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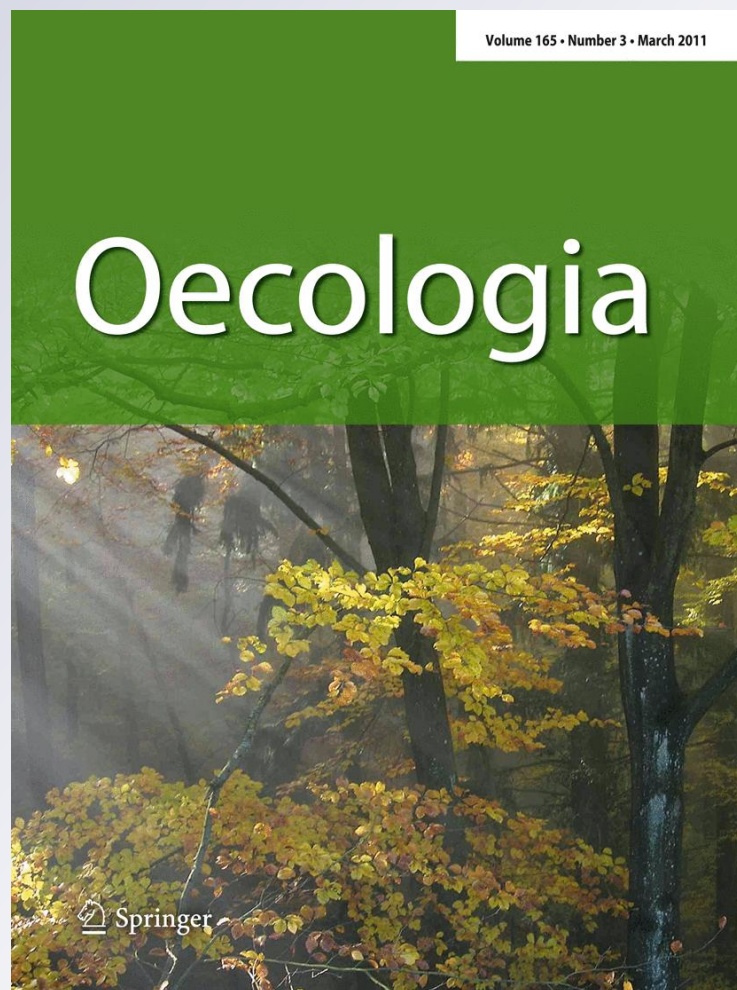
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Consequences of local Allee effects in spatially structured populations

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Abstract The ideal free distribution model incorporating the Allee effect was published by Fretwell and Lucas (1970), but went almost unnoticed within the ecological literature. The model is relevant to populations distributed among patchy habitats. It predicts a sporadic but substantial decline in populations at high densities, which in turn induces the rapid growth of new populations. In this paper, I show that the simple process explained by this model can be used to change our view of several phenomena within the field of population ecology, behavioural ecology and conservation. The ecological consequences of the model are well known. A key feature of Fretwell and Lucas's model is what I call the "Allee paradox:" there is a range of local population densities at which local individual fitness is less than the potential mean gain that could be obtained in the environment; however, individuals cannot disperse. This paradox can be used to explain why helping appears before suitable breeding areas are fully occupied, and why breeding females aggregate when male coercion is a reproductive cost. The model also predicts high clustering between related populations, and, in conservation biology, it can identify unfounded concerns about the dangers of extinction, delays in recolonisation processes after human-induced population decline, and latency periods in the initial phases of expansion of invasive species.

Keywords Growth rate · Breeding system · Cooperation · Extinction risk · Dispersion pattern

Introduction

The Allee effect refers to an increasing per capita growth rate with density at low densities (Courchamp et al. 2008). Numerous mechanisms have been reported to explain this effect, such as a decline in reproductive opportunities. In populations lacking the Allee effect, per capita growth rates decrease monotonically with density and there is one equilibrium point at which the population reaches carrying capacity (Fig. 1a). In populations experiencing the Allee effect, growth rates increase at low densities, then decline due to competitive interactions (Fig. 1b). This can result in a dynamic system with two carrying capacity (K) values, the first one being unstable. The lower K is critical; below this, growth is negative and the population or group is likely to become extinct (Courchamp et al. 1999). Therefore, $n = 0$ is a stable equilibrium point.

Several authors have applied Allee effect models to spatially structured subpopulations, based on metapopulation theory (Levins 1969). For example, Harding and McNamara (2002) presented a unifying framework for the Levins model via appropriate modification of the two basic functions of colonization and extinction rates. They incorporated several realistic biological processes, including the Allee effect.

In this paper, I address the question of the ecological consequences of the local Allee effect when populations (or subpopulations) are patchily distributed. I use an approach provided by game theory (Maynard Smith 1982). The relevance of the conceptual model of ideal free distribution (IFD) incorporating the local Allee effect (Fretwell and

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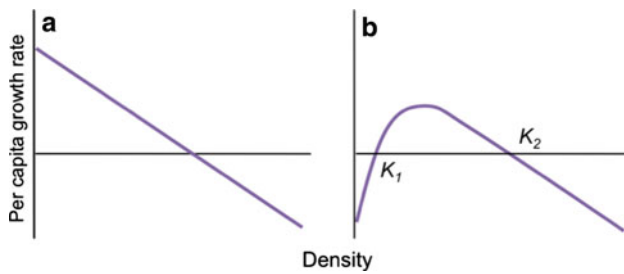


Fig. 1 Classical representations of the relationship between population growth rate and population density. **a** Without the Allee effect there is a continuous decrease in growth with density and only one stable equilibrium point when $r = 0$. **b** With the Allee effect, the function adopts an inverted U shape. As density increases, social benefits and other mechanisms improve growth until a maximal point is reached and growth begins to decrease due to intraspecific competition

Lucas 1970) has previously been highlighted by other authors (Greene and Stamps 2001; Morris 2002). In this paper I expand the description of some of its consequences and predictions for behavioural ecology, metapopulation dispersion patterns, and conservation biology.

The ecological literature uses terms such as “habitat” and “habitat selection” with different meanings, so it is best to define them explicitly. I use the definitions provided by Morris (2002). “Habitats” are spatially bounded subsets of physical and biotic conditions among which the population density of a focal species varies from other adjacent subsets. “Habitat selection” is the process whereby individuals preferentially use, or occupy, a nonrandom set of available habitats. These definitions connect habitat choice with population processes. IFD models can be applied at several ecological scales depending on the species and environments under study. Rosenzweig (1981), Sutherland (1996) and Doncaster (2000) developed IFD models that integrate across scales, ranging from foraging patches to communities.

Costs and benefits of habitat use

Ideal free distribution theory (IFD) is a game theory set of models about population distribution (Brown 1998). It is based on the assumption that animals choose patches of habitat that provide the maximum payoff in terms of individual fitness. At low densities, individuals congregate in the best initial habitats. However, intraspecific competition reduces the quality of the patch as the density of conspecifics increases (Fig. 2a). At equilibrium, the simplest ideal free model predicts that population abundance in different patches will match resource availability (Fretwell and Lucas 1970).

However, animal aggregations do not only involve social costs and resource competition. There may also be

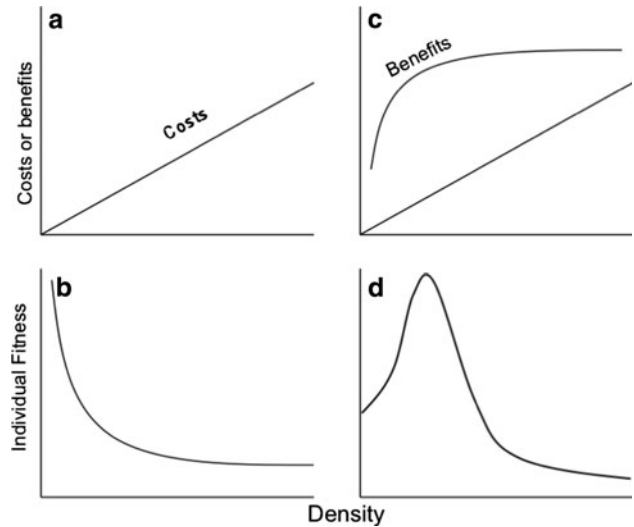


Fig. 2 Relationships between density and costs, benefits and individual fitness in populations without (**a**, **b**) and with (**c**, **d**) Allee effects (modified from Stephens et al. 1999)

benefits. A simple one is the reduction in predation risk due to the dilution effect (Hamilton 1971). Being a member of an aggregation reduces the chances of being attacked, as others are also potential prey. Such benefits of grouping (including breeding systems) have been important topics of research in behavioural ecology (Ruxton 2005). Figure 2c shows a schematic representation of the costs and benefits of population aggregations, and Fig. 2d demonstrates how the classical shape of the interference function (Fig. 2b) is altered by the Allee effect (Stephens et al. 1999).

Habitat occupancy process in a space with good and bad habitats

I describe a hypothetical example of the process of formation of two populations in an environment that contains two habitat types in a matrix of unsuitable habitat (Fig. 3). Patch I has a higher initial quality than patch II (Fig. 3a). According to IFD, the first individuals occupy the best patch (Fig. 3b). When the first population reaches 19 individuals (Fig. 3c), the patch types match in terms of quality, so the next animal that enters the system will be the founder of patch II. Due to the Allee effect, the entrance of that animal slightly improves patch quality such that it will be advantageous for another animal of the original population to migrate to the new one. A positive feedback loop results in rapid migration from I to II (Fig. 3d). This phenomenon continues until the qualities of the two habitat patches match again (Fig. 3e). From this point, both habitats are equally occupied (Fig. 3f).

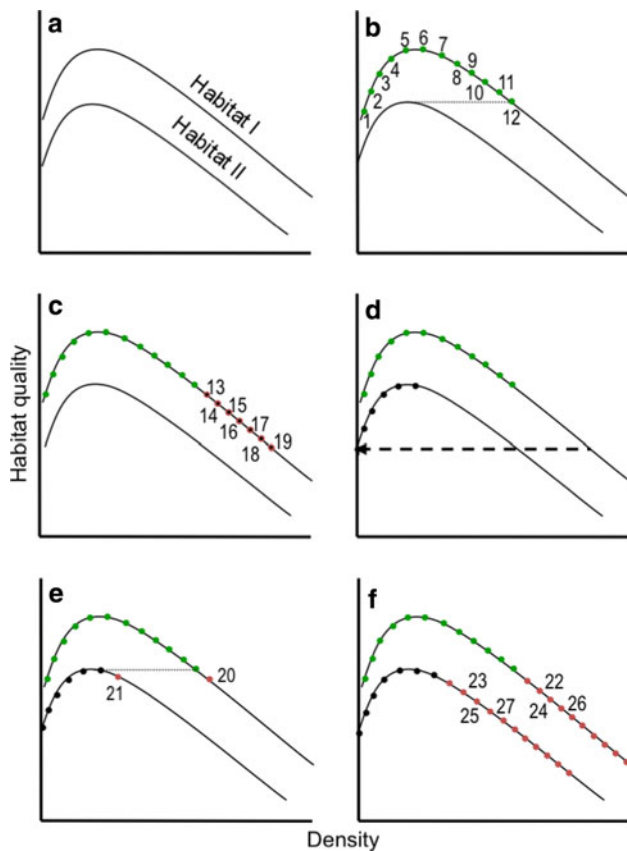


Fig. 3 Relationship between patch quality and local population density (modified from Bernstein et al. 1991a). **a** Two patches are represented; patch I has higher quality than II. **b** The process of colonization is initiated when the first individuals found a new population in the original best patch; when abundance reaches 12 individuals, the quality of the best patch matches the maximal possible quality of the poor one. **c** When the population reaches 12 individuals, the quality of the original good patch matches the initial quality of the poor one. **d, e** A migration process occurs from patch I to II until the quality of the original poor patch reaches its maximum. **f** Both colonies are equally occupied

A key feature of Fretwell and Lucas's model is what I call the "Allee paradox" (Bernstein et al. 1991a; Greene and Stamps 2001). There is a range of local population densities at which local individual fitness is less than the potential mean gain that could be obtained in the environment; however, individuals cannot disperse. They must "wait" until the density reaches the point at which their fitness (or "mean individual fitness") drops to a value that is less than the value for one individual in the new patch. In the example in Fig. 3, when the density in the original good patch reaches 18 individuals, the mean fitness is lower than if they distribute more homogeneously, e.g. 13 individuals in the good patch and 5 individuals in the poor one.

When the spatial dimension is incorporated, the most important result is that local densities in habitats shift suddenly as a function of overall population size. When patch quality in an initially good habitat approaches the

quality of an empty initially bad one, a very small increase in population size may result in a very large change in the distribution of individuals. Under the conditions of this model, species following Allee's principle may demonstrate erratic changes in distribution with small changes in the population (Fretwell and Lucas 1970).

Morris (2002) designed an explicit game model of habitat selection under the Allee effect. Morris's model searches for the solution in density space to the evolutionarily stable strategy of habitat selection. Morris showed how the instability generated by the Allee effect that I described graphically in Fig. 3 creates a hiatus or "hole" in abundance along habitat isodars (regressions of density between paired habitats when fitness is equalised between habitats). The presence of an Allee effect can easily be detected by comparing the exact probabilities of the observed frequency of data points in the hiatus area with those expected if fitness is positively density dependent at low density (Morris 2002). I recommend Morris's work for those interested in an explicit model on this subject and for the analysis of the ecological consequences of the Allee effect. Below I describe the concepts and ideas concerning the several roles that the Allee effect may have in a diverse range of disciplines such as behaviour, dispersal patterns and conservation.

Behavioural consequences

Evolutionary ecology of cooperative breeding

Cooperative breeding is a breeding system in which more than one pair of individuals shows parent-like behaviour towards the young of a single nest or brood. The evolution of this system has frequently been explained using the "habitat saturation" hypothesis (Emlen 1991). According to this, opportunities for independent breeding are limited because of the low availability of suitable breeding sites. Subordinate or inexperienced reproducers thus gain more by helping than by dispersing to poor patches. Several tests of this hypothesis failed because helping appears before suitable breeding areas are fully occupied (Komdeur 1992). Fretwell and Lucas's model can help to understand this result.

The evolution of cooperative breeding can usually be divided into two complementary processes: the decision to stay in the natal unit and the decision to help (Hatchwell and Komdeur 2000). In other words, delayed dispersal is a prerequisite for helping behaviour in most cooperative breeding systems. The "Allee paradox" is a possible context for delayed dispersal, and thus for the evolution of helping. Consider a population with the benefit of group formation and without territorial defence. The most plausi-

ble and frequent example is increased predator detection or foraging efficiency in winter flocks (e.g. Gardner 2004). At the beginning of the breeding season, breeding individuals can obtain the benefit of, for example, predation vigilance by other group members. As the breeding season progresses and breeder density increases, scramble competition causes individual fitness to decrease due to overexploitation of breeding resources. When the density reaches the values at which the Allee paradox operates (Fig. 3c), the new individuals that try to reproduce will do it poorly, but at the same time they will be prevented from leaving the group due to the Allee paradox. Under this context, helping behaviour can become a means of achieving individual fitness while remaining in the group. Thus, under the Allee paradox, helping is expected to improve the fitness of some individuals even though empty patches are available in the environment.

This hypothesis regarding the evolutionary process of cooperative breeding produces different predictions depending on the original benefit associated with group formation. If antipredation defence during the nonbreeding season is the origin of the positive trend between fitness and density, helping is expected to have evolved in species that live in open environments where group vigilance provides a clear advantage. A comparative analysis of South African birds by DuPlessis et al. (1995) found that regular cooperative breeding species live in open savannah habitats where predation pressure favours group living and where food supplies during the non-breeding season never fall below a baseline level.

Male coercion and the evolutionary ecology of mammalian mating systems

Because most mammalian systems of social organization ultimately depend on female dispersion (Davies 1991), the study of habitat selection by breeding females can help to understand the ecology of mammalian mating systems. Fretwell and Lucas's model can be used to explain female aggregations (harems, territories or leks) in mammals (Cassini 2000). Male harassment has been postulated as a major social factor influencing female movements and mate selection, ultimately affecting the evolution of mammalian mating systems (Bartholomew 1970; Clutton-Brock et al. 1992). Fretwell and Lucas's model can be applied to female habitat selection during breeding seasons, with (1) the probability of offspring survival as currency, (2) the increase in female–female competition for resources required for breeding as the cost of increasing density, and (3) a reduction in male coercion as the benefit. The model predicts that male coercion forces females to form denser aggregations than expected based on the distribution of resources alone, because a reduction in male harassment

compensates for the increase in female competition. The formal development of a model of habitat selection by breeding females under male coercion can be found in Cassini (2000).

Cassini (1999), Cassini and Fernández-Juricic (2003) and Cappozzo et al. (2008) tested the predictions of this model in pinnipeds. The order Pinnipedia is the only mammalian group that shows a combination of marine feeding and terrestrial breeding (Bartholomew 1970). The behaviour of colonial pinnipeds is consistent with the expectations of an IFD model incorporating the Allee effect, and evidence supports the advantage of female gregariousness in reducing the reproductive costs of interacting with males.

Dispersion consequences: population clustering

In spatially structured populations experiencing the Allee effect, solitary immigrants are expected to reach empty patches; however, they fail to produce a population due to the susceptibility to extinction produced by the Allee effect. When a source population reaches its threshold density, the emigration process starts and the nearby empty patch is rapidly occupied, provided a minimum-sized founder group simultaneously reaches the patch. The new population grows quickly due to this high immigration rate. Sink populations are formed when individual fitness in the source population is low due to density-dependent effects. The initial fitness in new populations is low but it should rapidly increase when density increases due to the arrival of new immigrants.

IFD assumes that animals are free to move between habitats. However, dispersal has costs and constraints (Bernstein et al. 1991b; Åström 1994; Kennedy and Gray 1997), so distant habitat patches are harder to reach than close ones. In addition, the random probability of finding a distant patch is lower. Therefore, when a new population (in habitat II in Figs. 3 and 4) is established from a founder population (from habitat I in the figures), the probability of the success of the colonisation process depends on the distance of dispersal. Close habitat patches have a greater chance of being occupied than distant patches of equal type. The slope of the relationship between the probability of a population forming and the distance to the source population depends on the ability of the species to move across the environment.

Thus, when the distance between source and sink habitat patches is small, the probability that several dispersers will meet in the same patch of habitat is relatively high, but it decreases with distance at a rate higher than expected by random. The expected consequence of this process is that sink populations are formed near the founder populations and show a clumped distribution. At the geographical level,

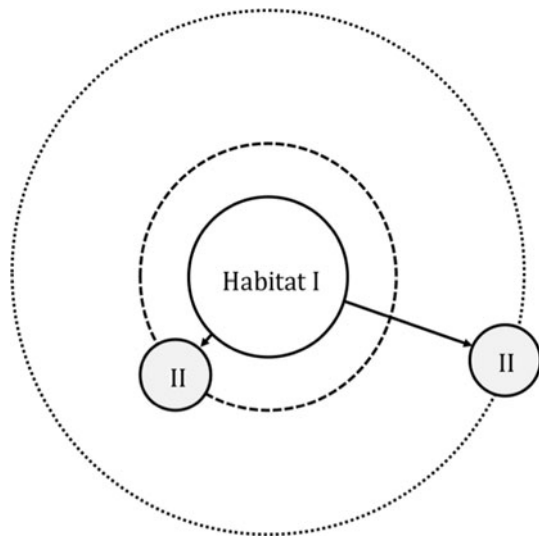


Fig. 4 Schematic representation of the formation of a new population in habitat II from a founder population located in habitat I at different distances

populations experiencing the Allee effect are expected to show a tendency to form clusters of populations within their range.

An interspecific comparison of dispersal distances and geographical patterns between social and solitary species in the same taxonomic group provides an opportunity to test this prediction of the high level of clustering produced by the Allee effect. For example, Cockburn (2003) analysed clades of oscine passerines from northern New Guinea in relation to social system and revealed an excellent negative correlation between cooperative breeding and dispersal ability.

Conservation consequences

Apparent tendency to extinction

The Allee effect has been extensively applied to the extinction of species that are low in numbers due to human influence (Courchamp et al. 2008). Fretwell and Lucas's model predicts substantial local population decay that is, paradoxically, the symptom of overall population recovery. Thus, substantial reductions in population density do not necessarily translate into concerns about conservation. There are two methods for distinguishing between a trend towards local extinction and Fretwell and Lucas's type of local population decrease. Since in the latter case emigration is the main cause of the decay, other symptoms in demographic parameters such as birth rates and fecundity are not expected. It is also recommended that neighbouring populations and empty patches of habitat are monitored for possible population growth in patches that receive the immigrants.

Delay in recolonisation

For species that have suffered strong impacts due to human exploitation and have been reduced to small and isolated populations, the recovery of the original distribution can be slow when they are under the Allee effect, even when the surviving local population can grow healthy under conservation protection plans. The reason is that recolonisation is expected to occur patch by patch, with the nearest patches first. In contrast, solitary species can have relatively low local population numbers due, for example, to territorial behaviour; however, they will probably show a faster pattern of recolonisation.

Latency period in the initial expansion of an invasive species

The prediction made for invasions regarding latency effects is well documented and standard for invading populations (see the review by Taylor and Hastings 2005). For a similar reason to that described above, the first population of an invasive species experiencing the Allee effect should require a relatively long period of time to start producing dispersers. The initial new populations should be close to the source population. However, if the species is a successful invader with a large reproductive capacity, an accelerated process of expansion is expected, as each new population that is formed is, at the same time, capable of producing new groups of colonisers.

Conclusions

In recent times, widespread evidence has been found for the Allee effect (Courchamp et al. 2008). However, most of this is related to negative effects at low population densities. Here, I emphasise the consequences when populations are spatially structured. These consequences have been largely ignored despite the early publication of Fretwell and Lucas's model, and subsequent publications by Bernstein et al. (1991a), Greene and Stamps (2001) and Morris (2002). Fretwell and Lucas's model generates predictions that are substantially different from the expectations produced by models for single populations or for metapopulations using Levin's approach.

Future tests of this model will require metapopulation studies in which several populations are followed and growth curves, dispersal, social behaviour and genetic flow are simultaneously estimated. Interspecific comparison is an additional method that could be used to test its predictions. For example, related species that differ in social behaviour could be compared, i.e. species with different Allee effect intensities. Such empirical efforts will be

worthwhile given the power of Fretwell and Lucas's model in producing new, unconventional predictions for a wide variety of disciplines such as population ecology, behavioural ecology and conservation biology.

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