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Inverse density dependence and the Allee effect

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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.

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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 ecology¹. 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 overcrowding, may be limiting’ (Box 1). One of Allee’s collaborators, E.P. Odum, first referred to this process as Allee’s Principle², 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 taxa³. These factors can be classified into three main categories⁴. 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

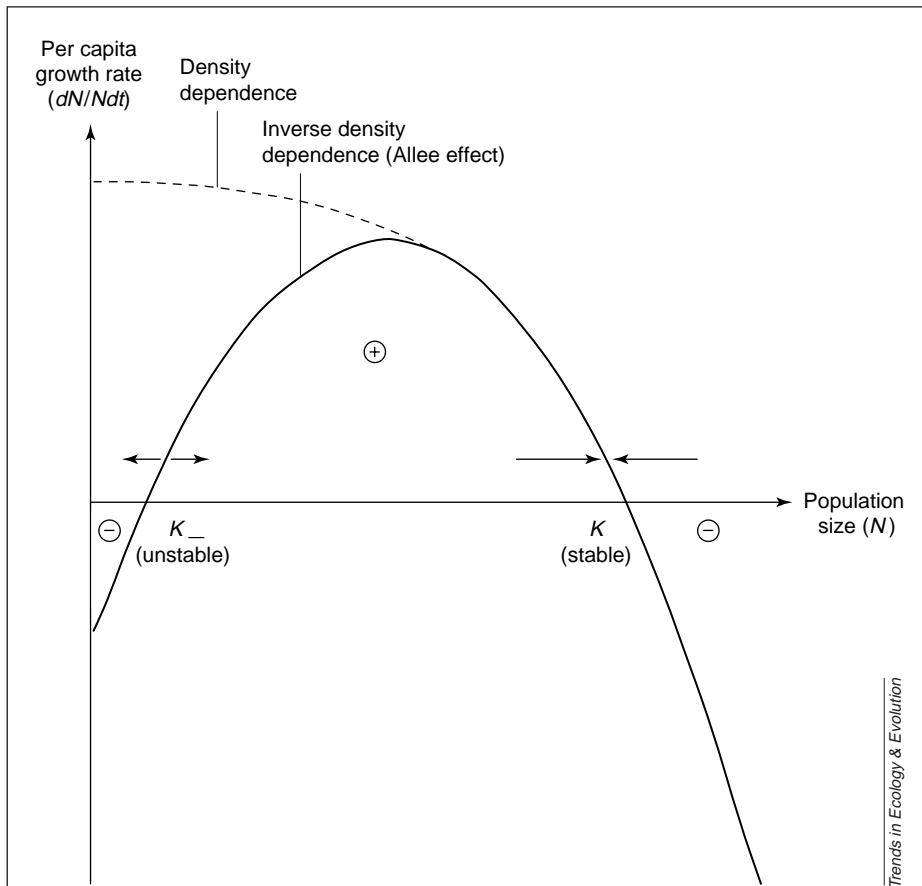


Fig. 1. Illustration of the Allee effect, from a very simple mathematical model of population dynamics:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) \left(\frac{N}{K_-} - 1 \right)$$

The per capita growth rate (dN/dt) is negative above the carrying capacity (K) and positive below. However, in the presence of an Allee effect, it also decreases below a given population size, and can even become negative below a critical population threshold (K_-). When a population displaying this type of population dynamics is driven below the critical threshold, the low, sometimes negative, per capita growth rate may lead it to extinction.

fertile), distributed across four islands⁷. A recent breeding program has resulted in the birth of nine chicks, but only two of these are female (R. Dennett, pers. commun.). The third category concerns the reduction in cooperative interactions when there are fewer individuals.

This last mechanism has attracted most research effort, probably partly because Allee himself proposed it, referring to it as 'proto-cooperation' or 'facilitation'¹. Given that cooperation usually implies active participation, we prefer to use the more generalist term of facilitation, except for particular cases. Shortage of receptive mate encounters during the mating period when density is too low⁸ is the most cited factor, although it represents only a small subset of social causes of inverse density dependence. Species in which fitness is enhanced by any type of conspecific facilitation might suffer from reduced density when intraspecific competitive processes are of secondary impor-

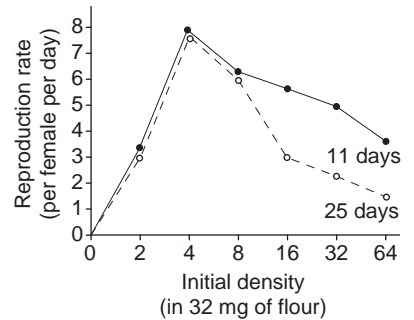
tance (Box 2). In this context, facilitation is taken in the broadest sense and sometimes includes sexual reproduction (where two organisms can be seen as 'cooperating' to pass on their genes to the next generation).

For example, decreased sexual reproduction owing to a lower probability of finding a mate at very low densities might generate a lower rate of recruitment, which in turn lowers the probability of finding mates in the next generation, thereby creating an extinction vortex, and ultimately the collapse of the population. Additionally, in cooperative animals, reduced recruitment may also be caused by higher juvenile mortality, owing to the cost of feeding or babysitting in small groups⁹ as in suricates, *Suricata suricatta*.

The Allee effect might also be generated by lower survival, such as when antipredator strategies become inefficient in small groups of prey. Examples of this include the passive protection of

Box 1. The floury little world of the *Tribolium*

One of the earliest illustrations of Allee's ideas of the existence of an optimal population size concerns his analysis of the laboratory work of three different researchers on the flour beetle, *Tribolium confusum*³⁵. This species showed the 'most rapid population growth at an intermediate population size rather than with too few or too many present', as shown in his figure, reproduced below.



Trends in Ecology & Evolution (Online: Fig. 1)

The higher growth rate at an intermediate population size was interpreted as the result of the interaction between two opposing processes. On one hand, 'adult beetles roam at random through their floury universe. They eat the flour, but they also eat their own eggs as they encounter these on their travels'³⁵. Because of this, eggs are less likely to escape oophagy at high densities. However, females lay more eggs, and eggs with a higher percentage of fertility, when they have been stimulated by successive copulation, which is more likely to occur at high densities. As a result, there is an intermediate optimal population density, above the possible minimum one, in which the growth rate is higher than at lower or higher population densities. Later, Allee and collaborators³⁵ showed that fish are better able to survive water poisoning if other fish had previously lived in it, because their secretions had conditioned the environment. This relationship between fitness and density was, however, positive only until competition became the principal factor influencing population dynamics. Such an interaction between two processes with an opposing relationship to density is a reasonably general feature of the Allee effect.

sea urchin larvae sheltered by adult spine canopies¹⁰, the early warning or confusion effects in fish schools and ungulate herds¹¹, or more active sentinel systems or defence strategies, as in suricates¹². However, because the extent of facilitation and/or cooperation might determine the strength of the Allee effect, many of these processes could be rather weak unless the populations are at very low density. In contrast, obligate cooperatively breeding species might experience a strong inverse density dependence, even when close to the carrying capacity, and may suffer from an Allee effect for most of their normal density range^{12,13}.

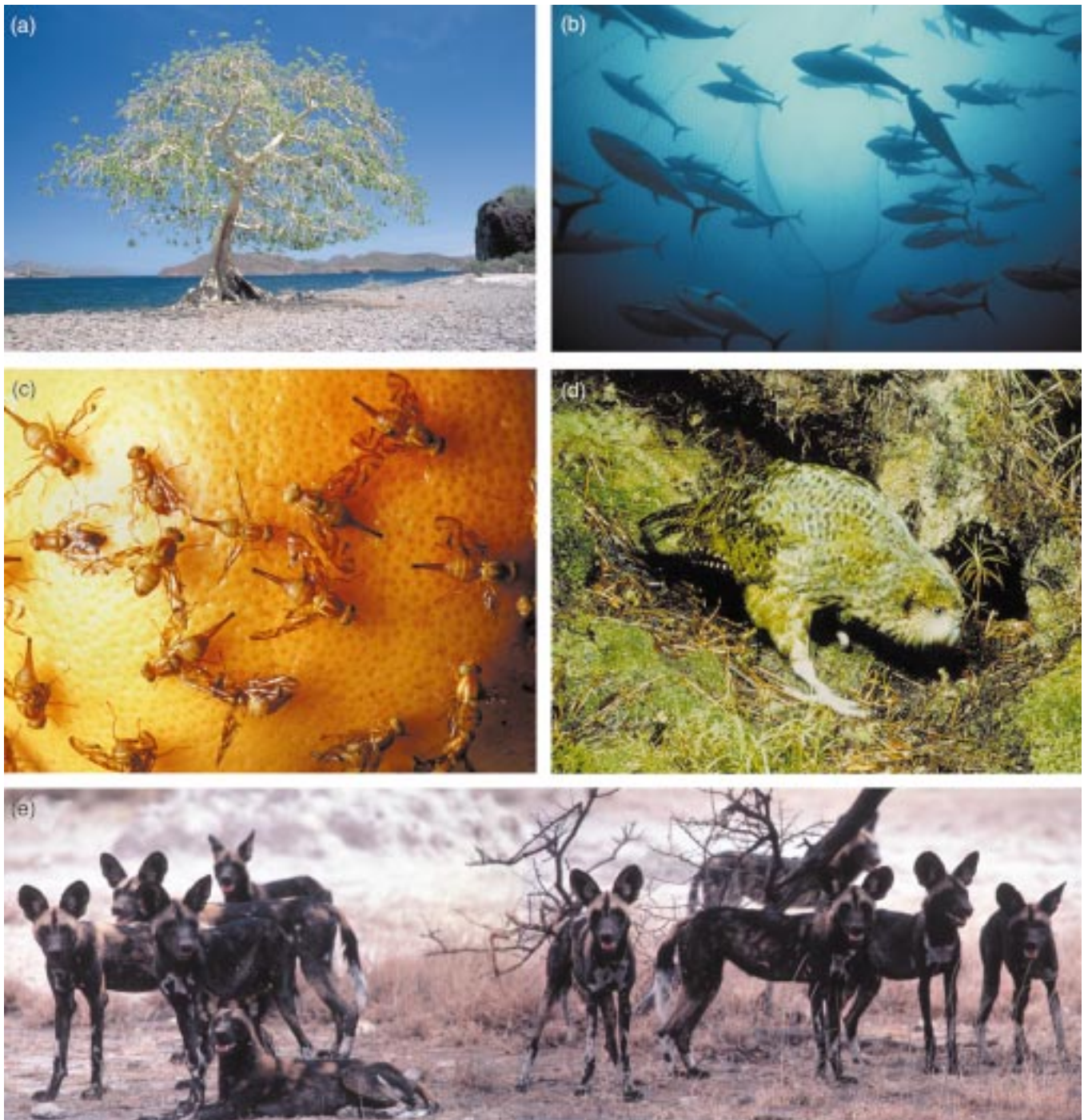


Fig. 2. Examples of the Allee effect in different taxa. (a) Because of a shortage of fertilization or of mating encounters, Allee effects can cause species extinction when density is too low. This is illustrated by pollination in fig trees (*Ficus* sp.), where small dispersed patches attract fewer pollinators or dispersers (photo reproduced, with permission, from Corbis/C. Mattison). (b) The Allee effect is important in group living animals, such as schooling fishes (here bluefin tunas *Thunnus thynnus* in fishing nets). It may also cause a population to collapse if harvesting pressure is too strong, as has happened for fisheries (photo reproduced, with permission, from Corbis/J.L. Rotman). (c) Because fruit flies attack more than 400 crops worldwide, they are considered to be one of the worst insect pests of agriculture. One of the techniques used to control them is the release of sterile males to create an Allee effect, as for these fruit flies, *Anastrepha ludens* (photo reproduced, with permission, from J. Dykinga, Agricultural Research Service, USDA). Another technique is to release natural enemies, in numbers large enough to ensure the Allee effect is avoided. (d) At very small population sizes, some endangered species, such as the Kakapo (*Strigops habroptilus*), have a low probability of finding receptive mates, and/or have a biased sex-ratio because of demographic stochasticity. There are only 54 individuals surviving of this giant parrot (photo reproduced, with permission, from D. Merton). (e) Obligate cooperative breeders, such as African wild dogs (*Lycan pictus*), may have a critical group size below which the group would be very likely to go extinct (photo reproduced, with permission, from J. Ginsberg).

Implications for population dynamics

For all these phenomena, and others, the major consequence of the Allee effect is the existence of a critical density below which the aggregation unit considered

(e.g. population, colony or social group) is likely to go extinct. This has been shown theoretically both with deterministic and stochastic mathematical models^{4,13,14}, and although still scarce, empirical evidence exists from very diverse

ecological systems (Box 2). Because the mechanism is quite straightforward, very basic population dynamic models (comparable in simplicity to the classical Verhulst logistic equation) can be used to mimic the Allee effect (Fig. 1).

Box 2. Allee effects, facilitation and cooperation

The Allee effect can be generated by a shortage of interactions among conspecifics at low density. These interactions range from strict cooperation to unconscious facilitation. At one extreme, strong cooperation, are taxa that form colonies (with different degrees of coloniality). For example, because offspring survival to maturity increases with colony size, the lifetime reproductive success of female social spiders, *Anelosimus eximius*, decreases in small colonies³⁶. Smaller colonies of reef-building coral populations are less likely to survive attacks by mucilage coverage³⁷ or catastrophic climatic events³³. In Damaraland mole-rats, *Cryptomys damarensis*, small colonies are more likely to fail because the colony work force is of insufficient size to locate food³⁸. In plants, lower survival can be caused by a lack of conditioning effects at low densities³⁹, and some colonial seabirds need a critical density to establish and reproduce^{1,40}.

At the other extreme of sociality are individuals of species whose only form of contact with conspecifics is for sexual reproduction (which can in this context be considered as proto-cooperation). They can also be subject to Allee effects. For example, pollination of many species of plants (especially by animal vectors), is less efficient when inter-individual distances become too large or patches too small^{39,41,42}. Fertilization in benthic invertebrates with free-spawn gametes, or with planktonic larvae, has also been shown to be insufficient at low population densities³³. A shortage of encounters with receptive mates during the mating period⁸ can increase the threat to small populations, such as those of the Glanville fritillary butterfly, *Melitaea cinxia*¹⁸, and the northern spotted owl, *Strix occidentalis*⁴³. An Allee effect may also delay the beginning of an invasion³², or even prevent its success, as seen in the House Finch, *Carpodacus mexicanus*, in North America. The same is true for species introductions (for their conservation or for biological control of another species), which generally require repeated releases of large numbers of individuals before successful establishment^{44,45}.

Between these two extremes, the atypical social system of obligate cooperative breeders can generate an Allee effect, potentially responsible for their high rates of group extinction¹³ (Box 3).

The implications of the Allee effect are potentially very important in most areas of ecology¹⁵ and evolution¹⁴, but we will focus here on population dynamics only. As we will see below, the practical management of population numbers, whether aiming to increase or reduce them, is strongly affected by this effect. The consequences of Allee effects are also likely to be significant for the theory of population dynamics, because most classic models imply a linear decrease of growth with density, as opposed to the non-linear relationship associated with the Allee effect¹⁴. Similarly, current mathematical models seem to overestimate persistence times for metapopulations of species exhibiting an

Allee effect, because even when explicitly considering small metapopulation sizes, they carry the implicit assumption that local populations always increase to their carrying capacity¹⁶. Other types of Allee effects have been demonstrated at the theoretical metapopulation level when the spatial dimension and stochasticity are taken into account^{4,17}. The importance of the Allee effect in metapopulation dynamics has also been shown empirically, as for the endangered Glanville fritillary butterfly (*Melitaea cinxia*)¹⁸.

Repercussions across trophic levels

Although it is an intraspecific phenomenon, some interspecific relationships

are strongly influenced by the Allee effect. It is well known that smaller groups of prey may be more exposed to predation than larger groups¹¹. It has also been shown, both theoretically and empirically, that if a species is a secondary prey item of a predator with a type II functional response, its death rate from predation will be inverse density dependent¹⁹. Similarly, the rate of infection for many parasitoid species has been shown to decrease with increasing host density²⁰. Other interspecific relationships, such as nest parasitism²¹ and kleptoparasitism²² can also be affected (Box 3).

The victims of interspecific relationships (e.g. prey or hosts) are not the only ones prone to the Allee effect: at low density, their natural enemies can also suffer inverse density dependence. Indeed, some cooperative hunters are not as efficient if they have a small hunting party, because some prey require a certain number of individual hunters if they are to be successfully isolated and attacked^{23,24} (Box 3). Other examples include kleptoparasites: hyenas (*Crocuta crocuta*) form large clans that spread out in search of prey and regroup once individuals have located a fresh kill and signalled to the others. A critical threshold in the clan size of hyenas is thus likely to limit the success of this type of foraging strategy when prey are scarce. This also seems to be true for many birds (whether predatory or not) regrouping in flocks to maximize resource location efficiency. In addition, it is reasonable to predict that inverse density-dependent mechanisms are likely to affect strongly the population dynamics of species such as parasitoids²⁰, because the difficulty of finding a mate at low densities compounds that of finding a host when the host density is also low.

Perhaps among the best known manifestations of population thresholds for extinction are some infectious pathogens, which do not persist below a critical host population size, as shown for human²⁵ as well as wildlife populations²⁶. This is because the life history of some pathogens (mostly their rates of transmission and induced mortality) makes it difficult for them to infect new hosts before dying out if the host density is too low. Although this is not an Allee effect *per se*, this critical community size, which can take different mathematical forms according to the system modelled²⁷, has interesting analogies with minimum viable populations and extinction thresholds generated by inverse density dependence. At a different scale, too few parasites (either micro- or macroparasites) in a host are less likely to overcome the host's immune defence, resulting in the extinction of the

Box 3. The Allee effect in African wild dogs

It has recently been proposed that the high rates of group extinction observed in obligate cooperative breeders are generated by a need for a critical number of helpers, which produce an Allee effect¹³. As a result, a social group driven below a critical threshold would have a lower chance of recovery and consequently become even smaller, with an increasing risk of extinction.

This can be illustrated by the African wild dog, *Lycaon pictus*, which is currently facing the threat of extinction throughout its remaining geographical range. Many causes have been proposed to explain its current decline, including human persecution, diseases, habitat fragmentation and competition with other predators⁴⁶. Although it has never been proposed, another, nonexclusive, factor is the existence of an Allee effect, which would render this species more sensitive to other mortality factors. Wild dogs live in groups of up to 20 adults and their dependent young²³. The hunting strategy of the group usually requires a critical size to be energetically efficient^{23,24,47}. A threshold group size might also be required for hunting because of kleptoparasitism by hyenas, which can be energetically very costly to small groups of wild dogs^{22,47,48}. In addition, helpers are required by the breeding female: litters are very large (up to 20 pups), and the breeding female, then the pups, need to be fed by other members of the group^{46,49}. Group members also help by chasing predators from the den area, and by staying at the den to protect the pups while the pack is hunting^{46,49}.

Consequently, a critical number of helpers might be needed for wild dog groups to survive. It has been suggested that groups of less than four adults are unable to reproduce successfully⁴⁶. Furthermore, the impact of environmental stochasticity (including random catastrophes, such as droughts and epidemics) and of natural enemies (competitors, predators, kleptoparasites) might increase the extinction probability of cooperators by driving them closer to or below the critical threshold. Human activities and pathogens might act in the same way, increasing the threat of the Allee effect by decreasing group sizes. For example, because of high contact rates owing to wild dogs' social structure, a virus can probably spread rapidly among group members. The disease-induced death of several dogs might then reduce the group to insufficient size for survival.

parasite. Consequently, there might be a critical threshold for many internal parasites.

Allee effects in more complex interspecific relationships, involving more than two species, have seldom been considered. However, given what is already known about the importance of this process on 'simple' competitive, predatory or parasitic relationships, it is reasonable to predict that models of processes such as predator- or parasite-mediated competition (which is an important ecological process²⁸) will generate different outcomes in the presence of inverse density dependence. At the niche scale, the Allee effect can prevent persistence of plants that ameliorate physically stressful habitats²⁹. This environmental conditioning is also important for many associated plant and animal species because it allows new colonization. At a larger scale, the Allee effect is likely to have a detectable influence on plant community dynamics and vegetation succession²⁹. It is very likely that species are affected by inverse density dependence generated by a combination of all these ecological forces. Even those species displaying no obvious Allee effect can be affected by others that do, which means that most species are probably influenced, either directly or indirectly, by this dynamic process.

Implications for applied ecology

Species subjected to a strong Allee effect might be more susceptible to catastrophic population collapses with only a slight increase in mortality, resulting either from harvesting or 'natural' causes. Two generally conflicting interests in ecosystem management, long-term optimal harvesting and biodiversity preservation, which both aim to prevent these collapses, have much to gain from acknowledging potential Allee effects. In fisheries, for example, the existence of multiple equilibria has been recognized (in theory at least), and the existence of a critical threshold for harvested populations has been advanced as a highly plausible explanation for the collapse of fisheries in several parts of the world³⁰ (Fig. 2). As exploited fish species are usually schooling species, and a large school is generally considered to be a defence against predators²¹, one should expect (and therefore attempt to prevent) Allee effects in these species.

Prevention of population collapses is also a priority in conservation biology¹⁵, where it is widely admitted that populations of small size are often at greater risk of extinction. However, even though many conservation programs (including reintroduction) focus on the extinction risks encountered by very small populations, and the existence of a minimum

Box 4. Biological control: helped and hindered by Allee effects

The primary aim of biological control, which is nothing more than a planned biological invasion to get rid of another invasion, is to minimize the establishment and persistence of pests and maximize that of their enemies. This is one of the few research areas in which the Allee effect is plainly recognized and fully used. The first successful attempts at biologically controlling a pest insect to meet with success artificially created an Allee effect in the pest population by inundating it with sterile males⁵⁰. This method is still widely used⁵⁰, as illustrated by the massive releases of sterile male Mediterranean fruit flies, *Ceratitis capitata*, last year in the USA. The emerging new concept of mammal control through virus-vectorized immunocontraception⁵¹ is likely to succeed because it should create an Allee effect.

An important issue in biological control programmes (and in the reintroduction of threatened species) concerns the minimum number of individuals that should be released to ensure the establishment of populations of natural enemies of the pest. Indeed, insufficient reproduction at low densities would result in a collapse of these populations because of at least two mechanisms⁴⁴. First, the low probability at finding a mate at low density may lead to a lack of recruitment⁸. Second, in arrhenotokous insect species (when virgin females produce only males), failure to mate may result in a male-biased sex ratio, and therefore in demographic stochasticity⁴. Both potentially create an Allee effect, and both can result in the failure of the introduction⁴⁴.

population size below which they cannot recover, the Allee effect is still seldom taken into account in this area¹⁵. That the Allee effect is indexed in only five out of 35 of the most recent major books on conservation biology illustrates this deficiency very well. Other research areas where the Allee effect plays a critical role are ecosystem invasions^{31,32} (Box 2) and, most importantly, biological control (Box 4).

What prospects for the Allee effect?

The early studies of population biology have been largely dominated by the importance of (negative) density dependence at high densities. In a time when anthropogenic disturbance has driven many populations to small sizes and/or low densities, we must now focus on the other extreme of population sizes. Indeed, studies demonstrating Allee effects and determining their causal mechanisms, either theoretically or empirically, ought to be more numerous in the future. There is a range of logistical problems associated with the study of very small natural populations, especially of mobile animals, rendering it difficult to demonstrate an Allee effect^{14,18,21}. Nevertheless, in several different areas of ecology, empirical evidence is needed on this still poorly documented but nonetheless important dynamic process.

With the notable exception of biological control, which provides excellent opportunities to study experimentally the effect of population size on establishment and persistence, experimental studies of the Allee effect are both impractical and unethical in natural conditions. Therefore, one has either to rely on 'natural experiments', such as catastrophic events³³, or to work on laboratory populations¹, which can compensate for the lack of replicability and control typical of 'natural experiments'. Although they are less scarce than empirical studies, theoretical studies of the consequences of the Allee effect are also needed, especially concerning the dynamics of interspecific relationships.

Future progress in understanding the dynamics of small populations will most likely be achieved by creatively combining these different scientific approaches.

Knowing a given species is prone to a strong Allee effect would not be of much help if the population collapse was inevitable. In many cases, however, it should be possible to artificially reverse the fate of a population that is dangerously close to, or even below, its critical threshold. For example, densities of some plants or trees could be increased by dispersing seeds, or by planting individuals obtained from nurseries or from other, more dense populations. Similarly, social groups of some endangered vertebrates could be artificially increased (e.g. during a short period of captivity), thereby avoiding the loss of the smallest groups. More importantly, knowing that an Allee effect threatens a given population would allow the redirection of harvesting pressure towards less threatened populations. Similarly, protection efforts for an endangered species, if proven sensitive to the Allee effect, should be redefined according to different priorities: for many species, density as much as population size should become a criterion of endangerment in conservation programmes. As the causes of decline of many populations still remain a puzzle (as for the recent amphibian declines³⁴), a more systematic investigation of potential Allee effects in endangered populations could be crucial to the better understanding of their dynamics, as well as efficiently protecting them against formally identified threats.

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