Esa Ranta

Integrative Ecology Unit, Division of Population Biology, Dept of Ecology and Systematics, PO Box 17 (Arkadiankatu 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

1 Koenig, W.D. (1999) *Trends Ecol. Evol.* 14, 22–36
2 Hudson, P.J. and Cattadori, I.M. (1999) *Trends Ecol. Evol.* 14, 1–2
3 Jansen, V.A.A. (1999) *Trends Ecol. Evol.* 14, 278–279
4 Moran, P.A.P. (1953) *Aust. J. Zool.* 1, 291–298
5 Royama, T. (1992) *Analytical Population Dynamics*, Chapman & Hall
6 Ranta, E. *et al.* (1995) *Proc. R. Soc. London Ser. B* 262, 113–118
7 Ranta, E. *et al.* (1997) *Oikos* 78, 136–142
8 Ranta, E., Kaitala, V. and Lindström, J. *Proc. R. Soc. London Ser. B* (in press)
9 Ranta, E., Kaitala, V. and Lundberg, P. (1997) *Science* 278, 1621–1623
10 Ranta, E., Kaitala, V. and Lundberg, P. (1998) *Oikos* 83, 376–382
11 Henttonen, H. *et al.* (1987) *Oikos* 50, 353–365
12 Hansen, T.F. *et al.* (1999) *Proc. Natl. Acad. Sci. U. S. A.* 96, 986–991
13 Hansson, L. (1999) *Oikos* 86, 159–169

Consequences of the Allee effect for behaviour, ecology and conservation

Philip A. Stephens
William J. Sutherland

Warder 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.

Philip Stephens and William Sutherland are at the School of Biological Sciences, University of East Anglia, Norwich, UK NR4 7TJ (philip.stephens@uea.ac.uk; w.sutherland@uea.ac.uk).

It is well recognized that individuals of many species can benefit from the presence of conspecifics, 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[1,2] (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[3–6]. Third, recent emphasis on the relevance of behavioural ecology to conservation[7–9] 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 conspecifics[10]. 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'[5] can be distinguished from facultative cooperators (e.g. the Seychelles warbler, *Acrocephalus sechellensis*[11]) 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[5,12].

The Allee effect can affect mating systems, not only of obligate cooperators but of other species also. The classic view of animal mating systems is that the spatial distribution of a species, particularly of its females, will determine the number of females that males can monopolize. Thus, mating systems become an issue of economical defensibility, or even 'optimal foraging'[13], by males[14], although it is now recognized that both male and female mate choice also play important roles[15]. Given that the spatial distribution, or degree of aggregation, of a species is, to a large extent, determined by the strength of the Allee effects to which it is subject, it is evident that Allee effects play an important role in dictating animal mating systems.

In addition to affecting the mating system of a species, the spatial distribution of individuals can impact on many other aspects of their ecology. One area of particular interest to conservationists is that of disease transmission. Dobson and Poole[16] 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

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Box 1. Mechanisms of the Allee effect

Following Allee's original work on the subject, any mechanism that can lead to a positive relationship between a component of individual fitness and either numbers or densities of conspecifics, can be termed a mechanism of the Allee effect. However, only those mechanisms that affect some measurable component of individual fitness should be included within the definition of Allee effects. It is thus sensible to discriminate, for example, between stochasticity of sex ratios (that can lead to skewed sex ratios in small populations, and can thus produce Allee effects by reducing mate availability) and stochasticity of births and deaths (that can produce increased extinction risks for small populations but that do not lead to reduced individual fitness at small population sizes, and hence cannot be termed mechanisms of the Allee effect)[45].

Recent reviews have discussed a variety of mechanisms of the Allee effect1,2,24. The beneficial effects of conspecific presence are well known and include classic mechanisms, such as predator dilution, antipredator vigilance, social thermoregulation, and reduction of inbreeding, genetic drift, or loss of integrity by hybridization, as well as a wide range of other mechanisms, for example:

Antipredator aggression. Colonial male bluegill sunfish (*Lepomis macrochirus*) spend less time pursuing predators than do solitary males. Colonial males thus have more time to aerate the nest, leading to reduced incidence of fungal disease in offspring[46].

Predator swamping. Synchronous mast-seeding in cycads (*Encephalartos* spp.) reduces predispersal seed predation, as a result of predator satiation[47].

Modification of the environment. At low densities, hemlock (*Tsuga heterophylla*) is less able to acidify soil and sequester water in the upper soil horizons. Production thus increases with density[48].

Social facilitation of reproduction. It is likely that females of several Callitrichid species would be energetically unable to forage efficiently, lactate and carry young, and thus would be unable to reproduce, without the presence of helpers who participate in transport of young[49].

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 individuals[17], and thus decoys or call playback can be employed to encourage preferential colonization in protected areas, or recolonization of deserted or recently restored patches of habitat[10,16].

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 unstable[18] and also that the relative abundance of a species between two habitat patches might be a poor indicator of habitat quality[19]. 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 presence. Pollock (*Pollachius virens*) 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, intertidal habitats they shoal[20]. The success of the first of these options is clearly subject to negative density dependence, whilst, in the second case, risk-dilution and predator-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 dynamics 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 suitability[21]. 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 extirpation. If the species is a good disperser, this will result in source–sink dynamics[22], 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 range[23].

Extinctions

The Allee effect greatly increases the likelihood of local and global extinction, a phenomenon that has received considerable attention from theoreticians[3,6,24] and has even been advanced as a principal factor mediating the discrete nature of species[25]. 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 Allee effect is strong, population growth will actually be negative when individuals become rare. Populations, groups or other aggregations (depending on the scale considered) will have two equilibria – a lower, unstable equilibrium and an upper, stable equilibrium. The lower equilibrium is critical and might be analogous to the minimum viable population concept or to minimum group size; below this, growth is negative and the population or group is likely to become extinct.

The marked differences between logistic growth and growth subject to Allee effects could have a profound influence on the population ecology of many species. The genetic consequences of population fragmentation are already well documented but these can be exacerbated by a range of less obvious Allee effects. The implications of Allee effects for metapopulation management could be critical[4,26]. Larger numbers of occupied patches can increase the number of migrants in a metapopulation, thus reducing the rate of local extinction (known as the rescue effect) and increasing the rate of successful colonization (by the establishment effect)[27]. This leads to a metapopulation analogue of the Allee effect, where there can be a lower threshold of patch occupancy, below which all subpopulations will be highly likely to go extinct. Allee effects can be alleviated by the mobility[28] or dispersal behaviour[29] of the species involved but this will depend on the costs of dispersal[5].

Populations fluctuate as a result of a range of biological and environmental factors. Furthermore, species with high intrinsic growth rates and overcompensating density dependence might show chaotic patterns of population growth. Should these species be subject to an Allee effect also, the fluctuations might take them into the zone of reduced growth, or even to below the critical threshold, rendering them especially vulnerable to extinction. A combination of fluctuating populations and the Allee effect has been invoked to account for one of the most dramatic extinctions of modern times – that of the passenger pigeon (*Ectopistes migratorius*). This North American bird might have been the most abundant bird species ever but fragmentation of the mast forests on which the species relied, intensive exploitation and large, natural fluctuations in population size[30] might have brought flocks below a lower, unstable equilibrium, resulting from decreased foraging efficiency at reduced flock sizes[31].

As a result of Allee effects, social species, particularly those that are obligate cooperators, might be especially vulnerable to extinction[5,12,32]. Species that live 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 could account for the slow recovery of the Ethiopian wolf (*Canis simensis*), following disease epidemics a decade ago, as described by Sillero-Zubiri *et al.*[33]

Exploitation

Sustainable harvesting is possible only because of compensation – the increase in population growth as a population is reduced. However, when populations are subject to an Allee effect, the population growth rate is depressed at reduced sizes and harvesting could have unforeseen consequences (Box 3). The most important impact of harvesting is to reduce the interval between the two equilibrium population sizes, with the result that natural fluctuations will be more likely to reduce the population to critical numbers and the harvested species will be more vulnerable to extinction[34]. Some species might be subject to increasing exploitation as the population becomes rarer, resulting in a particularly strong Allee effect. This is precisely the process that results when the value of a plant or animal specimen is strongly correlated with its rarity[35].

Allee-type dynamics are thought to have been responsible for the collapse of many fisheries operating under a system of maximum sustainable yields[36]. 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 compensating 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)[37]. 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[38]. 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

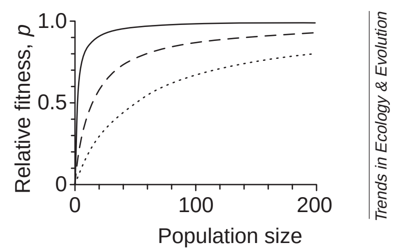
Box 2. The Allee effect and population dynamics

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.*[2] 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[24] 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 regulate the speed of approach to the asymptote. For example, the rectangular hyperbola model takes the form:

$$p = \frac{n}{(\theta + n)}$$

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

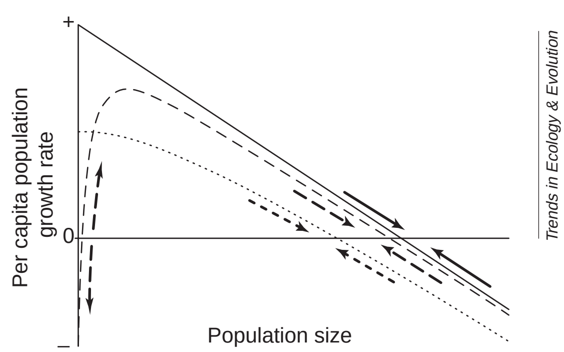


(Online: Fig I)

The relative fitness, p, is on a scale from zero to one. When $p = 0$, the Allee effect being considered will have its maximal effect on individual fitness; as $p \to 1$, the reduction in fitness owing to the Allee effect becomes insignificant. Whilst θ will scale the Allee effect, a further term of proportionality, α, will allow the severity of the Allee effect to be modelled. Logistic growth subject to an Allee effect will thus be given by:

$$\frac{dn}{ndt} = r - \frac{rn}{k} - \frac{\alpha\theta}{(\theta + n)}$$

where t is time, r is the intrinsic growth rate of the species, and k is the 'carrying capacity'. The difference between standard, logistic growth (unbroken line), and population growth incorporating Allee effects, is illustrated below. The dotted line shows growth with an Allee effect that is evident over a large range of population sizes, but is relatively weak (high θ, low α; this can be seen, for example, in a flock of birds, where collective vigilance is maximized only when large numbers of individuals are present, but small groups or individuals still suffer relatively low rates of predation). The dashed line shows growth with an Allee effect which is evident over a smaller range of population sizes but is much more severe (low θ, high α; a situation that might arise in a flock of another species, where collective vigilance shows little increase above a small number of birds, but in flocks below that size, mortality due to predation is almost 100%).



(Online: Fig II)

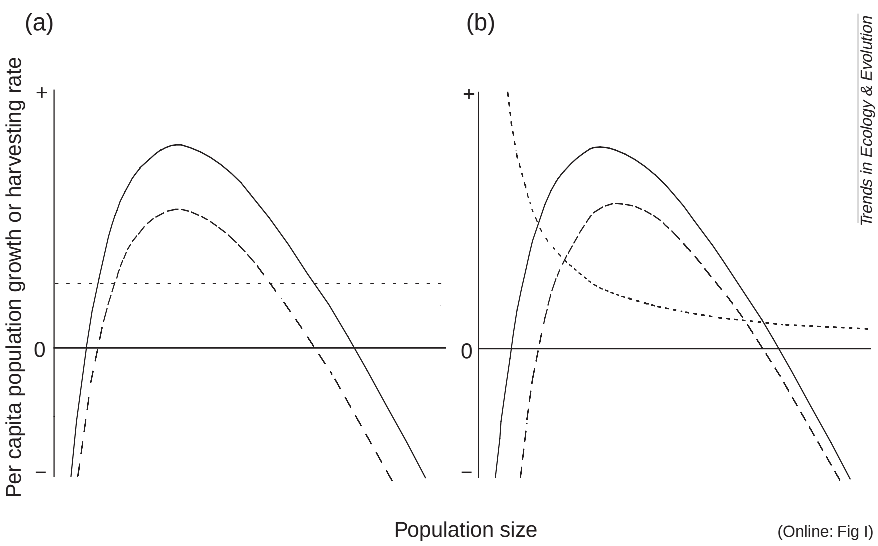
The per capita (or 'specific') rate of population growth indicates whether the population is likely to increase, decrease, or remain constant. When this is zero, the population is stable, and thus where the growth curves cross the abscissa, the population is at an equilibrium point. When the specific 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 3. Harvesting and the Allee effect

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 (dashed 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.



(Online: Fig I)

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.

sparse for the range of spawner abundances in which the Allee effect would be most apparent.

Introductions

Introductions, whether desirable or not, can be affected by Allee effects. Allee effects can reduce rates of spread of invading organisms[39] and depress early growth rates for introduced populations – an observation used to explain the accelerating spread of house finches (*Carpodacus mexicanus*) through Eastern North America[40]. A period of latency before rampant growth of an invasive population might lead to underestimation of the viability of recently introduced populations, promoting complacency at the time when the species would be most readily eradicated.

For those species deliberately introduced, Allee effects should be incorporated into decisions regarding founder population sizes, release sites and release procedure. Increasing likelihood of establishment with number released has been shown for both insects[41] and birds[42]. A tendency for long-range, post-release dispersal might favour soft-release protocols involving temporary penning at the release site, whilst an understanding of social systems is also important. Simultaneous release of male and female bush-tailed phascogales (*Phascogale tapoatafa*) resulted in dispersing males failing to find the few females released; staggered releases, with females establishing territories before males were released, reduced male dispersal and prevented a mate-finding Allee effect[43].

Conclusions

The consequences discussed here mean the Allee effect has ramifications in many other areas of ecology and conservation. Of particular importance to conservationists are the many, potentially synergistic, component Allee effects that might impact on the viability of subpopulations and affect policies of metapopulation management. Such factors must be incorporated into population viability analyses[44]. An awareness of the diverse array of mechanisms that lead to Allee effects and an appreciation of their consequences are important components in understanding the ecology and conservation of many systems.

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References

1 Fowler, C.W. and Baker, J.D. (1991) **A review of animal population dynamics at extremely reduced population levels,** *Report to the International Whaling Commission* 41, 545–554
2 Courchamp, F., Clutton-Brock, T. and Grenfell, B. (1999) **Inverse density dependence and the Allee effect,** *Trends Ecol. Evol.* 14, 405–410
3 McCarthy, M.A. (1997) **The Allee effect, finding mates and theoretical models,** *Ecol. Model.* 103, 99–102
4 Amarasekare, P. (1998) **Allee effects in metapopulation dynamics,** *Am. Nat.* 152, 298–302
5 Courchamp, F., Grenfell, B. and Clutton-Brock, T. (1999) **Population dynamics of obligate cooperators,** *Proc. R. Soc. London Ser. B* 266, 557–563
6 Poggiale, J.C. (1998) **From behavioural to population level: growth and competition,** *Math. Comput. Model.* 27, 41–49
7 Caro, T.M., ed. (1998) *Behavioral Ecology and Conservation Biology*, Oxford University Press
8 Sutherland, W.J. (1998) **The importance of behavioural studies in conservation biology,** *Anim. Behav.* 56, 801–809
9 Gosling, L.M. and Sutherland, W.J., eds *Behaviour and Conservation*, Cambridge University Press (in press)
10 Reed, J.M. and Dobson, A.P. (1993) **Behavioural constraints and conservation biology: conspecific attraction and recruitment,** *Trends Ecol. Evol.* 8, 253–256
11 Komdeur, J. (1992) **Importance of habitat saturation and territory quality for the evolution of cooperative breeding in the Seychelles warbler,** *Nature* 358, 493–495
12 Creel, S. (1998) **Social organization and effective population size in carnivores,** in *Behavioral Ecology and Conservation Biology* (Caro, T.M., ed.), pp. 246–265, Oxford University Press
13 Srivastava, A. and Dunbar, R.I.M. (1996) **The mating system of Hanuman langurs: a problem in optimal foraging,** *Behav. Ecol. Sociobiol.* 39, 219–226
14 Davies, N.B. (1991) **Mating systems,** in *Behavioural Ecology: an Evolutionary Approach* (Krebs, J.R. and Davies, N.B., eds), Blackwell
15 Reynolds, J.D. (1996) **Animal breeding systems,** *Trends Ecol. Evol.* 11, 68–72
16 Dobson, A. and Poole, J. (1998) **Conspecific aggregation and conservation biology,** in *Behavioral Ecology and Conservation Biology* (Caro, T.M., ed.), pp. 193–208, Oxford University Press
17 Muller, K.L. *et al.* (1997) **The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*),** *Am. Nat.* 150, 650–661
18 Sibly, R.M. (1983) **Optimal group size is unstable,** *Anim. Behav.* 31, 947–948
19 Fretwell, S.D. (1972) *Populations in a Seasonal Environment*, Princeton University Press
20 Rangeley, R.W. and Kramer, D.L. (1998) **Density-dependent antipredator tactics and habitat selection in juvenile pollock,** *Ecology* 79, 943–952

21 Brown, J.H. (1984) **On the relationship between abundance and distribution of species,** *Am. Nat.* 124, 255–279
22 Pulliam, H.R. (1988) **Sources, sinks, and population regulation,** *Am. Nat.* 132, 652–661
23 Lennon, J.J., Turner, J.R.G. and Connell, D. (1997) **A metapopulation model of species boundaries,** *Oikos* 78, 486–502
24 Dennis, B. (1989) **Allee effects: population growth, critical density, and the chance of extinction,** *Nat. Res. Model.* 3, 481–538
25 Hopf, F.A. and Hopf, F.W. (1985) **The role of the Allee effect in species packing,** *Theor. Popul. Biol.* 27, 27–50
26 Gruntfest, Y., Arditi, R. and Dombrovsky, Y. (1997) **A fragmented population in a varying environment,** *J. Theor. Biol.* 185, 539–547
27 Lande, R., Engen, S. and Sæther, B.E. (1998) **Extinction times in finite metapopulation models with stochastic local dynamics,** *Oikos* 83, 383–389
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* 81, 449–457
29 Stacey, P.B. and Taper, M. (1992) **Environmental variation and the persistence of small populations,** *Ecol. Appl.* 2, 18–29
30 Halliday, T.R. (1980) **The extinction of the passenger pigeon *Ectopistes migratorius* and its relevance to contemporary conservation,** *Biol. Conserv.* 17, 157–162
31 Bucher, E.H. (1992) **The causes of extinction of the passenger pigeon,** *Current Ornithol.* 9, 1–36
32 Reed, J.M. (1999) **The role of behavior in recent avian extinctions and endangerments,** *Conserv. Biol.* 13, 232–241
33 Sillero-Zubiri, C., King, A.A. and Macdonald, D.W. (1996) **Rabies and mortality in Ethiopian wolves (*Canis simensis*),** *J. Wildl. Dis.* 32, 80–86
34 Alvarez, L.H.R. (1998) **Optimal harvesting under stochastic fluctuations and critical depensation,** *Math. Biosci.* 152, 63–85
35 Allee, W.C. (1938) *The Social Life of Animals*, William Heinemann
36 Lande, R., Engen, S. and Sæther, B.E. (1994) **Optimal harvesting, economic discounting and extinction risk in fluctuating populations,** *Nature* 372, 88–90
37 Myers, R.A. *et al.* (1995) **Population dynamics of exploited fish stocks at low population levels,** *Science* 269, 1106–1108
38 Liermann, M. and Hilborn, R. (1997) **Depensation in fish stocks: a hierarchic Bayesian meta-analysis,** *Can. J. Fish. Aquat. Sci.* 54, 1976–1984
39 Lewis, M.A. and Kareiva, P. (1993) **Allee dynamics and the spread of invading organisms,** *Theor. Popul. Biol.* 43, 141–158
40 Veit, R.R. and Lewis, M.A. (1996) **Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America,** *Am. Nat.* 148, 255–274
41 Hopper, K.R. and Roush, R.T. (1993) **Mate finding, dispersal, number released, and the success of biological–control introductions,** *Ecol. Entomol.* 18, 321–331
42 Green, R.E. (1997) **The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand,** *J. Anim. Ecol.* 66, 25–35
43 Soderquist, T.R. (1994) **The importance of hypothesis testing in reintroduction biology: examples from the reintroduction of the carnivorous marsupial *Phascogale tapoatafa*,** in *Reintroduction Biology of Australian and New Zealand Fauna* (Serena, M., ed.), pp. 156–164, Surrey Beaty and Sons
44 Boyce, M.S. (1992) **Population viability analysis,** *Annu. Rev. Ecol. Syst.* 23, 481–506
45 Stephens, P.A., Sutherland, W.J. and Freckleton, R.P. **What is the Allee effect?** *Oikos* (in press)
46 Côté, I.M. and Gross, M.R. (1993) **Reduced disease in offspring: a benefit of coloniality in sunfish,** *Behav. Ecol. Sociobiol.* 33, 269–274
47 Donaldson, J.S. (1993) **Mast-seeding in the cycad genus *Encephalartos* – a test of the predator satiation hypothesis,** *Oecologia* 94, 262–271
48 Ferson, S. and Burgman, M.A. (1990) **The dangers of being few: demographic risk analysis for rare species extinction,** *Ecosystem Management: Rare Species and Significant Habitats. New York State Museum Bulletin* 471, 129–132
49 Sussman, R.W. and Garber, P.A. (1987) **A new interpretation of the social organisation and mating system of the Callitrichidae,** *Int. J. Primatol.* 8, 73–92

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 CB2 3EJ (fc219@cam.ac.uk; thcb@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[1]. 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 conspecific individuals are not numerous enough: 'undercrowding, as well as overcrowding, may be limiting' (Box 1). One of Allee's collaborators, E.P. Odum, first referred to this process as Allee's Principle[2], 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 inverse density dependence are numerous and have been described for most major animal taxa[3]. These factors can be classified into three main categories[4]. The first is genetic inbreeding and loss of heterozygosity, leading to decreased fitness (such as demonstrated for plants[5,6]). The second is demographic stochasticity (including sex-ratio fluctuations)[4], as illustrated by the failure of many biological control programmes that released control insects in too small numbers. Another example concerns threatened species with low fecundity and small population size, such as the Kakapo *Strigops habroptilus*, the world's largest parrot (Fig. 2). In 1997, the total population of this flightless bird consisted of 54 individuals, of which only 20 were female (with few of these being

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