

Importance of the Allee effect for reintroductions¹

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Abstract: Many factors, both biotic and abiotic, impede the success of reintroductions. Among these is the difficulty that small populations have in surviving and thriving. For many species of animals and plants, populations at low density or of small size suffer from a weak or even a negative growth rate, either of which increases their extinction risk; this is called the Allee effect. As reintroductions are almost invariably characterized by small propagule sizes, the importance of the Allee effect must be considered in order to assess its potential impact on the probability of success in reintroductions. In this paper, we highlight the ubiquity of the Allee effect, the importance of this process as predicted by theoretical models, and its potential role in the failure of previous reintroduction attempts. We emphasize that although previous reintroduction programs have shown that release size is paramount to the success of reintroductions, no link has yet been formally demonstrated between Allee effects and reintroduction success. We encourage researchers in ecology to further investigate the role of the Allee effect on the probability of reintroduction success, using available data on comparable processes such as invasive species and the propagation of biological control agents where possible. We also urge biodiversity managers to consider this potential impediment to the survival, increase, and spread of small groups of reintroduced individuals in conservation programs.

Keywords: Allee effect, number released, propagule size, reintroductions.

Résumé : Parmi les facteurs qui limitent le succès des réintroductions se trouvent les difficultés à survivre et à se développer que rencontrent les populations en faibles effectifs. Pour de nombreuses espèces animales et végétales, les populations à faible densité ou de faible taille subissent un taux d'accroissement très faible, voire négatif, ce qui augmente leur risque d'extinction; ce processus est appelé effet Allee. Comme les réintroductions concernent presque invariablement des petits nombres d'individus, il est crucial de déterminer l'importance de l'effet Allee afin d'identifier son impact potentiel sur la probabilité de succès des réintroductions. Dans cet article, nous montrons l'omniprésence de l'effet Allee, l'importance de ce processus et enfin son rôle potentiel dans l'échec de réintroductions passées. Nous soulignons que malgré l'importance capitale, et désormais évidente, du nombre d'individus relâchés pour le succès des programmes de réintroductions, il n'existe pas encore de lien formel entre ces programmes et l'effet Allee. Il nous semble essentiel de poursuivre les efforts de recherche fondamentale en écologie pour caractériser le rôle de l'effet Allee dans la probabilité de succès des réintroductions. À cet égard, l'utilisation de données provenant de processus similaires, comme les invasions biologiques ou le contrôle biologique, peut s'avérer fructueuse. D'autre part, il est important que les gestionnaires de la biodiversité réalisent pleinement l'importance de la taille des groupes d'individus réintroduits pour le succès des programmes de conservation.

Mots-clés : effet Allee, nombre d'individus relâchés, réintroductions.

Nomenclature: Throughout, latin binomials are those used by the original authors.

Introduction

As population extinctions and the general loss of biodiversity throughout different biomes increase, ecosystem conservation and restoration is becoming a predominant concern in ecology. Reintroduction of species into habitat whence they have disappeared is an increasingly important tool in scientific wildlife management (Griffith *et al.*, 1989; Fischer & Lindenmayer, 2000). As is the case for most ecosystem management approaches, reintroductions are plagued with technical and ecological difficulties, a significant part of which are unexpected. These hindrances often generate failures (Griffith *et al.*, 1989; Fischer & Lindenmayer, 2000). Reintroduction programs may be economically costly, and failure is thus a waste of resources and efforts (Lindburg, 1992). Additionally, it can be difficult to argue that the experience gained from failed attempts

partly balances the economic loss, and negative outcomes often erode potential financial support for subsequent, better-designed programs (Freckleton, 2000). Finally, reintroduction failures may also be considered to be a waste of "valuable individuals", since these programs generally involve already reduced endangered populations or species. Consequently, it is important to determine the factors that are responsible for these program failures. As a result, the characterization of the ecological factors that facilitate or hinder establishment and spread of new populations is a major aim in applied ecology. One general aspect of population reintroduction programs concerns the relatively small number of individuals either remaining in the host ecosystem or available to be introduced in that ecosystem. Here we focus on one important aspect relative to the intrinsic dynamics of populations with small numbers of individuals: the Allee effect.

We very briefly redefine Allee effect and then highlight its potentially crucial importance for the survival of small, reintroduced populations. By reviewing empirical data on reintroduction, we highlight the potential role of this pro-

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cess in the failure of previous reintroduction attempts. We also show that the limited pool of available empirical data on the effect of propagule size on the success probability of a reintroduced population can be considerably expanded by taking advantage of the available data on comparable processes such as invasive species and propagating agents of biological control. We conclude by advocating an increase in studies on Allee effects as potential factors influencing the success probability of reintroductions. We also recommend that biodiversity managers take into account this process of population dynamics not only when designing and implementing reintroduction programs, but also when using restocking programs to tackle the consequence of Allee effects in declining populations.

Reintroductions and Allee effects

According to the Re-introduction Specialist Group of the IUCN, Species Survival Commission (Re-introduction Specialist Group, 1995), a reintroduction is any attempt to establish a species (or any other unambiguously defined lower taxonomic unit) in an area that was once part of its historical range, but from which it has been extirpated or become extinct. We will also use the term translocation (“deliberate and mediated movement of wild individuals or populations from one part of their range to another”; Re-introduction Specialist Group, 1995), which is often equivalent with respect to the process under consideration here. In general, reintroductions concern endangered populations, which implies a limited number of individuals available for reintroduction. Because of this shortage of individuals, the founder populations will be confronted by different dynamic problems typical of small populations or populations at low density, among which is the Allee effect.

In many species, individuals benefit from the presence of conspecifics. The level at which intraspecific competition exceeds the benefits of conspecific presence varies much between species. There is a growing realization that this level can be relatively high in many species. In fact, in some cases, this benefit can greatly outweigh the cost of intraspecific competition, meaning that individual fitness is reduced at low population size or density. This has been called the Allee effect, and it results in a decrease of the population growth rate at low size or density. Although it is difficult to disentangle Allee effects from stochasticity, one simple point is that Allee effects are processes that can—deterministically—produce increased extinction risks for small populations through reduced individual fitness at small population sizes. Depending on particular studies, the term “Allee effect” does not always have the same definition and often refers only to a restricted part of the larger phenomenon or encompasses processes independent of the Allee effect. Thus, it is worth reviewing the different existing kinds of Allee effects.

Different types of Allee effects

In an attempt to build a clarifying framework, Stephens, Sutherland and Freckleton (1999) introduced an important distinction. They distinguished the “component Allee effect”, a positive relationship between any component of individual fitness and either number or density of con-

specifics, from the “demographic Allee effect”, a positive relationship between density or population size and per capita growth rate, the latter phenomenon being the result of the sum of every component Allee effect and of negative density-dependence (due to intraspecific competition). A component Allee effect may thus exist without leading to a demographic one. Behavioural ecologists and conservation biologists, who often work on different scales, generally focus on only 1 of these 2 definitions, and care should be taken not to confuse them. It is likely that, when unspecified, Allee effects will often be component Allee effects for researchers and demographic Allee effects for biodiversity managers (Gascoigne & Lipcius, 2004).

Focusing implicitly on the “demographic Allee effect”, several authors additionally have distinguished variable strengths in the Allee effect (Brassil, 2001; Wang & Kot, 2001; Boukal & Berec, 2002). The Allee effect is described as “weak” when population growth is slowed down for small densities but not to the point of becoming negative and as “strong” when there is a density (size) threshold (where per capita growth rate becomes null) below which the population will decrease and probably go extinct (Figure 1). Although the distinction between weak and strong effect is important, most authors neglect the former and almost exclusively consider the strong Allee effect as if it were the only one. Also, it is important to realize that, as has been previously stated (Stephens, Sutherland & Freckleton, 1999), populations suffering from an Allee effect are not necessarily characterized by the existence of a threshold at low density. Such an error could lead to mistaking a demographic/component effect for a strong/weak Allee effect (e.g., Fowler & Ruxton, 2002). Figure 2 encapsulates the distinction between demographic/component and weak/strong Allee effects.

Biological processes behind the Allee effect

An Allee effect may be due to different biological processes. Three main phenomena are responsible: difficulty in

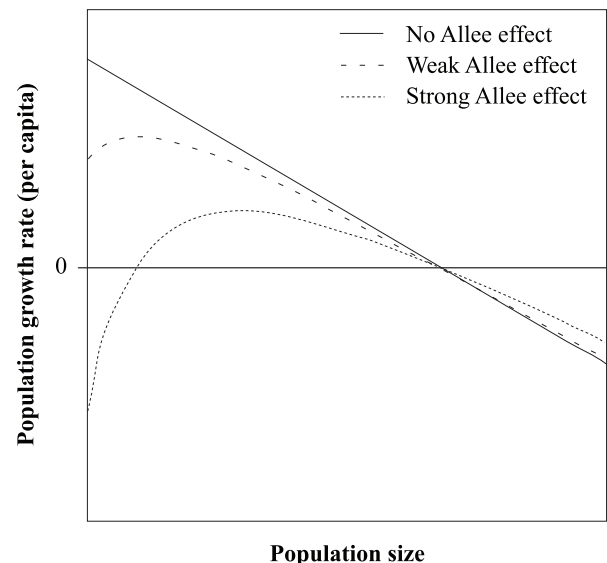


FIGURE 1. Comparison of per capita growth rates of populations with no Allee effect, weak Allee effect, and strong Allee effect.

sexual reproduction, lack of chemical or physical facilitation of necessary processes, and reduction of cooperative interactions in social species.

The most commonly cited cause of Allee effects is the decreased likelihood of encountering a reproductive partner at low density. This can be the case for species as different as insects and large mammals, for which receptive partners may be lacking in the accessible area during the reproduction period (Fauvergue, Hopper & Antolin, 1995; Wells *et al.*, 1998; Larkin *et al.*, 2002). A similar pattern appears in the low reproduction rate of water-spawning invertebrates, for which a minimum density of mixing gametes is needed for significant impregnation (Levitan & Young, 1995; Stoner & Ray-Culp, 2000; Baker & Tyler, 2001), and of flowering plants, for which a sufficiently large patch is needed to attract enough specialist pollinators or generalist pollinators with enough intraspecific pollen (Groom, 1998; Colas, Olivieri & Riba, 2001; Hackney & McGraw, 2001). Demographic stochasticity that induces a highly biased sex-ratio thus contributes to this kind of Allee effect. The mechanism for an Allee effect in some animals might be related to high levels of male–male aggression and/or male harassment of females when there are relatively few mature females in the population, especially if the sex ratio is in favour of males. This has been suggested as a cause of concern for the Arabian Oryx, *Oryx leucoryx* (P. Seddon, pers. comm.). Saltz, Rowen, and Rubenstein (2000) show that at larger densities male territories become smaller and females associate with more males, thus increasing the ratio of breeding males to females, which could result in a genetic-based Allee effect. Plants or animals that have evolved mechanisms to avoid inbreeding among close relatives may have developed several methods for restricting mate choice, which may lead to a lack of acceptable mates if fragmentation of habitats becomes serious (Tainaka & Itoh, 1996). More generally, it has been suggested that sexual selection, in particular female mate preferences, could be a previously neglected component that gives rise to an Allee effect (Sorci, Møller & Clobert, 1998; Møller & Legendre, 2001).

The second general process contributing to an Allee effect, namely the lack of improved habitat that would

normally be induced by the presence of sufficiently large numbers of conspecifics, was historically one of the first suggested causes of the Allee effect. Here again, there are examples for organisms as different as plants and mammals. This facilitation may be chemical, as in the case of the hemlock *Tsuga heterophylla*, which is less able to acidify soil and sequester water in the upper soil when at lower density (Ferson & Burgman, 1990). It may also be physical: hibernating individuals may benefit from social thermoregulation, as in the case of alpine marmots (Stephens *et al.*, 2002).

Thirdly, a decrease in group size necessarily induces a reduction of social interactions. In some populations, individuals cooperate to protect the group from predators, develop anti-predator vigilance, and/or carry out collective aggression. For example, predation risk is directly linked to individual vigilance in desert bighorn sheep (*Ovis canadensis*), and as a result, predation by mountain lion (*Felis concolor*) is higher in smaller groups, with groups of < 5 individuals subject to the greatest predation risk (Mooring *et al.*, 2004). In species where social interactions are particularly important such as cooperative species, some individuals (helpers) may be devoted to nest or pup guarding and to feeding the offspring of other members of the group. They may also regroup or split tasks when hunting or defending resources. In these cases, the number of adults plays a key role in the survival and growth of the population and the Allee effect can be very significant (Courchamp, Grenfell & Clutton-Brock, 1999b). Other, more specific or less common biological processes may lead to an Allee effect, such as strong natural selection acting on habitat choice in ecological traps (Kokko & Sutherland, 2001) or high dispersal levels, which quickly lower density of new populations (Fagan, 1999; South & Kenward, 2001). Note that as specified by Stephens and Sutherland, consequences of demographic stochasticity should not be considered as Allee effects unless they reduce a component of individual fitness (Stephens & Sutherland, 1999).

Unequivocal field (or laboratory) evidence of the Allee effect remains rare, as it is difficult to demonstrate and characterize dynamic processes in small populations. Therefore, studies on the Allee effect are mostly theoretical. Yet, theoretical studies of Allee effects produce important results. For instance, the Allee effect may be important for the persistence of a population becoming established at a given site (Dennis, 1989; Veit & Lewis, 1996; Grevstad, 1999), when this population must face interactions with other species in the community (competition, predation, parasitism) (Amarasekare, 1998; Wang, Liang & Wang, 1999; Courchamp, Grenfell & Clutton-Brock, 2000; Etienne *et al.*, 2002; Ferdy & Molofsky, 2002; Deredé & Courchamp, 2006), and when it spreads spatially (*e.g.*, Kot, Lewis & vandenDriessche, 1996; Amarasekare, 1998; Gyllenberg, Hemminki & Tammaru, 1999; Keitt, Lewis & Holt, 2001; South & Kenward, 2001; Cantrell & Cosner, 2002; Ferdy & Molofsky, 2002). In all these stages of population development, the Allee effect appears to either slow down or block further progress. As these situations constitute the 3 main stages in the dynamics of an establishing population (Hastings, 1996; Shea & Chesson, 2002), the Allee effect is likely to affect the success of reintroductions at all stages.

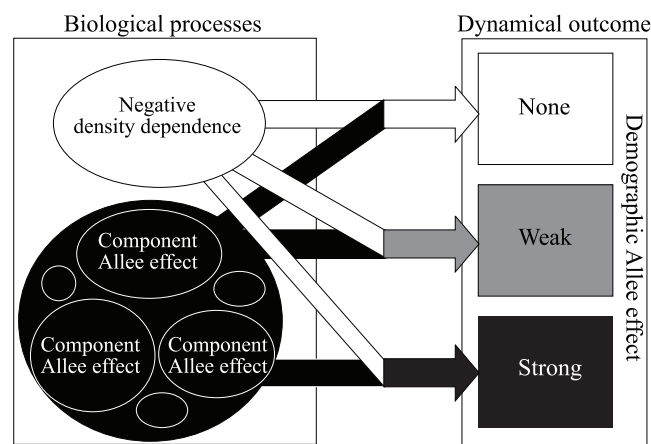


FIGURE 2. Representation of the different types of Allee effects. Component Allee effects in conjunction with classical negative density dependence may lead to demographic Allee effects.

Another type of theoretical study is of great importance for reintroduction studies: those using models applied to concrete cases. Although potentially very informative, these studies are still extremely scarce (but see Tenhumberg *et al.*, 2004). However, most information on the link between reintroduction and release sizes is currently provided by empirical evidence.

Importance of release sizes and numbers for reintroductions: Evidence from experience

Although the definition of success is not always clear (Seddon, 1999; Fischer & Lindenmayer, 2000), in general most reintroduction programs have low success rates, despite an over-emphasis on successful reintroductions in the published literature (Kleiman, 1989; Wolf *et al.*, 1996; Fischer & Lindenmayer, 2000). Comprehensive reviews have reported low overall success rates of bird and mammal translocations (44%) and considerably lower rates for reptiles and amphibians (19%) (Griffith *et al.*, 1989; Dodd & Seigel, 1991). The success rate of Australian macropod (Marsupialia) reintroductions was 11% on the mainland and 60% on islands (Short *et al.*, 1992). Because these programs can be very expensive (Lindburg, 1992; Fischer & Lindenmayer, 2000), there is an urgent need to determine the causes of failure. Several studies have therefore focused on finding correlates to reintroduction success and/or failure (Griffith *et al.*, 1989; Wolf *et al.*, 1996; Wolf, Garland & Griffith, 1998; Fischer & Lindenmayer, 2000). From these studies, many factors have been shown to influence reintroduction success: there are ecological factors, such as habitat quality, genetics, predation, competition, and impregnation consequences, and non-ecological factors, including public relations and education, good team management, socio-economic factors, legal considerations and litigation costs, and the length of time committed to the reintroduction project (see references in Fischer & Lindenmayer, 2000). Among these factors, one has often been correlated with a higher probability of introduction success: the number of release events and the number of individuals per release (Griffith *et al.*, 1989; Hopper & Roush, 1993).

Some species are less prone to extinction at small population sizes, especially when the habitat is particularly favourable (*e.g.*, closed islands), and thus initial number of animals released is not always related to persistence in reintroductions of these species. This is the case, for example, for saddlebacks (*Philesturnus carunculatus*) and robins (*Petroica australis*) (Taylor, Jamieson & Armstrong, 2005). Yet, the number of animals released is one of the most important parameters predicting reintroduction success probability. When studied, the number of released animals was more important in determining the probability of success than the number of release events (Wolf *et al.*, 1996), and the total number of animals released was a consistent predictor of reintroduction success irrespective of analytical technique (Griffith *et al.*, 1989; Wolf *et al.*, 1996; Wolf, Garland & Griffith, 1998). For example, in a review of 180 case studies, Fischer and Lindenmayer found that releasing more than 100 animals led to higher chance of reintroduction success (Fischer & Lindenmayer, 2000). In another comprehensive review, Griffith *et al.* (1989) found that

successful translocations released more animals relative to unsuccessful translocations (160 compared to 54) and suggested a plateau at releases of 80 to 120 individuals for birds and 20 to 40 individuals for large native game mammals. Releases of a greater number of individuals significantly increased the establishment success of birds introduced to Australia (Newsome & Noble, 1986) and New Zealand (Veltman, Nee & Crawley, 1996; Green, 1997), of birds introduced in Europe (unpubl. data, cited in Ebenhard, 1991), and of a variety of mammals and birds translocated in Pacific countries (Griffith *et al.*, 1989). In comprehensive reviews on single taxa, a larger number of individuals released has been shown to favourably influence reintroduction success for carnivores (Breitenmoser *et al.*, 2001), ungulates (Komers & Curman, 2000), and diurnal raptors (Cade, 2000) (see Figure 3).

It is not the aim of the present paper to review all reintroduction programs with respect to the effect of release number and size; the extent of the current published literature precludes it. Suffice to say, it is increasingly recognized by scientists and conservation managers alike that a substantial number of individuals must be introduced in order to obtain a good chance of success in the long term (McCarthy, 1994). Although this is partly due to various other factors, the mean number of animals released per project (Wolf *et al.*, 1996) has increased over the past 2 decades (for example, the median number of animals translocated increased from 31.5 in 1987 [Griffith *et al.*, 1989] to 50.5 six years later [Wolf *et al.*, 1996]), which may illustrate a growing awareness. Yet, much remains to be done to highlight the importance of release size in reintroduction programs even nowadays. Current guidelines for reintroducing endangered species into the wild fail to mention explicitly the importance of release size or numbers (Kleiman, 1989; Stanley Price, 1991; Re-introduction Specialist Group, 1995).

Causative link with the Allee effect

One obvious question is whether the reported positive correlation between number of individuals released and release success is a demonstration of a causative effect. It is clear that the data are generally insufficient to allow a direct test of this, especially because the available syntheses fail to provide details of the number of times and sites at which the stated numbers of animals were released. For example, since releases of large numbers usually take place at more sites and in more years than small releases, the perceived correlation could be due simply to a greater chance of at least 1 founding population encountering, by chance, places or years with favourable conditions for population growth (Green, 1997). In addition, a likely bias in correlating success with population size may come from the fact that people generally release fewer animals in situations where the reintroduction is anticipated to fail (D. Armstrong, pers. comm.). One good example, however, is the 30-y study of 21 translocations of the vulnerable black-faced impala (*Aepyceros melampus petersi*) in Namibia, which demonstrated not only that initial population size was paramount to the success of those translocations, but also that it was probably linked to a predation-driven Allee effect: in the

presence of cheetah, small translocated populations were significantly less likely to be viable than larger populations (Matson, Goldizen & Jarman, 2004). This led to clear recommendations regarding reintroduction strategies: introducing large initial populations, ideally more than 15 animals, should be more efficient than attempting to eliminate cheetah following translocations of impalas (Matson, Goldizen & Jarman, 2004). Nevertheless, given the current paucity of data to show otherwise, we must consider the likely pos-

sibility of a direct causative link between numbers of individuals released and reintroduction success.

Next is the question of whether the observed importance of release size is an indication of an acting Allee effect. There is a strong theoretical basis for linking the number of individuals involved in the establishment of a new population and the success of this establishment. There are also numerous pieces of evidence from empirical studies on successful and unsuccessful introductions of insects, birds, and mammals (Forsyth & Duncan, 2001 and references therein). In particular, it is unambiguous that the likelihood of population extinction from random catastrophes and demographic and environmental stochasticity is inversely related to population size (Leigh, 1981; Lande, 1993; 1998). In addition, the Allee effect has been shown to play an important role in small population extinctions (Dennis, 1989; Courchamp, Clutton-Brock & Grenfell, 1999a; Stephens & Sutherland, 1999).

A correlation between reintroduction success and number released is however insufficient to infer an Allee effect. Such a correlation could also be attributed to demographic stochasticity or to confounding factors, and it is often impossible to disentangle both types of processes once a population has disappeared. Yet, as the Allee effect has a catastrophic impact on many small populations and as reintroduction programs are often characterized by low availability of individuals to be released, one should always assess the likelihood of this process affecting the species to be reintroduced. The Allee effect is potentially significant for a wide range of species (probably to some degree for all sexually reproducing species); since small releases were more often unsuccessful, the Allee effect might have played a major role in past reintroduction failures.

Mention of Allee effects is almost absent from the reintroduction literature, however. In addition to the above example of the black-faced impala, another example concerns study of management strategies for the Arabian Oryx in Saudi Arabia (Treydte *et al.*, 2001). The authors found evidence of a possible Allee effect when analyzing birth-rate data from 10 y of records. At low population size (< 100 individuals) females showed a low individual birth rate; the birth rate increased at medium population size and then declined at high population size. Because it was a single population monitored over time, there may have been other influences as well, such as variations in annual rainfall. However, the plot of birth rate against population density was best described by a quadratic equation typical of an Allee effect. Probably because releases of oryx were made over a number of years and the initial founder population was thus supplemented, the consequences of any Allee effect were not critical (P. Seddon, pers. comm.).

Yet, there are indications that some other authors have found evidence of Allee effects in reintroduced populations, although they did not identify them as such. For example, Griffith *et al.* (1989) showed that there is an asymptotic relationship between the number of animals released and the probability of success. This relationship is consistent with the existence of a critical population size below which extinction (or establishment failure) is likely.

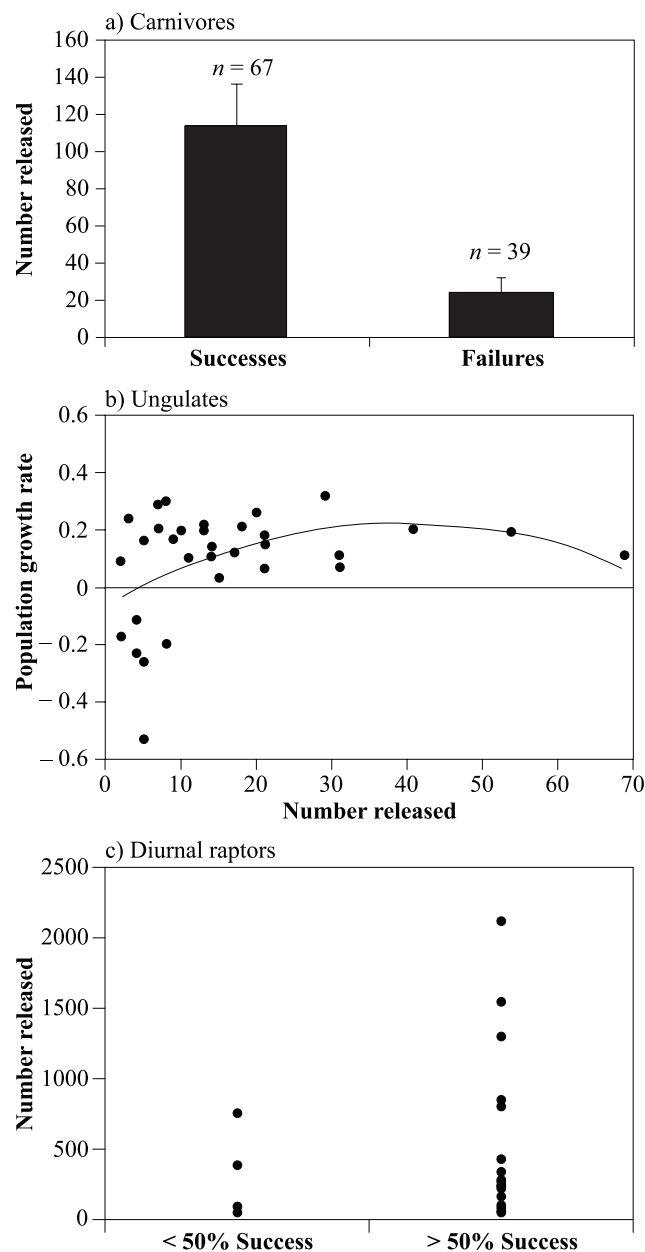


FIGURE 3. Relationships between the number of individuals released and release success for programs concerning carnivores (a), ungulates (b) and diurnal raptors (c). Release success is measured in terms of appreciation of success/failure by the authors of the review (a), population growth rate (b), and as appreciation of percentage of success by the authors of the review (c), respectively. In the last case, we arbitrarily divided the programs between those with higher and those with lower than 50% success. Data from Breitenmoser *et al.*, 2001 (a), Komers & Curman, 2000 (b), and Cade, 2000 (c).

Discussion

INCREASING NUMBERS OF REINTRODUCTION PROGRAMS

The suite of conservation options is limited. Thus, despite the major drawbacks of reintroduction programs (they are expensive, time intensive, and logistically complex), reintroduction remains a commonly used and potentially powerful instrument for the conservation of biodiversity. Its use is very likely to increase in the future, as local populations decline and species become extinct in the wild. The growing interest in reintroduction programs by biodiversity managers is well illustrated by the increase in the total number of reintroduction programs over the past decades (Griffith *et al.*, 1989; Wolf *et al.*, 1996).

It has long been advocated that conservation biology should develop a theoretical framework (Caughley, 1994), and although this is now generally accepted, much remains to be done in subdivisions of this ecological field, for example in population reintroductions. In this context, the small-population paradigm in conservation biology has failed to meet the needs of conservation managers for scientifically based guidelines. Unlike the similar dilemma over the use of a single large or several small nature reserves (SLOSS), the release size issue has only recently received some theoretical interest (Grevstad, 1999). There are still no theoretical rules for deciding the release number and size for population reintroductions, the majority of which are based on trial and error and on non-scientific considerations such as logistic reality.

The general lack of scientifically based guidelines for reintroduction programs may in fact have a simple explana-

tion. The increasing impact of humans on ecosystems and species, and the resulting augmented loss of biodiversity, has led to an increase in studies concerning two domains: processes implied in extinction (dynamics of small populations) and restoration actions for extirpated populations (reintroductions). In both domains, the current level of attention is recent and represents an explosive increase over the last decade (Figure 4). The lack of interaction between the 2 areas of study is surely due to the newness of the interest in them, and to the common falsehood that one cannot start theorizing on a subject before it is sufficiently well known. In addition, the alarming threats faced by some populations have forced urgent actions that may not have been driven by scientific considerations. However, it is striking to see the continuing lack of overlap between "reintroduction" and "Allee effect" articles, despite the existence of nearly 1000 publications in the scientific literature in one domain or the other (ISI Web of Science, September 2006).

IMPLEMENTING RELEASE STRATEGIES FOR REINTRODUCTIONS

We advocate not only that future reintroduction programs be based on progressive results in ecological research, but also that scientific studies on reintroductions take full advantage of the growing number of available results to analyze factors likely to influence the success probability and in turn to set up scientifically based guidelines for new reintroductions. We begin by giving some recommendations concerning the Allee effect. It is usually suggested that release size be as large as possible in order to increase chances of population establishment. However, because the number of individuals to be released is often low, it is in

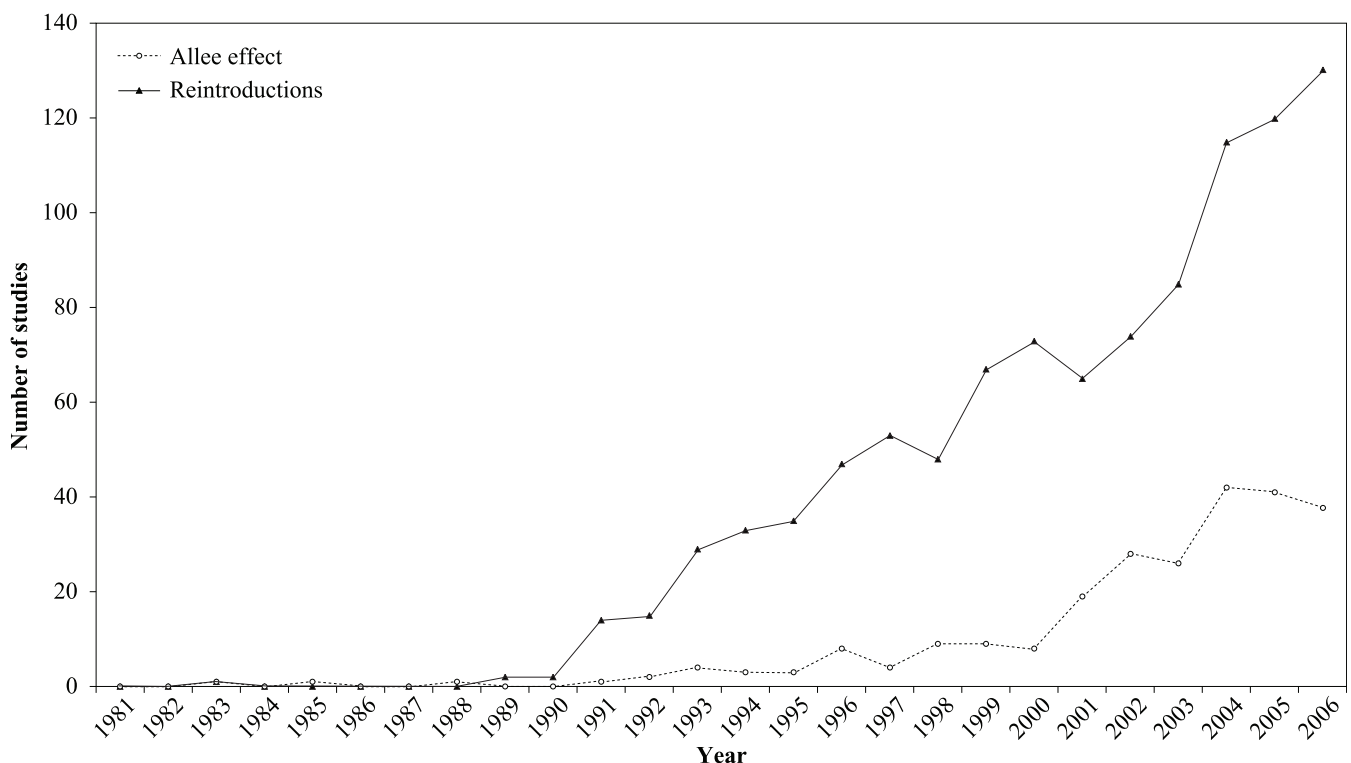


FIGURE 4. Comparison of the incidence over time of the use of "Reintroduction" and "Allee effect" in the title, abstract or keywords in the scientific literature, from *ISI Web of Science*, September 2006. The exponential-like increase in use of both keywords highlights the recent interest in both study domains. Yet, of the nearly 1000 publications shown here, not a single one mentioned both keywords.

general impossible to make releases both large and numerous. This raises an obvious question: how should the available release stock be divided up?

WHAT IS A LARGE RELEASE SIZE?

A simple answer would be to make as many releases as possible provided each release event is sufficiently large to prevent any Allee effect. But this simple answer leads to another obvious question: What is a sufficiently large release size?

When one goes back to published literature on this point, the question remains unanswered. In several papers, reintroduction success has been related to numbers of animal released. For example, releasing more than 100 animals led to higher chance of success (Fischer & Lindenmayer, 2000). However, in this case, the animals studied were diverse, including mammals, birds, amphibians, reptiles, and invertebrates, and it seems that the choice of 100 for the analysis was based more on our decimal system than on the species studied. At more precise taxonomic levels, attempts to set thresholds have been limited to the advice that release size may be important, without providing precise quantification (surely the intention of the cited authors). It has been shown that releases of more than 100 individuals led to success in 83% of bird species surveyed, compared with only 35% when releases were smaller (Green, 1997). But, surely, releasing 100 Seychelles warblers is not the same as releasing 100 bearded vultures. Hopper and Roush (1993) mention a critical release size of 100–1000 insects, which is more realistic, but less precise. There is of course a trade-off between admitting that minimum successful release size may vary within a specific taxonomic level and the reduced application benefits if the range of values is too wide.

Comparison of ungulate and bird introductions suggests that taxa vary with regard to the minimum number of individuals required for introductions to have a high chance of success (Forsyth & Duncan, 2001). Similarly, once the other variables are controlled for, translocated mammals were more likely to establish than translocated birds (Griffith *et al.*, 1989; Wolf *et al.*, 1996). In fact, propagule sizes leading to successful colonization have been shown to vary greatly according to species (see Berggren, 2001 and references therein). It seems clear that different species have different life history traits, behaviour, and resulting dynamics (as do different populations of the same species) and therefore different susceptibilities to Allee effects (and other related processes). Therefore, setting thresholds at 100 or 500 individuals is meaningless, unless these thresholds are applied to precise taxonomic levels or ecological functional groups (see Figure 3). Even then, generalizations may lead to important errors. For example, a study on dichromatic birds showed that reintroduction of highly sexually selected species requires a much larger number of individuals released (Sorci, Møller & Clobert, 1998) than less sexually selected monochromatic bird species, because strong sexual selection may exacerbate an Allee effect (as effective mate encounter will be lower than actual mate encounter; Sorci, Møller & Clobert, 1998; Møller & Legendre, 2001). In addition, reintroduced animals can have lower reproduction and survival in the first year(s) follow-

ing translocation (Novellie *et al.*, 1996; Armstrong & Ewen, 2001), thereby increasing the risk of Allee effects, and some species could be more sensitive than others to translocation stress (see also Letty *et al.*, 2003). Moreover, in many cases, the majority of animals in failed reintroductions either died shortly after release or dispersed away from the release site (D. Armstrong, pers. comm.), meaning the effective propagule size was much lower than the actual number released, low enough to easily lose populations through demographic stochasticity or to Allee effects. For animal species with strong dispersal tendencies, there may be an increased probability that the released animals will suffer from an Allee effect (Fagan, 1999; South & Kenward, 2001).

Each species thus needs to be assessed separately for susceptibility to demographic and genetic weaknesses at small population size, in order to optimize the size and number of releases. Matson, Goldizen, and Jarman (2004) proposed that groups of more than 15 black-faced impalas be released, while Mooring *et al.* (2004) suggested not releasing fewer than 10 male and 10 female desert bighorn sheep. In addition, as discussed by Wolf, Garland, and Griffith (1998), determination of some minimum viable number of animals for release will depend on the unique circumstances of each translocation. Thus, it appears that the question is not well formulated: one should ask instead “what is a sufficiently large release size for the species we are concerned with in the specific context of our reintroduction program”? One way to answer this question is to conduct release trials with different release sizes, keeping all other things equal, and then to assess establishment “success” (Berggren, 2001; Letty *et al.*, 2003). One problem with characterizing a program as a success, however, is that the definition is limited in time, and therefore what may be a success within 5 y may not remain so after a few more years (Seddon, 1999). Another problem is the risk of “wasting” valuable individuals through such trials. In both regards, mathematical models would certainly be useful tools to help answer this question.

SPREADING THE RISK, OR NOT?

It has been suggested that releasing all available individuals at the same time is not the best strategy as it precludes spreading the risk among several releases. It is even possible that releases at multiple sites or at different times would provide a better chance of success (J. Clobert & R. Ferrière, unpubl. data). Veltman, Nee, and Crawley (1996) found that successful species had been introduced to significantly more localities. It is possible that these multiple releases encounter a good rate of success because this approach increases the chance that at least one release will meet favourable conditions for population establishment. In addition, animals from early releases may act as a cue for animals of later releases, enabling them to establish a home range faster (Dolev *et al.*, 2002). This is important because if home range establishment affects reproductive success, the results may falsely appear as an Allee effect.

Spreading releases across time or across space can be advantageous for several reasons, but both decrease the chance of establishment if there is an Allee effect. In this case, spreading the releases does not amount to spreading

the risk, but rather to increasing it: as the availability of the individuals may not be extended at will, it implies making smaller releases. Grevstad (1999) showed that the best strategy for “classical populations” (as many releases as possible) is the opposite of that for populations with an Allee effect (releases as large as possible) and that in the presence of an Allee effect, environmental variability can doom larger releases as well as rescue smaller ones. He argues that appropriate release strategies are much more important for populations with an Allee effect, since ignoring such effects not only decreases success probability but can make the difference between certain success and certain failure. Similarly, spatial separation may decrease the chances of reintroduction success, as shown for the helmeted honeyeater (McCarthy, 1994).

Once again, the lack of studies on the relationship between release size and the outcome of the release precludes any definitive conclusions on the best strategy to adopt in any given case. In particular, it is unfortunate that studies describing reintroduction failures are exceedingly difficult to publish, as this eliminates the possibility of analyzing the impact of various factors on reintroduction success probability. We think such analyses are extremely important and would contribute to an increase in the success of reintroduction programs. At the present time, we suggest that these analyses be conducted on data from studies in neighbouring disciplines, 2 of which are richer in available data on similar processes.

ALTERNATIVE WAYS TO STUDY THE IMPORTANCE OF RELEASE SIZE

One of the neighbouring fields of research in ecology concerns biological invasions. This domain studies the establishment and spread of populations in ecosystems from which their congeners are absent. The main difference from reintroductions is that the species in question is systematically put into ecosystems outside its normal historico-geographical range. In both cases, the species are introduced by people (sometimes more tenaciously for biological invasions than the average reintroduction program) and must pass through the different phases of population survival, establishment, growth, and spread, often from relatively low numbers. Because biological invasions are numerous, widespread, increasingly well documented, and have occurred sometimes decades or centuries ago, they provide an excellent opportunity to complement analyses on reintroductions. For example, one may examine the proportion of exotic species deliberately introduced by humans to a new area that have become established (Veltman, Nee & Crawley, 1996; Green, 1997; Cassey, 2001; Forsyth & Duncan, 2001; Cassey *et al.*, 2003). As the samples of introduced species can be large and the time elapsed since the introductions can be long, there is a greater opportunity to assess long-term persistence (Green, 1997).

A study on the relative success of exotic ungulate and bird introductions to New Zealand showed that both were strongly linked to number of individuals introduced (Forsyth & Duncan, 2001). The initial population size, measured as the number of releases and the initial number of propagules liberated in New Zealand, significantly increased the probability of successfully establishing bird

populations (Veltman, Nee & Crawley, 1996). Despite a wide range of bird taxa analyzed and the crude estimates of the number of birds released during the introductions in New Zealand, Green (1997) found a clear positive effect of the number of birds released on the probability of successful establishment, whether across all species or only within families. Overall, 83% of species released in large numbers (> 100 individuals) became established, compared with only 35% when fewer than 100 birds were released (Green, 1997). He also provided a discussion of the issue, citing other published examples of the effect of propagule size on the success of population establishment (Green, 1997). More recent theoretical studies aiming to investigate the impact of Allee effect on invasion success through modeling (Drake, 2004; Leung, Drake & Lodge, 2004; Taylor & Hastings, 2005) may also provide precious information in the context of reintroductions.

The second domain of ecology where past experience can help in reintroduction programs is biological control (or biocontrol). Biological control can be defined as the intentional introduction of individuals with the aim of reducing or eliminating their competitors or prey; in general, it concerns invertebrates. Biological control too can be regarded as a process similar to reintroduction, with the important difference that, as for biological invasions, the topic benefits from a large array of published literature, in particular from the perspective of correlates of establishment and propagation success. We suggest that, in the context of the relative paucity of data regarding the causes of reintroduction failure, this convenient parallel could be used to increase the available knowledge on population persistence and spread, with probable beneficial effects on our understanding of how to optimize reintroductions.

For example, until recently, there were no theoretical rules for deciding the release number and size for biological control (Grevstad, 1999). The recent progress on this point in biological control (Shea & Possingham, 2000) should provide new impetus to the effort to elaborate a theoretical framework for population reintroductions.

ALLEE EFFECT AND RESTOCKING

Similarly, follow-up translocations (*i.e.*, when the release is staggered into 2 or more occasions) lack criteria with a clear logical basis (Armstrong & Ewen, 2001). Follow-up translocations have been correlated with higher probability of success, probably in part because dividing the release facilitates a test of the fit between the habitat and the released individuals before all the individuals are released (Griffith *et al.*, 1989). However, one must first clearly assess the potential problems linked with small release size before deciding whether or not to release more available individuals. On the other hand, the asymptotic nature of the relationship associated with the better success of longer translocation programs suggests that the minimum number of animals may be released over several years if insufficient animals are available for a single release (Griffith *et al.*, 1989). In addition, if few individuals are available for the first release, follow-up releases can be a good way to reinforce newly established populations, especially since data can be obtained about the first released individuals that will

facilitate improvement of the protocols used in subsequent releases. Augmentations (or restocking) can similarly benefit from spreading the release over several years.

Unlike re-establishment reintroductions, augmentation reintroductions aim to boost genetic and demographic support for wild populations that are on the brink of extinction (Lindburg, 1992). It is noteworthy that both follow-up and augmentation releases have the potential to counter the adverse dynamic and genetic effects of low population size or density, including the Allee effect.

ALTERNATIVE MEASURES TO REDUCE THE IMPACT OF ALLEE EFFECTS IN REINTRODUCTIONS

Manipulating the number of released individuals is the main way to counteract the consequences of Allee effects. However, that is not always possible. Fortunately, other means to limit Allee effects and prevent the drawbacks of small release size are possible. Depending on the biological processes involved in the Allee effect, it may be effective to work on improving the composition of the release propagules or the environment where reintroduction takes place. Indeed when a sufficient stock of individuals is available, the composition of the group deserves careful consideration. If the Allee effect is linked to rarity of mating events, favouring such events is crucial. In some cases, the release of already fertilized females may limit this type of Allee effect. In other cases, the sex ratio of the propagule must be chosen according to the reproduction system of the species in order to optimize the chance of reproduction opportunities. Released individuals must also be chosen to maximize the likelihood of mating events. In species where sexual selection is important, introducing individuals known to be attractive should favour release success. For species where genetic distance between partners is crucial (incompatibility system), introducing related individuals may contribute to program failure, whereas for species where genetically close partners are more attractive it would enhance reintroduction success. If the Allee effect is related to social behaviour in cooperative species, the individuals must be chosen to favour group cohesion. For instance, it may be more successful to introduce genetically related individuals to ensure group formation than to choose genetically distant individuals, despite the advantages of higher genetic diversity.

Momentarily modifying the environment may also enhance reintroduction. In the case of zoophilous or entomophilous plant species, regular introduction of pollinators or dispersers may help to avoid a reproduction-related Allee effect. For Allee effects linked to a paucity of facilitation, artificial initial physical enhancement of the environment may provide a counterbalance. If the Allee effect is related to predation, a reduction of the predator population may help the establishment of the propagule until it has passed the critical size.

A first stage of penning on the release site could help to prevent dispersion of individuals and reduce Allee effects (Stephens & Sutherland, 1999). Releasing females first could enable them to establish territories before males are released, thus reducing male dispersion and Allee effects related to mate finding, as reported in brush-tailed phascogales (*Phascogale tapoatafa*) (Soderquist, 1994).

Obviously, many of these proposed measures (not an exhaustive list) would have been taken regardless of Allee effects; nonetheless, taking into account the phenomenon may modify perceptions of the advantages and drawbacks of these measures and change the final release protocol.

Conclusion

Reintroductions are an increasingly used tool in conservation biology, but there is still a distressingly large number of failures in reintroduction programs. Such failures have been conspicuously correlated with the number of individual released, and there is little doubt now among practitioners that increasing the number of individuals to be reintroduced can increase the likelihood of population establishment in numerous species.

Despite the low success rate of reintroduction programs, conservation researchers have failed to provide practitioners with a scientific framework with which to increase success, in particular concerning guidelines relating to release size. Fundamental research on small or founding populations is, however, becoming of greater interest to ecologists, notably with respect to the Allee effect. The diversity of biological processes giving rise to Allee effects contributes to making the phenomenon ubiquitous in small populations, and theoretical studies underline the potential impact of this dynamic process. Despite the fact that the role of Allee effects has rarely been studied and explicitly demonstrated in reintroduction failures, it appears that such effects may play a substantial role in the outcome of reintroductions.

It is thus crucial to determine the threat posed by the Allee effect in current and future reintroduction programs and therefore to assess the role it has played in past failures. We see 2 complementary ways to proceed: (1) study the biology of the species of concern to assess the risk of an Allee effect and (2) check for the importance of small release sizes in past programs involving similar species. It is clear from the literature that published results are biased towards success, as failures are more rarely reported. This precludes a formal statistical analysis of the importance of release size on the probability of success of reintroductions. However, we think that if such data could be compiled by scientists or managers having access to information on past reintroduction programs, for instance in the grey literature, great progress could be made towards clarifying the consequences of release size in given taxonomic groups. Widening these analyses to datasets from biological invasions and biological control attempts would be invaluable in enlarging the information pool.

If Allee effects are suspected to have an influence on reintroduction projects of particular species and the importance of release size has been unequivocally linked to past reintroduction failures for this species, then managers can begin to adopt specific strategies of release, focused on increasing population size or density. Meanwhile, as definitive evidence and robust scientific guidelines are both currently lacking, caution is required, and in particular we suggest that the Allee effect be critically assessed in current and future reintroduction programs.

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