I

recent reviews have shown that there is viewed as relatively unimportant, but from a lack of recognition and from being intriguing phenomenon of population relatively recently, however, the concept reference of conspecifics, a concept broadly referred to as the Allee effect. Until rela-
tively recently, however, this concept was generally regarded as an intriguing but relatively unimportant aspect of population ecology. Increasing appreciation that Allee effects must be incorporated into models of population dynamics and habitat use, together with recent interest in the implications of sociality for conservation, have shown that for ecology and conservation the consequences of the Allee effect are profound. The Allee effect can be regarded not only as a suite of problems associated with rarity, but also as the basis of animal sociality. Warden C. Allee brought attention to the possibility of a positive relationship between aspects of fitness and population size 50 years ago. Until recently, however, this concept was generally regarded as an intriguing but relatively unimportant aspect of population ecology. Increasing appreciation that Allee effects must be incorporated into models of population dynamics and habitat use, together with recent interest in the implications of sociality for conservation, have shown that for ecology and conservation the consequences of the Allee effect are profound. The Allee effect can be regarded not only as a suite of problems associated with rarity, but also as the basis of animal sociality.

It is well recognized that individuals of many species can benefit from the presence of conspecics, a concept broadly referred to as the Allee effect. Until relatively recently, however, the concept was viewed as rather idiosyncratic—an intriguing phenomenon of population growth but of limited relevance to most natural populations. The term suffers from a lack of recognition and from being viewed as relatively unimportant, but recent reviews have shown that there is widespread evidence for Allee effects (Box 1). The importance of this phenomenon has been emphasized by recent developments in three areas of ecology and conservation. First, developing interest in conservation over recent decades has prompted increasing attention on rarity and associated population dynamics. Second, recent modelling approaches have allowed the consequences of Allee effects to be understood for a wide range of systems. Third, recent emphasis on the relevance of behavioural ecology to conservation has heightened interest in the importance of conspecific interactions for the viability of populations. Developments in all of these areas have illustrated the fact that, directly or indirectly, the ramifications of Allee effects can be seen in almost every area of ecology and conservation. We restrict the following review to five areas in which the direct consequences of the Allee effect are of particular interest and importance.

Aggregative behaviour and group living

Animal aggregations, beyond the level expected from habitat limitations or aggregation of resources, can be attributed to conspecific attraction. Such attraction, arising as a result of the benefits of conspecific presence, is a direct product of the Allee effect. Conspecific attraction can explain breeding aggregations in colonial species and also why some noncolonial species preferentially settle near conspecics. The Allee effect can thus be seen as a major driving force behind animal sociality. The degree of sociality of a species might reflect the degree of severity of the Allee effects to which it is subject. For many species, survival of solitary individuals can be low and a minimum group size (or number of helpers) might be required for successful reproduction. These ‘obligate cooperators’ can be distinguished from facultative cooperators (e.g. the Seychelles warbler, Acrocephalus sechellensis) by the presence of nonreproductive helpers, even in the absence of habitat constraints. The severe Allee effects to which obligate cooperators are subject can have serious impacts on their population dynamics.

The Allee effect can affect mating systems, not only of obligate cooperators but of other species as well. The classic view of animal mating systems is that of disease transmission. Dobson and Poole presented a simple model to show the increased susceptibility of aggregative species to disease outbreaks, demonstrating the reduced threshold for establishment of a pathogen within aggregated host populations. Clearly, there

Consequences of the Allee effect for behaviour, ecology and conservation

Philip A. Stephens
William J. Sutherland

Warden C. Allee brought attention to the possibility of a positive relationship between aspects of fitness and population size 50 years ago. Until recently, however, this concept was generally regarded as an intriguing but relatively unimportant aspect of population ecology. Increasing appreciation that Allee effects must be incorporated into models of population dynamics and habitat use, together with recent interest in the implications of sociality for conservation, have shown that for ecology and conservation the consequences of the Allee effect are profound. The Allee effect can be regarded not only as a suite of problems associated with rarity, but also as the basis of animal sociality.

It is well recognized that individuals of many species can benefit from the presence of conspecics, a concept broadly referred to as the Allee effect. Until relatively recently, however, the concept was viewed as rather idiosyncratic—an intriguing phenomenon of population growth but of limited relevance to most natural populations. The term suffers from a lack of recognition and from being viewed as relatively unimportant, but recent reviews have shown that there is widespread evidence for Allee effects (Box 1). The importance of this phenomenon has been emphasized by recent developments in three areas of ecology and conservation. First, developing interest in conservation over recent decades has prompted increasing attention on rarity and associated population dynamics. Second, recent modelling approaches have allowed the consequences of Allee effects to be understood for a wide range of systems. Third, recent emphasis on the relevance of behavioural ecology to conservation has heightened interest in the importance of conspecific interactions for the viability of populations. Developments in all of these areas have illustrated the fact that, directly or indirectly, the ramifications of Allee effects can be seen in almost every area of ecology and conservation. We restrict the following review to five areas in which the direct consequences of the Allee effect are of particular interest and importance.

Aggregative behaviour and group living

Animal aggregations, beyond the level expected from habitat limitations or aggregation of resources, can be attributed to conspecific attraction. Such attraction, arising as a result of the benefits of conspecific presence, is a direct product of the Allee effect. Conspecific attraction can explain breeding aggregations in colonial species and also why some noncolonial species preferentially settle near conspecics. The Allee effect can thus be seen as a major driving force behind animal sociality. The degree of sociality of a species might reflect the degree of severity of the Allee effects to which it is subject. For many species, survival of solitary individuals can be low and a minimum group size (or number of helpers) might be required for successful reproduction. These ‘obligate cooperators’ can be distinguished from facultative cooperators (e.g. the Seychelles warbler, Acrocephalus sechellensis) by the presence of nonreproductive helpers, even in the absence of habitat constraints. The severe Allee effects to which obligate cooperators are subject can have serious impacts on their population dynamics.

The Allee effect can affect mating systems, not only of obligate cooperators but of other species as well. The classic view of animal mating systems is that of disease transmission. Dobson and Poole presented a simple model to show the increased susceptibility of aggregative species to disease outbreaks, demonstrating the reduced threshold for establishment of a pathogen within aggregated host populations. Clearly, there

Esa Ranta
Integrative Ecology Unit, Division of Population Biology, Dept of Ecology and Systematics, PO Box 17 (Arkonadukatu 7), FIN-00014, University of Helsinki, Finland (esa.ranta@helsinki.fi)

Veijo Kaitala
University of Jyväskylä, Dept of Biological and Environmental Science, PO Box 35, FIN-40351 Jyväskylä, Finland (vkaitala@cc.jyu.fi)

Per Lundberg
Dept of Theoretical Ecology, Ecology Building, Lund University, SE-223 62 Lund, Sweden (per.lundberg@wallace.teorekol.lu.se)

References

PERSPECTIVES

are many other factors that will influence disease transmission, but it is likely that species that aggregate as a behavioural response to strong Allee effects will be especially vulnerable to disease.

Finally, conspecific attraction arising from Allee effects could be useful as a conservation tool. Conspecific presence can be an important factor influencing patch choice, especially for younger individuals17, and thus decoys or call playback can be employed to encourage preferential colonization in protected areas, or reclamation of deserted or recently restored patches of habitat14,16.

Patch choice and range

Incorporating the Allee effect into the ideal free distribution might impact on several aspects of the distribution of individuals between patches. Conspecific attraction has been used to argue that optimal group sizes can be unstable18 and also that the relative abundance of a species between two habitat patches might be a poor indicator of habitat quality19. If the suitability of a patch of habitat is elevated by conspecific presence, further individuals will settle preferentially in an occupied patch, irrespective of whether an alternative patch of equal quality exists. Furthermore, shifting distributions might also result from the benefits of conspecific presence20. Pollock (Pollockiounus rivesi) employ two antipredator strategies for protection from avian predators in structured habitats, such as algal beds, the fish disperse to reduce detection by predators, whereas in open, internal habitats they shoul20. The success of the first of these options is clearly subject to negative density dependence, whilst, in the second case, risk-dilution and predation-confusion effects are positively density dependent. Thus, increases in local density might cause pollock to switch from algal habitat to open habitat. At an even greater spatial scale, the Allee effect might influence the dynamic of species ranges. It has been suggested that many species show declines in local density towards the extremes of their range, as a result of decreasing habitat suitability20. Towards the edge of a species’ range, less suitable habitat might support smaller local populations or lower population densities. If these are close to, or below, critical levels of local abundance (see the following section on extinctions), peripheral populations will have a greater likelihood of extinction. If the species is a good disperser, this will result in source-sink dynamics21, with individuals dispersing from the more productive centre of the range to the less productive extremes. For less mobile species, however, range truncation is more likely, with individuals failing to occupy all of the available range20.

Extinctions

The Allee effect greatly increases the likelihood of local and global extinction, a phenomenon that has received considerable attention from theoreticians12,24 and has even been advanced as a principal factor mediating the discrete nature of species25. Incorporating Allee effects into traditional models of population dynamics, such as the logistic equation, leads to several important observations (Box 2). It is evident that fitness will be depressed at low levels of abundance and, if the
in large groups with few reproductive individuals can respond to population declines in one of two ways: they can either form fewer optimal sized groups (and hence fewer reproductive units), or they can form higher numbers of suboptimal, smaller groups. In either case, population growth will be reduced. Such a process has been responsible for the collapse of many fisheries operating under a system of maximum sustainable yields. Data from a range of fisheries have been examined to test this assertion. Myers et al. assessed data from 128 fish stocks to compare the fit of a standard Beverton-Holt recruitment model (predicting compensation per capita recruitment at lower spawner densities) with a model modified to allow for either hypercompensation (greatly increased per capita recruitment at lower spawner densities), or depensation (reduced per capita recruitment at lower spawner densities, essentially analogous to the Allee effect). Of 26 stocks where data allowed for sufficient statistical power, a model indicating depensatory dynamics gave the significantly better fit in only three cases, with a further two stocks showing some nonsignificant evidence of depensation. However, a more recent examination of the data has indicated that the possibility of depensation cannot be rejected with confidence in most cases. Many exploited fish species are strong schoolers and therefore might be expected to show Allee effects. It is possible that for those species subject to Allee effects, data are insufficient to reject the depensation model even though there may be some evidence for depensation in some cases. Furthermore, the depensation model is not sensitive enough to detect some depensation levels. In general, it is possible to introduce inverse density dependence at low population sizes. The effect of this is to produce a relationship between per capita growth rate and population size, where negative density dependence at an upper threshold (K, the ‘carrying capacity’) is mirrored by inverse density dependence at the lower threshold. For increased control over the shape of this relationship, for example, to modify the slope of the relationship around the lower equilibrium, it is necessary to add a further parameter. Dennis showed that empirical data on mating frequencies of azuki bean weevils with increasing population density could be modelled using either a negative exponential or a rectangular hyperbola function. Both of these functions use a single parameter to model the speed of approach to the asymptote. For example, the rectangular hyperbola model takes the form:

\[
p = \frac{aK}{K - n}
\]

where \(p\) is the relative fitness due to an Allee effect and \(n\) is the population size, \(K\) is the population size at which fitness is half its maximum value, hence the greater the value of \(K\), the greater the reduction in fitness owing to the Allee effect. This is shown below for a range of values of \(K\): (for \(K = 2\), unbroken line; \(K = 15\), dashed line; and \(K = 50\), dotted line).

![Graph showing Allee effect with varying \(K\) values](Online Fig 2)

The per capita (or ‘specific’) rate of population growth indicates whether the population is likely to increase, decrease, or remain constant. When this is zero, the population is stable, and thus where the growth curves cross the abscissa, the population is at an equilibrium point. When the specific growth rate is positive, the population will increase, and when it is negative, the population will decrease.

Two crucial observations arise from these models. First, per capita growth of populations experiencing Allee effects is lower than would be expected from the logistic model, with the most marked reductions at small population sizes. Second, although all of the models retain the stable, upper equilibrium characteristic of logistic growth (illustrated by the convergent arrows in all three instances), where the Allee effect is strong, there is also a lower, unstable equilibrium (illustrated by the divergent arrows). The lower equilibrium is critical: below this, populations are highly likely to become extinct.

**Box 2. The Allee effect and population dynamics**

At low population sizes or densities, Allee effects lead to reduced reproduction or survival. Simple mathematical models can reveal much about the dynamics and, therefore, the important implications of this phenomenon. Courchamp et al. show that simply by adding one extra parameter (K, the lower unstable equilibrium point) to the classic logistic equation of population growth, it is possible to introduce inverse density dependence at low population sizes. The effect of this is to produce a relationship between per capita growth rate and population size, where negative density dependence at an upper threshold (K, the ‘carrying capacity’) is mirrored by inverse density dependence at the lower threshold.

For increased control over the shape of this relationship, for example, to modify the slope of the relationship around the lower equilibrium, it is necessary to add a further parameter. Dennis showed that empirical data on mating frequencies of azuki bean weevils with increasing population density could be modelled using either a negative exponential or a rectangular hyperbola function. Both of these functions use a single parameter to model the speed of approach to the asymptote. For example, the rectangular hyperbola model takes the form:

\[
p = \frac{aK}{K - n}
\]

where \(p\) is the relative fitness due to an Allee effect and \(n\) is the population size, \(K\) is the population size at which fitness is half its maximum value, hence the greater the value of \(K\), the greater the reduction in fitness owing to the Allee effect. This is shown below for a range of values of \(K\): (for \(K = 2\), unbroken line; \(K = 15\), dashed line; and \(K = 50\), dotted line).

![Graph showing Allee effect with varying \(K\) values](Online Fig 2)

The per capita (or ‘specific’) rate of population growth indicates whether the population is likely to increase, decrease, or remain constant. When this is zero, the population is stable, and thus where the growth curves cross the abscissa, the population is at an equilibrium point. When the specific growth rate is positive, the population will increase, and when it is negative, the population will decrease.

Two crucial observations arise from these models. First, per capita growth of populations experiencing Allee effects is lower than would be expected from the logistic model, with the most marked reductions at small population sizes. Second, although all of the models retain the stable, upper equilibrium characteristic of logistic growth (illustrated by the convergent arrows in all three instances), where the Allee effect is strong, there is also a lower, unstable equilibrium (illustrated by the divergent arrows). The lower equilibrium is critical: below this, populations are highly likely to become extinct.
Traditional models of population growth, such as the logistic model, incorporate negative density dependence only: population growth rates are expected to increase as a population is harvested, because of the reduction in negative density dependence. From Box 2, however, it is evident that populations subject to Allee effects will show reduced growth at low population sizes, indeed, under strong Allee effects, growth can actually become negative below a certain size. Harvesting of populations under these conditions might have serious consequences.

The major consequences of harvesting populations which are subject to Allee effects can be inferred from the figures below. In these, population growth in an unexploited population (unbroken line) is contrasted to that in an exploited population (hashed line), for two harvesting regimes. (a) shows constant effort harvesting, where harvesting effort does not vary with population size. For every individual, there is a constant risk of harvesting mortality regardless of population size, as indicated by the per capita harvesting mortality rate (dotted line). (b) shows constant yield harvesting, where a given number of individuals are always harvested, irrespective of population size. In this case, effort must increase as the population decreases, and per capita harvesting mortality rate (dotted line) increases accordingly.

Box 3. Harvesting and the Allee effect

In both cases the most serious consequences result from the reduction of the upper, stable population equilibrium and simultaneous increase in the lower, unstable equilibrium. The two equilibria are pushed closer together, and the population will be markedly more vulnerable to extinction.

Introductions

Introductions, whether desirable or not, can be affected by Allee effects. Allee effects can reduce rates of spread of invading organisms and depress early growth rates for introduced populations – an observation used to explain the accelerating spread of house finches (Carpodacus mexicanus) through Eastern North America40. A period of latency – an observation used to explain the growth rates for introduced populations shown for both insects and birds41 – through Eastern North America40. A period of latency – an observation used to explain the growth rates for introduced populations shown for both insects and birds41. A period of latency – an observation used to explain the growth rates for introduced populations shown for both insects and birds41. A period of latency – an observation used to explain the growth rates for introduced populations shown for both insects and birds41. A period of latency – an observation used to explain the growth rates for introduced populations shown for both insects and birds41.

In both cases the most serious consequences result from the reduction of the upper, stable population equilibrium and simultaneous increase in the lower, unstable equilibrium. The two equilibria are pushed closer together, and the population will be markedly more vulnerable to extinction.

Acknowledgements

Thanks to Franck Courchamp, Rob Freckleton and two anonymous referees for comments and suggestions. This work was partly funded by a grant from the Natural Environment Research Council to PAS.

References

Inverse density dependence and the Allee effect

Franck Courchamp
Tim Clutton-Brock
Bryan Grenfell

The Allee effect describes a scenario in which populations at low numbers are affected by a positive relationship between population growth rate and density, which increases their likelihood of extinction. The importance of this dynamic process in ecology has been under-appreciated and recent evidence now suggests that it might have an impact on the population dynamics of many plant and animal species. Studies of the causal mechanisms generating Allee effects in small populations could provide a key to understanding their dynamics.

Franck Courchamp, Tim Clutton-Brock and Bryan Grenfell are at the Dept of Zoology, University of Cambridge, Downing Street, Cambridge, UK. CR2.35 (fc219@cam.ac.uk; tbc@hermes.cam.ac.uk; bryan@zoo.cam.ac.uk).

In 1931, Warder Clyde Allee proposed that intraspecific cooperation might lead to inverse density dependence, an idea that he later extended in his famous 1949 book on animal ecology. Exactly half a century later, it is timely to review the influence of his concept on current ecological research, and assess future prospects. Allee observed that many animal and plant species suffer a decrease of the per capita rate of increase as their populations reach small sizes or low densities (Fig. 1). Under such conditions, the rate of increase can reach zero, or even negative values, because of a decrease in reproduction and/or survival when con-

specific individuals are not numerous enough: "undercrowding, as well as over-crowding, may be limiting" (Box 1). One of Allee's collaborators, E.P. Odum, first referred to this process as Allee's Principle, but it is now generally known as the Allee effect.

Causes of inverse density dependence

The Allee effect strictly refers to inverse density dependence at low density. Factors involved in generating Allee effects in small populations could provide a key to understanding their dynamics.

28 Kindvall, O. et al. (1998) Individual mobility prevents an Allee effect in sparse populations of the bush cricket Metrioptera roeseli: an experimental study, Oikos 83, 440–457
45 Stephens, P.A., Sutherland, W.J. and Freckleton, R.P. What is the Allee effect? Oikos (in press)

TREE vol. 34, no. 10 October 2009 0109-5547/09/$ see front matter © 2009 Elsevier Science Ltd. All rights reserved. PI 0109-5547(09)51663-3