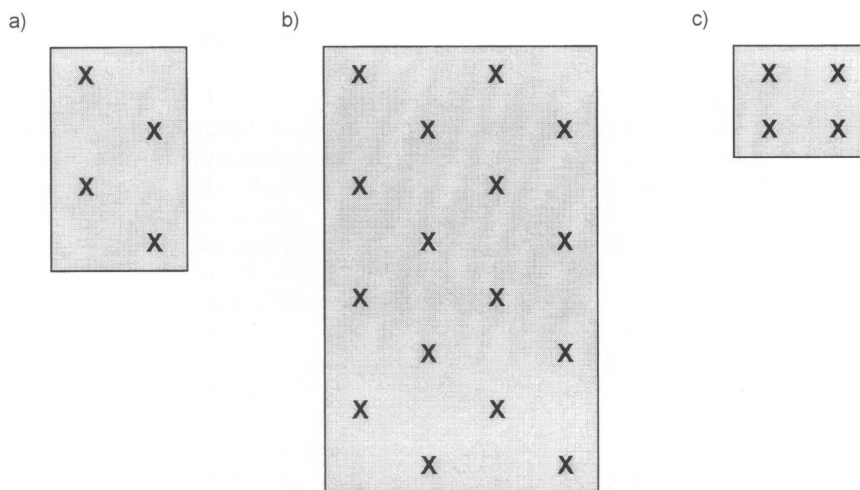

Fig. 3. Allee effects, population size and population density. Determining whether an Allee effect results from low numbers (n) or low densities (δ) of individuals may be thought of in terms of isolated patches or islands of habitat. The three diagrams show a) $n = 4$, $\delta = 2$, b) $n = 16$, $\delta = 2$, and c) $n = 4$, $\delta = 4$. Consider a mechanism such as the maintenance of balanced sex ratios. Such a mechanism may fail as a species becomes rarer, reducing average individual fitness and causing an Allee effect. In patch (a), there is a high chance that both individuals may be of one sex and that mating may not take place at all. Higher numbers of individuals in patch (b) reduce the probability of such a biased sex ratio, demonstrating that increasing numbers may alleviate the Allee effect, without an increase in density. Indeed, a highly skewed sex ratio is less likely in patch (b) than in patch (c), despite the fact that individuals in patch (c) are at the higher density. Thus Allee effects arising from sex ratio skews result from low numbers of individuals, or small population sizes. By contrast, consider a mechanism such as the modification of soil characteristics, a phenomenon by which plants may improve local conditions for growth. Assuming that an individual plant may have a given effect on, say, the pH of a given volume of soil, then plants in patches (a) and (b) will be equally well off, and only an increase in density (as in patch (c)) will lead to an increase in individual fitness.

such as modification of soil properties that is dependent on density of individuals present (Fig. 3).

Translation of Allee effects from one temporal or spatial scale to another is also dependent on the mechanism involved. Temporal changes in aggregative behaviour may indicate temporal changes in the strength of Allee effects. A striking example is that of the mara (*Dolichotis patagonum*) (Taber and Macdonald 1992). Patchy habitat quality and rapid depletion lead to the highly territorial, monogamous behaviour of maras for most of the year. However, despite an abundance of warrens, pupping is communal, probably as a result of the benefits to pups of increased vigilance and improved thermoregulation in communal crèches.

Spatial inconsistencies in Allee effects may also occur. Howler monkeys (*Alouatta palliata*) on Barro Colorado Island, Panama, live in troops of 6–31 individuals (Smith 1977). Individuals within a group may gain considerable benefits from the presence of conspecifics, including increased anti-predator behaviour, and cultural transmission of food-finding and anti-predator information. Troops show considerable range overlap. Over a period of time, high recruitment into a single small group of howler monkeys may elevate their numbers considerably. Thus at the local scale of the group, a demographic Allee effect may be seen. At a wider scale however, such an increase in the number of howler monkeys in one troop may cause a marked increase in the resource depletion, lowering the average fitness in other groups.

Demographic stochasticity

Demographic stochasticity arises as a consequence of the discrete rather than continuous nature of biological population sizes (May 1973); it leads to fluctuations in per capita growth rates that may threaten the persistence of small populations. It has been suggested that demographic stochasticity represents a type of Allee effect (Lande 1998) but whether this is the case depends on both the definition of the Allee effect used and the type of demographic stochasticity considered. The definition of the Allee effect that we propose above is framed in terms of the effects of population size, or density, on the fitness of individuals and the consequences that this may or may not have for population change. In this respect we contrast two categories of demographic stochasticity: first we consider the most commonly invoked source of demographic stochasticity – the random variation resulting from discrete individual (rather than continuous) birth and death events (May 1973, Lande 1993); second we consider sex ratio fluctuations, also commonly cited as a form of demographic stochasticity (Caughley 1994, Lande 1998). Taking these categories in isolation, we show that despite the important implications of both for population dynamics and persistence, only sex ratio

fluctuations may be usefully considered as a mechanism of the Allee effect.

In general terms an Allee effect resulting from demographic stochasticity is proposed to arise as a consequence of an increase in the variance in the rate of population change or mean fitness at low numbers. The mechanism for this change in variance is directly analogous to the familiar phenomenon of increased sampling variance of the population mean as sample sizes become small, for example as predicted by the central limit theorem. The long-term stochastic dynamics of a population may be predicted by transformation of the original population size (N) to a new scale (x), such that $x = g(N)$ where the transformation g has the property that variance about the mean fitness is homogenised as x varies. The most familiar example of this 'isotropic' transformation is the geometric mean population growth rate for population growth of discrete generations in a stochastic environment, i.e. when $g(N) = \ln N$ (e.g. Lewontin and Cohen 1969). The key feature of this method is that patterns of dynamics are predicted correctly by x, but not by N. In particular, the mean value of x, which may be termed the 'dynamic mean' of the population, correctly predicts population persistence or growth.

In the particular case of the effect of demographic stochasticity on the variance in mean fitness, if the variance resulting from demographic stochasticity is given by $\sigma^2 N$, then $\mu(x)$, the mean value of the change in x at a given value of N, is (Lande 1998):

$$\mu(x) = \frac{\partial g}{\partial N} \bar{r} N + \frac{\partial^2 g}{\partial N^2} \frac{\sigma^2 N}{2} \qquad (1)$$

In this case it is assumed that change is modelled by a density independent model ($\Delta N = r_t N$) defined by growth parameter r and that demographic stochasticity is the only form of variability. For this model, the appropriate variance homogenising transformation is $x = 2\sqrt{N}$.

Eq. 1 therefore becomes:

$$\mu(x) = \bar{r}\sqrt{N} - \frac{\sigma^2}{4\sqrt{N}} = \frac{\bar{r}x}{2} - \frac{\sigma^2}{2x} \qquad (2)$$

The variance resulting from demographic stochasticity reduces the mean rate of change of x to below $\bar{r}/2$, its maximum value in the absence of demographic stochasticity. The strength of this reduction is proportional to the reciprocal of x, i.e. the effect becomes more important as x becomes smaller, leading to the proposal that there is an Allee effect.

The important feature of eq. (2), however, is that it is assumed that demographic stochasticity affects *only* the variance about the mean of N, and not the mean or expected rate of change ($\bar{r}$). This applies, for example, to demographic stochasticity resulting from births and

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deaths. If, for example, the mean probability of death is d, and the numbers surviving are predicted by a binomially distributed random variable, then the variance in population size is given by $Nd(1 - d)$. The variance is a function of N, but the probability of a randomly chosen individual surviving remains constant at a value of $(1 - d)$. A similar argument could, for example, be developed for natality or rates of recruitment. Although for any population this mechanism would lead to increasing probabilities of extinction with decreasing population sizes, expected individual fitness would not decline concomitantly.

The other form of demographic stochasticity that is commonly proposed to lead to reduced rates of change at low densities is the effect of population size on sex ratios, in particular sex ratio skews at low densities. In this case the effect of population size on individual fitness is rather different. Consider a species which produces young with, on average, an equal ratio of males (M) to females (F), i.e. the probability of producing either is $p(M) = p(F) = 0.5$. At very low population sizes (e.g. $N = 2$), there are three possible population compositions (all male, MM; male and female, FM; and all female, FF) which arise with probabilities $p(MM) = 0.25$, $p(MF) = p(FM) = 0.25$, and $p(FF) = 0.25$. The probability of a reproductive pair is thus $p(MF) + p(FM) = 0.5$ and hence the probability of any individual being in a position to reproduce is also 0.5. As population sizes become high ($N \rightarrow \infty$), however, the population sex ratio will approach 1:1, and nearly every individual within the population will be able to find a mate of the opposite sex. Hence the probability of an individual being in a position to reproduce approaches unity.

The key point to emerge is that the effect of demographic stochasticity through births and deaths arises in a very different way from the effects of demographic stochasticity through population sex ratios. In the former case there is no measurable component of individual fitness that is affected by population size or interactions with other population members. The fate of an individual, in terms of its probability of dying or reproducing, is unaffected by the size of the population within which it finds itself. In the case of demographic stochasticity through population sex ratios, on the other hand, the probability of an individual being able to mate *is* affected by population size, i.e. there is a measurable component of individual fitness that can be related to the size of the population and interactions between organisms. The fate of the population as a whole *is* affected by its size when demographic stochasticity through births and deaths occurs. This, however, is *not* a consequence of changing fates of the individuals within the population and hence cannot be considered as an example of the Allee effect.

A similar argument can be used to categorize other phenomena arising from low population density or size. Inbreeding depression, for example, is commonly proposed to lead to reduced fitness at low densities. Inbreed-

ing could be considered to generate an Allee effect since the degree of inbreeding depression to which an individual is subject depends on the size of the population into which it is born.

One of the important conclusions we derive from these distinctions between component and demographic Allee effects as well as between the forms of demographic stochasticity is that Allee effects do not inevitably lead to impacts on net population growth, such as positive density dependence and unstable lower equilibria; neither do the existence of these imply underlying Allee effects. An Allee effect at the level of the population implies that positive density dependence results from the effects of density on the fates of, and interactions between, individuals within the population.

In summary, following our definition of the Allee effect, which is closely based on Allee's original work, it is reasonable to include stochastic sex ratio fluctuations as a mechanism leading to Allee effects but misleading to group stochastic birth and death processes together with Allee effects. Although stochastic mortality and natality produce increased extinction risks for small populations, they are qualitatively different from Allee effect mechanisms and will occur even in the absence of a requirement for conspecific interactions. It is important to emphasise this difference by retaining these within the separate idea of demographic stochasticity, rather than subsuming them into a relaxed definition of Allee effect mechanisms.

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