

Multiple Allee effects and population management

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Allee effects, strongly related to the extinction vulnerability of populations and gradually becoming acknowledged by both theoretically oriented and applied ecologists, have already been shown to have important roles in the dynamics of many populations. Although not yet widely recognized, two or more Allee effects can occur simultaneously in the same population. Here, we review the evidence for multiple Allee effects and show that their interactions can take several forms, many of which are far from inconsequential. We suggest that more research is needed to assess the prevalence and interactions of multiple Allee effects, as failing to take them into account could have adverse consequences for the management of threatened or exploited populations.

Introduction

The Allee effect is a concept that, having been poorly studied for decades, is now once again recognized as an important phenomenon in many fields of ecology and evolution. Allee effects occur whenever fitness of an individual in a small or sparse population decreases as the population size or density also declines [1,2].

Various mechanisms generating Allee effects have been suggested (Table 1), having been largely studied as singular entities. However, despite accumulating evidence (Table 2), the possibility that two or more Allee effect-generating mechanisms act simultaneously upon a single population is not yet widely recognized. Here, we demonstrate their ubiquity, with examples from terrestrial and marine ecosystems, from plants, invertebrates and vertebrates, and from natural and exploited populations.

Implications of multiple Allee effects for population growth are also not yet understood. For example, if each single Allee effect were to yield different extinction thresholds, what would be the value of the threshold resulting from the simultaneous presence of several Allee effects? We propose several plausible scenarios of how multiple Allee effects might interact, and emphasize the importance of the outcomes of these scenarios for biodiversity conservation. Overall, we suggest that multiple Allee effects could markedly affect the dynamics of the species concerned, and that the importance of multiple effects is concealed by the current lack of information about their prevalence.

Phenomenological classification of Allee effects

Understanding the importance of multiple Allee effects requires a clarification of the terminology used for single Allee effects. The two main pairs of concepts related to these effects are component–demographic and weak–strong Allee effects (see Glossary).

Component–demographic Allee effects

Component Allee effects designate a positive relationship between any measurable component of individual fitness and either numbers or density of conspecifics. For instance, plants occurring at low density can receive a reduced

Glossary

Allee threshold: critical population size or density below which the per capita population growth rate becomes negative (Figure 1).

Anthropogenic Allee effect: mechanism relying on human activity, by which exploitation rates increase with decreasing population size or density: values associated with rarity of the exploited species exceed the costs of exploitation at small population sizes or low densities.

Component Allee effect: positive relationship between any measurable component of individual fitness and population size or density.

Demographic Allee effect: positive relationship between total individual fitness, usually quantified by the per capita population growth rate, and population size or density.

Dormant Allee effect: component Allee effect that either does not result in a demographic Allee effect or results in a weak Allee effect and which, if interacting with a strong Allee effect, causes the overall Allee threshold to be higher than the Allee threshold of the strong Allee effect alone.

Double dormancy: two component Allee effects, neither of which singly jointly produce an Allee threshold (i.e. the double Allee effect becomes strong).

Genetic Allee effect: genetic-level mechanism resulting in a positive relationship between any measurable fitness component and population size or density.

Human-induced Allee effect: any component Allee effect induced by a human activity.

Multiple Allee effects: any situation in which two or more component Allee effects work simultaneously in the same population.

Nonadditive Allee effects: multiple Allee effects that give rise to a demographic Allee effect with an Allee threshold greater or smaller than the algebraic sum of Allee thresholds owing to single Allee effects.

Predation-driven Allee effect: a general term for any component Allee effect in survival caused by one or multiple predators whereby the per capita predation-driven mortality rate of prey increases as prey numbers or density decline.

Strong Allee effect: demographic Allee effect with an Allee threshold (Figure 1).

Subadditive Allee effects: multiple Allee effects that give rise to a demographic Allee effect with an Allee threshold smaller than the algebraic sum of Allee thresholds owing to single Allee effects.

Superadditive Allee effects: multiple Allee effects that give rise to a demographic Allee effect with an Allee threshold greater than the algebraic sum of Allee thresholds owing to single Allee effects.

Weak Allee effect: demographic Allee effect without an Allee threshold (Figure 1).

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Table 1. Main mechanisms generating component Allee effects

Mechanism	How it works	Examples	Refs
Component Allee effects in reproduction			
(1) Mate finding	Harder to find a (compatible and receptive) mate at low population size or density	Cod <i>Gadus morhua</i> ; queen conch <i>Strombus gigas</i> ; Glanville fritillary butterfly; alpine marmot <i>Marmota marmota</i>	[4,6,9,27–29]
(2) Broadcast spawning	Harder for sperm and egg to meet at low population density	Crown-of-thorns starfish <i>Acanthaster planci</i> ; sea urchins	[9]
(3) Reproductive facilitation	Individuals less likely to reproduce if not perceiving others to reproduce, the situation more probable in small populations	Whiptail lizards; snail <i>Biomphalaria glabrata</i> ; queen conch; many colonial seabirds	[9,30,31]
(4) Pollen scarcity	Decreased pollinator visitation frequencies in small or sparse populations; lower probability of compatible pollen on pollinator at low plant density; lower probability of pollen grain to find stigma in wind-pollinated plants	Haleakala silversword <i>Argyroxiphium sandwicense</i> ; smooth cord grass <i>Spartina alterniflora</i>	[17,32,33]
(5) Cooperative breeding	Breeding groups less successful in producing and/or rearing young when small	African wild dog <i>Lycaon pictus</i>	[16]
Component Allee effects in survival			
(6) Cooperative anti-predator behaviour	Prey groups less vigilant and/or less efficient in cooperative defence when small; fleeing small groups confuse predators less easily	Meerkat <i>Suricata suricatta</i> ; desert bighorn sheep <i>Ovis canadensis</i> ; African wild dog	[13,34–36]
(7) Predator dilution (predator satiation or swamping)	As prey groups get smaller or prey populations sparser, individual prey vulnerability increases	Cod; meerkat; crown-of-thorns starfish; woodland caribou <i>Rangifer tarandus caribou</i>	[25,37]
(8) Allee effect through exploitation	When exploitation rates do not decrease as fast as the exploited population, the probability of an individual being caught increases	Potentially any commercially important species; currently debatable in many marine species	[2,9,25,38]
(9) Anthropogenic Allee effect	Rare species considered more valuable suffer enhanced exploitation and hence become more rare	Related to activities including collecting, trophy hunting, luxury products or exotic pets acquisition	[12]
Allee effects in reproduction and/or survival			
(10) Foraging efficiency	Ability to locate food, kill prey or overrule kleptoparasites decline in small foraging groups and can, in turn, reduce individual survival and/or fecundity	African wild dog; black-browed albatross <i>Thalassarche melanophris</i>	[16,39]
(11) Environmental conditioning	Amelioration of environmental stress through large numbers via many specific mechanisms, such as more efficient social thermoregulation (marmots) or improved winter ice resistance (mussels)	Alpine marmot; ribbed mussel <i>Geukensia demissa</i> ; bark beetles; fruit fly <i>Drosophila melanogaster</i> ; alpine plants	[11,28,40,41]
(12) Cultivation effect	Fewer adult fish imply higher juvenile mortality; fewer adult urchins worsen settlement success and feeding conditions of their young, and lessen protection from predation	Cod; many freshwater fish species; sea urchins	[10,42]
Genetic Allee effects			
(13) Sampling effect and genetic drift	Reduced number of beneficial alleles, accumulation of detrimental mutations, and/or reduced evolutionary potential in small populations	Herb <i>Ranunculus reptans</i> ; Florida panther <i>Felis concolor coryi</i>	[43,44]
(14) Inbreeding	Increased selfing rate and/or number of matings between close relatives in small populations	Herb <i>R. reptans</i> ; marsh gentian <i>Gentiana pneumonanthe</i>	[14,43,44]

amount of pollen and, hence, suffer a lowered seed set, as observed in plant taxa ranging from herbaceous temperate plants to tropical trees [1]. By contrast, a demographic Allee effect refers to a positive density dependence observed at the overall fitness level, classically measured by the per capita population growth rate [3]. For example, small populations of the Glanville fritillary butterfly *Melitaea cinxia* grow at a lower rate owing to a reduced ability of females to find mates [4]. Although component Allee effects need not result in demographic Allee effects [5], an observation of a demographic Allee effect is, by definition, always evidence of an underlying component Allee effect. When talking about multiple Allee effects, interactions occur between two or more component Allee effects but are assessed at the level of demographic Allee effects.

Weak–strong Allee effects

Whether a demographic Allee effect is weak or strong depends on the opposing strengths of positive density dependence (i.e. Allee effect mechanism) and negative density dependence (i.e. intraspecific competition). Demographic Allee effects are characterized by a hump-shaped relationship between the per capita population growth rate and population size or density (Figure 1). Provided that the growth rate becomes negative at small population sizes or low densities, the population faces a strong Allee effect. The size or density at which the growth rate becomes negative is termed the Allee threshold [6]; populations that drop below it go extinct. When the per capita population growth rate remains positive (although still hump-shaped) the Allee effect is weak, with no extinction threshold. As we show

Table 2. Examples of systems with multiple Allee effects

Habitat ^a	Species	Multiple component Allee effects ^b	Refs
T	Marsh gentian <i>Gentiana pneumonanthe</i>	Small populations have lower fecundity owing to a reduced pollination success (4) and increased inbreeding (14)	[14]
T	Monarch butterfly <i>Danaus plexippus</i>	Individuals in small overwintering groups suffer multiple costs: mating depression in spring (1), less efficient predator dilution (7), and decreased protection against cold (11)	[7,8]
T	Social spider <i>Anelosimus eximius</i>	Small colonies have a reduced number of eggs per sac (? ^c) and reduced offspring survival to maturation, owing to reduced protection against predators (6) and low ability of colonies to acquire resources (10)	[45]
A	Red sea urchin <i>Strongylocentrotus franciscanus</i>	Individuals in low-density populations have reduced fertilization efficiency (2) and survival of new recruits owing to a cultivation effect ^d (12) (e.g. adult urchins, when at high densities, protect juveniles from predation in their canopy of spines and facilitate their feeding)	[9,10]
A	Ribbed mussel <i>Geukensia demissa</i>	Low-density populations suffer from increased mortality owing to crab predation (7) and winter ice (11)	[11]
A	Cod <i>Gadus morhua</i>	Individuals in small-sized populations have reduced fertilization efficiency (2) and juvenile survival owing to a cultivation effect ^d (12) (e.g. adult cod prey on species that prey on juvenile cod; fewer adult cod imply higher juvenile mortality)	[23,42]
A	White abalone <i>Haliotis sorenseni</i>	Individuals at small density have reduced fertilization efficiency (2); some populations suffer overexploitation (8) and the species being considered a luxury item is subject to an anthropogenic Allee effect (9)	[12,22,26]
T	Lesser kestrel <i>Falco naumanni</i>	Small colonies suffer from increased nest predation (7) and lower adult survival (7 ^e)	[46]
T	Speckled warbler <i>Chthonicola sagittata</i>	Small overwintering flocks might face reduced vigilance to predators ^d (6) and foraging efficiency ^d (10)	[15]
T+A	Sooty shearwater <i>Puffinus griseus</i> ; Hutton's shearwater <i>P. huttoni</i> ^d	Birds in small colonies have lower breeding success (7) and higher mortality (7 ^e), both owing to predation by the stoat <i>Mustela erminea</i>	[47]
T	African wild dog <i>Lycaon pictus</i>	Smaller packs are less efficient in cooperative breeding (5), cooperative anti-predator behaviour (6), and cooperative hunting (10)	[16]
A	Southern fur seal <i>Arctocephalus australis</i>	Small populations face reduced pup survival owing to habitat change (plain to more rugged) (11) elicited by human disturbance, and to predation by southern sea lions <i>Otaria flavescens</i> (7); these effects were not observed in the same population	[48,49]
A	Southern sea lion <i>Otaria flavescens</i>	Small breeding groups suffer a 'constant-yield-like exploitation' by killer whales <i>Orcinus orca</i> ^d (7) and a reduced survival of pups caused by displaced mating behaviour of adult males ^d (7 ^e)	[50]
T	Alpine marmot <i>Marmota marmota</i>	Individuals in smaller overwintering groups have difficulties in finding mates (1) and decreased survival, owing to less efficient social thermoregulation (11)	[28]
T	Desert bighorn sheep <i>Ovis canadensis</i>	Individuals in smaller groups suffer higher predation risk because of lower vigilance (6) and the species rarity makes it a valuable item for trophy hunters (9)	[12,13]

^aA, aquatic habitat, T, terrestrial habitat.

^bThe numbers in parentheses correspond to the Allee effect mechanisms in Table 1.

^cExact mechanism unknown.

^dThese mechanisms have been hypothesized by the authors of the respective studies.

^eThe same mechanism operates on two distinct life stages.

below, the presence or absence of Allee thresholds in single Allee effects determines the way in which multiple Allee effects interact.

Examples of multiple Allee effects

Given the number of recognized Allee effect mechanisms (Table 1), it is reasonable to assume that multiple mechanisms might be working simultaneously in a population. We discuss evidence of multiple Allee effects from a general perspective, with specific examples given in Table 2. We find it convenient to distinguish natural and exploited systems, given that exploited systems can contain human-induced Allee effects.

Natural systems

Table 2 contains examples from a variety of taxa from both marine and terrestrial ecosystems. This diverse spectrum of species has a heterogeneous set of life-history parameters (e.g. life span, fecundity, sociality or food-web position), suggesting that multiple Allee effects are not limited to taxa with a specific life history and are not uncommon in different ecosystems.

Component Allee effects can co-occur in several ways. Table 2 includes examples in which a component Allee

effect affecting reproduction interacts with another affecting survival (e.g. monarch butterfly *Danaus plexippus* [7,8] or red sea urchin *Strongylocentrotus franciscanus* [9,10]), where two component Allee effects affecting survival interact (e.g. ribbed mussel *Geukensia demissa* [11] or desert bighorn sheep *Ovis canadensis* [12,13]) and where two component Allee effects affecting reproduction interact (e.g. marsh gentian *Gentiana pneumonanthe* [14]).

In some cases, the same mechanism can affect reproduction and survival. For example, reduced efficiency of foraging (e.g. speckled warbler *Chthonicola sagittata* [15]) or cooperative hunting (e.g. African wild dog *Lycaon pictus* [16]) in a small group might lead not only to starvation and increased mortality of its members, but also to a reduced reproductive output of those that survive (Table 2). Genetic Allee effects could also affect reproduction and survival, could operate in most small or sparse populations and, thus, could interact with any non-genetic Allee effect present (Table 1). However, there is currently little evidence for this (but see the marsh gentian example; Table 2).

One can think of other situations in which multiple Allee effects could occur, even though empirical evidence is lacking. For example, rare plants can be both pollen limited

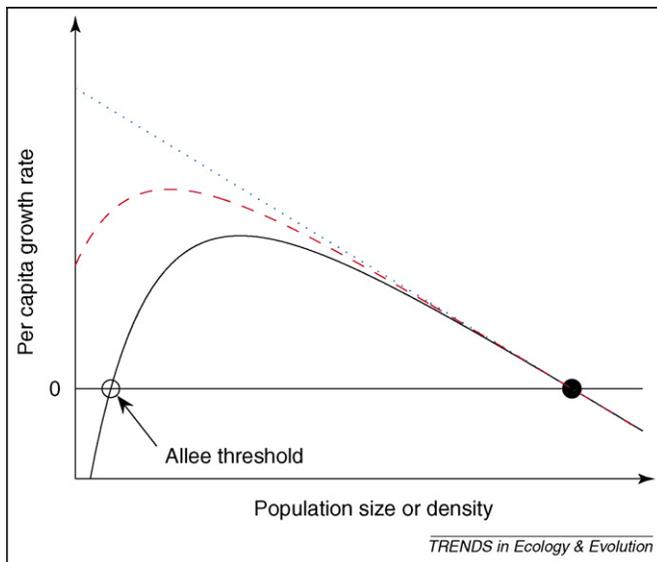


Figure 1. The relationships between the per capita population growth rate and either population size or density for negative density dependence (dotted curve), and weak (dashed curve) and strong (solid curve) Allee effects. In weak or strong Allee effects, the relationship is positive at low population sizes or densities, where positive density-dependent (Allee effect) mechanisms overpower negative density-dependent (intraspecific competition) ones. It is negative at high population sizes or densities, where the converse is true.

[17] and subject to herbivore-driven Allee effects, analogous to Allee effects owing to predator dilution [18] (Table 1). Also, reduced seed set in small or sparse populations of trees could be coupled with a disproportionate predation on resulting seeds, owing to failure to satiate seed predators.

Exploited systems

Exploitation can affect systems with Allee effects in several ways. It can reduce population size or density to a level close to or below an Allee threshold [1] or increase the Allee effect strength [2]. More importantly, positive density dependence can be a direct consequence of exploitation [9,12,19].

As soon as exploitation rates decrease at a slower rate than does the population size, the probability of any individual being caught increases, generating a component Allee effect. The constant-yield exploitation strategy is an example of this relationship: the annual catch of the Norwegian herring fishery remained almost constant until the stock size was very small [19]. Also, once an exploited species is a bycatch of the exploitation of another, a decline in the secondary species does not act as an economic incentive to reduce its exploitation, which is driven by the target species, again creating a component Allee effect. In the Irish Sea, at least four species of skate and shark have been exploited to extinction while being 'only' a bycatch of fisheries for cod, plaice, sole and other more valuable species [20].

Finally, there is a new type of human-induced Allee effect, the anthropogenic Allee effect, which characterizes situations where exploitation rates actually increase as the population declines [12]. When rarity is associated with value, high exploitation costs of the few remaining individuals are no longer an economic constraint, and ecological extinction can precede economic extinction. The human activities involved include trading species as luxury

products or exotic pets, trophy hunting or ecotourism [12]. In all these cases, a species that becomes rare would be considered more valuable, and would, consequently, suffer enhanced exploitation, and become even rarer.

If an exploited population with a human-induced Allee effect already has a 'natural' Allee effect, the two can interact to produce a double Allee effect. Many marine species suffer heavy exploitation, which has been suggested to generate an Allee effect, and a reduced fertilization success at low densities [9,10,21–23]. Combined with reduced juvenile survival at low densities in cod and red sea urchins, these two species could suffer a triple Allee effect (Table 2). Desert bighorn sheep are subject to a component Allee effect resulting from higher predation by mountain lions *Felis concolor* in smaller groups because of lower vigilance [13]. This species is also likely to be subjected to the anthropogenic Allee effect, as its rarity makes it an especially valuable item for trophy hunters [12]; hunts for these animals are currently selling for US\$50 000 and over, per trophy.

Interactions between component Allee effects

How do the multiple Allee effects interact? Although there is currently no answer, an interaction is likely and potential consequences for the concerned populations are sufficient to warrant careful consideration by ecologists. Given that the most distinctive feature of (strong) Allee effects is the occurrence of an Allee threshold, we focus on the magnitude of the Allee threshold that results from the interacting component Allee effects.

It is difficult to imagine cases in which the combined effect of multiple Allee effects is less than that of any single Allee effect. Therefore, we propose that the overall Allee threshold is equal or greater than the largest of the individual Allee thresholds. Although any conclusive demonstration is so far lacking, two lines of evidence make us believe that Allee effects could interact, and that their interaction is far from inconsequential. Indirect evidence comes from the rare marsh gentian [14]. In this species, lowered fecundity caused by a pollen-limitation Allee effect had little influence on the population viability, whereas increased inbreeding in small populations had a small yet significant effect; a strong reduction in population viability was found when the two acted simultaneously.

More straightforward although theoretical support comes from a simple population model, which was developed to illustrate some of the possible outcomes of an interaction of two component Allee effects (Box 1). The outcomes of the model vary depending on parameter values determining the strength of the individual component Allee effects. To distinguish weak and strong interaction, the outcomes were classified according to whether the overall Allee threshold is higher or lower than the sum of the two individual Allee thresholds. We call these cases super-additive and subadditive Allee effects, respectively (the terms were borrowed from mathematics; note that super-additivity is in fact a synergistic interaction). Of special interest are the cases in which none of the single Allee effects are strong, yet the double Allee effect is strong; we then speak of dormant Allee effects. A dormant Allee effect also occurs when only one of the single Allee effects is

Box 1. Interaction of two Allee effects: a modelling study

How can two component Allee effects interact to produce an overall demographic Allee effect (Figure 1)? To illustrate some of the possible outcomes, we present a simple model of dynamics of a population that is subject to two component Allee effects, one linked to reproduction and the other to survival (Equation 1):

$$dN/dt = \sigma[1 - (1 - \theta)\exp(-\varepsilon N)]N - \delta(1 + N/K)N - \alpha N/(1 + \beta N) \quad [\text{Eqn 1}]$$

where N is population density. Divided by N , all terms are per capita, and the three terms on the right-hand side of Equation 1 represent, in sequence, positively density-dependent birth rate (mate-finding Allee effect), negatively density-dependent survival rate, and positively density-dependent survival rate owing to predation (predation-driven Allee effect). Positive constants $\theta < 1$ and ε define intensity of the mate-finding Allee effect, σ is the maximum birth rate, δ is the mortality rate at low densities and in the absence of the predation-driven Allee effect, $K > 0$ scales the carrying capacity of the population, and positive constants α and β scale the predation rate given by the type II

functional response (which implies positively density-dependent probability of an individual escaping predation). Because setting $\theta = 1$ and $\alpha = 0$ switches off the component Allee effect in reproduction and survival, respectively, we can assess the effects of both component Allee effects both in isolation and simultaneously.

A straightforward analysis of Equation 1 shows that the trivial steady state $N=0$ is unstable provided that $\delta + \alpha < \sigma\theta$, and locally stable if the opposite inequality holds. In the first case, there is one globally stable interior equilibrium corresponding to the carrying capacity of the population; the population is subject to a weak Allee effect provided that $\sigma(1 - \theta)\varepsilon - \delta/K + \alpha\beta > 0$, and there is no demographic Allee effect if < 0 . If the origin $N=0$ is locally stable, there can be either none or two interior equilibria depending on actual parameter values. In the first case, the origin is globally stable; in the second, the higher interior equilibrium is locally stable (carrying capacity) and the lower unstable (Allee threshold). There is no analytical expression that would distinguish these two cases in the parameter space, thus, one has to resort to numerical techniques.

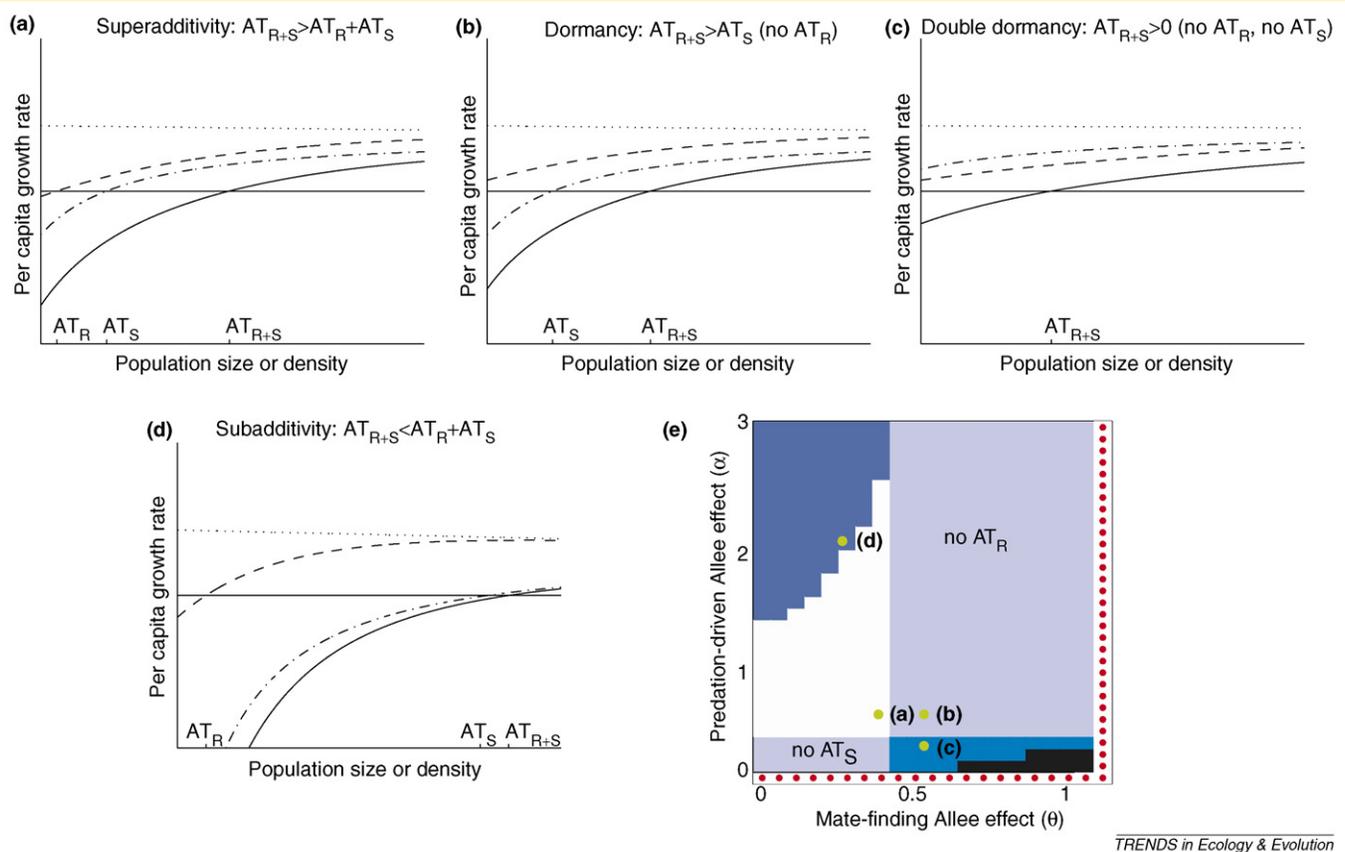


Figure 1. Distribution of patterns in a section of the parameter space of how two component Allee effects interact. The fixed parameters of $\sigma = 0.5$, $\varepsilon = 2$, $\delta = 0.2$, $K = 10$ and $\beta = 4$ were chosen to represent a wide spectrum of possible interaction outcomes. (a–d) demonstrate how the per capita population growth rate depends on population size or density in the vicinity of Allee thresholds corresponding to single and double Allee effects, for specific parameter combinations shown in (e); dotted line, no Allee effect; dashed line, Allee effect in reproduction; dash-dot line, Allee effect in survival; solid line, double Allee effect. AT_R , AT_S and AT_{R+S} represent the Allee threshold owing to Allee effects in reproduction, survival and both components, respectively. In (e), red dots represent the combinations where there is only either a single or no component Allee effect. Six different patterns of how the two Allee effects (predation driven and mate finding) interact were observed for the parameter values examined, four of which are of particular importance here [corresponding to (a–d)]: superadditivity (white), $AT_{R+S} > AT_R + AT_S$; dormancy (lighter blue), either no AT_R or no AT_S , $AT_{R+S} > AT_S$ or $AT_{R+S} > AT_R$; double dormancy (mid blue), neither AT_R nor AT_S , $AT_{R+S} > 0$; subadditivity (dark blue), $AT_{R+S} < AT_R + AT_S$. The remaining two patterns correspond to the cases where two weak Allee effects combine to produce a joint weak Allee effect, and where a weak Allee effect and a strong Allee effect combine such that the overall Allee threshold equals that of the strong Allee effect (black).

strong but the Allee threshold owing to the double Allee effect is higher than that of the single strong Allee effect. An implication of an occurrence of dormancy is that even a weak Allee effect represents a risk that should be accounted for: should another Allee effect occur, for example through human activities, it could cause the population

to go extinct much faster than would be expected from the disturbance alone.

Interactions in managed and exploited populations

We argue that management efforts can be optimized by considering multiple Allee effects, and can be negated by

overlooking them. The consequences of failure to recognize all component Allee effects will largely be determined by the way in which these Allee effects interact.

If only one component Allee effect is taken into account when two or more exist, the interaction of Allee effects can raise the overall Allee threshold to such an extent that conservation measures taken to cope with the recognized Allee effect will be inadequate. For example, introducing individuals so as to reach a given population size or density might prove insufficient if overlooked Allee effects raise the value of the extinction threshold. Mooring *et al.* [13] proposed the release of more than five individual desert bighorn sheep at any one time to overcome the Allee threshold owing to predation; however, managers might consider increasing this number to overcome safely its interaction with the anthropogenic Allee effect owing to trophy hunting [12]. As it is impossible to estimate accurately the Allee threshold from a given component Allee effect, and to fine-tune management around this value, management of populations with Allee effects should be risk averse.

To eradicate a pest population with a strong Allee effect, it is, in theory, sufficient to bring it below its Allee threshold [24]. The higher this extinction threshold, the less effort might be needed to achieve this goal. Several biocontrol strategies can artificially induce an Allee effect, by disrupting fertilization through the release of sterile males or sex pheromones (mate-finding Allee effect), by introducing a predator or parasitoid with a proper functional response (predation-driven Allee effect), or by removing individuals at a fixed rate (Allee effect owing to constant yield exploitation) [2,19,25]. If there were two or more Allee effects interacting in the pest population, the overall Allee threshold might disproportionately increase, and effort could be saved accordingly. Although to our knowledge there is currently no documented example in this field, the plausibility of this idea calls for investigations of the conditions under which multiple Allee effects could help optimize pest control.

Some exploitation strategies can themselves be a source of a component Allee effect, as explained earlier. If a natural Allee effect acts in the same population, the overall Allee threshold might increase owing to an interaction of the two, and there is a significant risk of overexploitation if that interaction is not recognized or if the Allee threshold owing to the natural Allee effect is considered the safety limit for the stock size. Even if eventually halted, exploitation can bring the population close to or even below the Allee threshold corresponding to the natural Allee effect. Several species of California abalones could be a typical example of stocks being unable to bounce back even after complete cessation of fishing, because of an unsuspected Allee effect acting in concert with overexploitation [22]. More than ten years after closing the fishery, it appears that an overlooked mating-related Allee effect (abalones as broadcast spawners need to exceed a critical density for an efficient fertilization [9,26]) might have combined with an anthropogenic Allee effect [12] to drive the population below the levels that were then considered safe for exploitation (Table 2).

Conclusions and future research

We show here that positive density dependence (Allee effect) in two or more fitness components might not be

uncommon and that consequences of multiple Allee effects for population dynamics can, in theory, be far from inconsequential. Multiple Allee effects occur by combining a variety of component Allee effects affecting reproduction and/or survival, in a range of taxa and habitats, and appear to interact so that the overall effect can be disproportionately large, relative to the effect of any single component Allee effect. We propose that multiple Allee effects cannot be disregarded whether managing threatened, pest, or exploited populations.

The challenge now is to demonstrate the prevalence and strength of these effects, both theoretically and empirically. We envisage three main avenues for further research. First, we call for a continued search for empirical evidence of multiple Allee effects, with particular emphasis on their interaction. Second, general-purpose population models with two or more component Allee effects should be developed and analysed. Third, specific population models of species listed in Table 2 could help reveal how component Allee effects interact in nature. This endeavour is especially important in systems where human activity has a significant role, if sustainable development and conserved biodiversity are to remain primary goals of conservation biology.

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References

- 1 Courchamp, F. *et al.* (1999) Inverse density dependence and the Allee effect. *Trends Ecol. Evol.* 14, 405–410
- 2 Stephens, P.A. and Sutherland, W.J. (1999) Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol. Evol.* 14, 401–405
- 3 Stephens, P.A. *et al.* (1999) What is the Allee effect? *Oikos* 87, 185–190
- 4 Kuussaari, M. *et al.* (1998) Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos* 82, 384–392
- 5 Levitan, D.R. (1991) Influence of body size and population density on fertilisation success and reproductive output in a free-spawning invertebrate. *Biol. Bull.* 181, 261–268
- 6 Boukal, D.S. and Berec, L. (2002) Single-species models of the Allee effect: extinction boundaries, sex ratios and mate encounters. *J. Theor. Biol.* 218, 375–394
- 7 Calvert, W.H. *et al.* (1979) Mortality of the Monarch butterfly (*Danaus plexippus* L.): avian predation at five overwintering sites in Mexico. *Science* 204, 847–851
- 8 Wells, H. *et al.* (1998) Mate location, population growth and species extinction. *Biol. Conserv.* 86, 317–324
- 9 Gascoigne, J.C. and Lipcius, R.N. (2004) Allee effects in marine systems. *Mar. Ecol. Prog. Ser.* 269, 49–59
- 10 Ramirez-Felix, E. and Manzo-Monroy, H.G. (2004) Modelling the use of two fishery assess rights, concessions and licences, in the red sea urchin, *Strongylocentrotus franciscanus* (Agassiz), fishery at Santo Tomás, Baja California, Mexico. *Cienc. Mar.* 30, 547–560
- 11 Bertness, M.D. and Grosholz, E. (1985) Population dynamics of the ribbed mussel, *Geukensia demissa*: the costs and benefits of an aggregated distribution. *Oecologia* 67, 192–204
- 12 Courchamp, F. *et al.* (2006) Rarity value and species extinction: the anthropogenic Allee effect. *PLoS Biol.* 4, e415, DOI: 10.1371/journal.pbio.0040415

- 13 Mooring, M.S. *et al.* (2004) Vigilance, predation risk, and the Allee effect in desert bighorn sheep. *J. Wildl. Manage.* 68, 519–532
- 14 Oostermeijer, J.G.B. (2000) Population viability analysis of the rare *Gentiana pneumonanthe*: importance of genetics, demography, and reproductive biology. In *Genetics, Demography and Viability of Fragmented Populations* (Young, A.G. and Clarke, G.M., eds), pp. 313–334. Cambridge University Press
- 15 Gardner, J. (2004) Winter flocking behaviour of speckled warblers and the Allee effect. *Biol. Conserv.* 118, 195–204
- 16 Courchamp, F. and Macdonald, D.W. (2001) Crucial importance of pack size in the African wild dog *Lycaon pictus*. *Anim. Conserv.* 4, 169–174
- 17 Ghazoul, J. (2005) Pollen and seed dispersal among dispersed plants. *Biol. Rev. Camb. Philos. Soc.* 80, 413–443
- 18 Gross, J.E. *et al.* (1993) Functional response of herbivores in food-concentrated patches: tests of a mechanical model. *Ecology* 74, 778–791
- 19 Hilborn, R. and Walters, C.J. (1992) *Quantitative Fisheries Stock Assessment. Choice, Dynamics and Uncertainty*, Chapman & Hall
- 20 Dulvy, N.K. *et al.* (2003) Extinction vulnerability in marine populations. *Fish. Fish.* 4, 25–64
- 21 Stoner, A.W. and Ray-Culp, M. (2000) Evidence for Allee effects in an over-harvested marine gastropod: density-dependent mating and egg production. *Mar. Ecol. Prog. Ser.* 202, 297–302
- 22 Hobday, A.J. *et al.* (2001) Over-exploitation of a broadcast spawning marine invertebrate: decline of the white abalone. *Rev. Fish Biol. Fisher.* 10, 493–514
- 23 Rowe, S. *et al.* (2004) Depensation, probability of fertilization, and the mating system of Atlantic cod (*Gadus morhua* L.). *ICES J. Mar. Sci.* 61, 1144–1150
- 24 Liebhold, A. and Bascompte, J. (2003) The Allee effect, stochastic dynamics and the eradication of alien species. *Ecol. Lett.* 6, 133–140
- 25 Gascoigne, J.C. and Lipcius, R.N. (2004) Allee effects driven by predation. *J. Appl. Ecol.* 41, 801–810
- 26 Babcock, R. and Keesing, J. (1999) Fertilization biology of the abalone *Haliotis laevis*: laboratory and field studies. *Can. J. Fish. Aquat. Sci.* 56, 1668–1678
- 27 Møller, A.P. and Legendre, S. (2001) Allee effect, sexual selection and demographic stochasticity. *Oikos* 92, 27–34
- 28 Stephens, P.A. *et al.* (2002) Model complexity and population predictions. The alpine marmot as a case study. *J. Anim. Ecol.* 71, 343–361
- 29 Berec, L. *et al.* (2001) Linking the Allee effect, sexual reproduction and temperature-dependent sex determination via spatial dynamics. *Am. Nat.* 157, 217–230
- 30 Crews, D. *et al.* (1986) Behavioural facilitation of reproduction in sexual and unisexual whiptail lizards. *Proc. Natl. Acad. Sci. U. S. A.* 83, 9547–9550
- 31 Vernon, J.G. (1995) Low reproductive output of isolated, self-fertilising snails: inbreeding depression or absence of social facilitation? *Proc. R. Soc. B* 259, 131–136
- 32 Davis, H.G. *et al.* (2004) Pollen limitation causes an Allee effect in a wind-pollinated invasive grass (*Spartina alterniflora*). *Proc. Natl. Acad. Sci. U. S. A.* 101, 13804–13807
- 33 Forsyth, S. (2003) Density-dependent seed set in the *Haleakala silversword*: evidence for an Allee effect. *Oecologia* 136, 551–557
- 34 Aukema, B.H. and Raffa, K.F. (2004) Does aggregation benefit bark beetles by diluting predation? Links between a group-colonisation strategy and the absence of emergent multiple predator effects. *Ecol. Entomol.* 29, 129–138
- 35 Clutton-Brock, T.H. *et al.* (1999) Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *J. Anim. Ecol.* 68, 672–683
- 36 Courchamp, F. *et al.* (2002) Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behav. Ecol.* 13, 20–27
- 37 Wittmer, H.U. *et al.* (2005) The role of predation in the decline and extirpation of woodland caribou. *Oecologia* 144, 257–267
- 38 Frank, K.T. and Brickman, D. (2000) Allee effects and compensatory population dynamics within a stock complex. *Can. J. Fish. Aquat. Sci.* 57, 513–517
- 39 Grünbaum, D. and Veit, R.R. (2003) Black-browed albatrosses foraging on Antarctic krill: density-dependence through local enhancement? *Ecology* 84, 3265–3275
- 40 Gascoigne, J.C. *et al.* (2005) Density dependence, spatial scale and patterning in sessile biota. *Oecologia* 145, 371–381
- 41 Wertheim, B. *et al.* (2002) Allee effect in larval resource exploitation in *Drosophila*: an interaction among density of adults, larvae, and micro-organisms. *Ecol. Entomol.* 27, 608–617
- 42 Walters, C. and Kitchell, J.F. (2001) Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Can. J. Fish. Aquat. Sci.* 58, 39–50
- 43 Fischer, M. *et al.* (2000) Genetic Allee effects on performance, plasticity and developmental stability in a clonal plant. *Ecol. Lett.* 3, 530–539
- 44 Willi, Y. *et al.* (2005) A threefold genetic Allee effect: population size affects cross-compatibility, inbreeding depression and drift load in the self-incompatible *Ranunculus reptans*. *Genetics* 169, 2255–2265
- 45 Avilés, L. and Tufiño, P. (1998) Colony size and individual fitness in the social spider *Anelosimus eximius*. *Am. Nat.* 152, 403–418
- 46 Serrano, D. *et al.* (2005) Colony size selection determines adult survival and dispersal preferences: Allee effects in a colonial bird. *Am. Nat.* 166, E22–E31
- 47 Cuthbert, R. (2002) The role of introduced mammals and inverse density-dependent predation in the conservation of Hutton's shearwater. *Biol. Conserv.* 108, 69–78
- 48 Stevens, M.A. and Boness, D.J. (2003) Influences of habitat features and human disturbance on use of breeding sites by a declining population of southern fur seals (*Arctocephalus australis*). *J. Zool.* 260, 145–152
- 49 Harcourt, R. (1992) Factors affecting early mortality in the South-American fur-seal (*Arctocephalus-australis*) in Peru – density-related effects and predation. *J. Zool.* 226, 259–270
- 50 Thompson, D. *et al.* (2005) The size and status of the population of southern sea lions *Otaria flavescens* in the Falkland Islands. *Biol. Conserv.* 121, 357–367

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