

Mate-location failure, the Allee effect, and the establishment of invading populations

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In recent years, increased global trade and travel have provided potent invasion pathways for ever-increasing numbers of alien species. Although many species from distant parts of the world have increased productivity and taken on critical roles in agriculture, horticulture, forestry, and aquacultural industries, many other alien species have had serious deleterious effects on these same industries as well as on human health (Pimentel et al. 2000). Additionally, invasions by many non-indigenous species are known to negatively affect important ecological processes and properties in a variety of natural ecosystems (Mack et al. 2000; McNeely et al. 2001).

The immense impacts of invading species provide ample motivation for undertaking measures to prevent more species from establishing. Though prevention of the arrival of new species is often a desirable option, it may not always be possible to shut down all invasion pathways (Lodge et al. 2006). In cases where a newly arrived population is considered to pose a considerable risk, there may be justification to attempt eradication, i.e., the total elimination of a species over a given area. Large-scale eradication programs are often complex, involving both government agencies and public stakeholders (Myers et al. 1998). Eradication is much more likely to be successful if it is carried out in the early phase of an invasion rather than after a species has been present for an extended period

(Wittenberg and Cock 2001). Given the difficulty of eradication as well its critical importance, it is vital that the population processes operating during the invasion process be understood and considered when formulating a strategy for achieving eradication (Liebhold and Tobin 2008).

Perhaps the single most important population process that affects establishment success is the Allee effect, which refers to the phenomenon of increasing per capita population growth with increasing density (Taylor and Hastings 2005; Courchamp et al. 2008). The concept of the Allee effect is not new: it originates from observations made by Warder Allee in the 1930s that survival and reproduction are often limited by a lack of conspecifics, and that this can lead to population decline at low densities (Allee 1931). This effect, probably one of the most exciting concepts in ecology, was long neglected but more recently re-discovered because of its profound implications for a variety of problems. Although Allee's concept was first resurrected by conservation biologists because they recognized its importance to the persistence of rare and endangered species (e.g., Lande 1987; Dennis 1989), applied ecologists eventually began to realize that the Allee effect has important implications for both the establishment and eradication of invasive alien species (Hopper and Roush 1993; Yoshimura et al. 1999; Liebhold and Bascombe 2003).

Several factors are known to cause the Allee effect in low-density populations: these include the absence of cooperation (e.g., cooperative feeding), genetic inbreeding, and predator satiation. However, the most prevalent cause of Allee dynamics is the failure of mates to locate each other at low population densities (Courchamp et al. 1999; Taylor and Hastings 2005). At low densities, populations may likely decline because of mate-location failure, but as populations increase, growth rates increase as individuals

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more easily encounter mates. The Allee effect may be intensified by the spatial isolation of founding individuals (Berec et al. 2001) and by temporal asynchrony in the development of the two sexes (Calabrese and Fagan 2004; Robinet et al. 2007). There are many other factors that may affect the strength of the Allee effect arising from mate-location failure, and this is a very active area of research.

Given the many recent important advances in understanding the role of the Allee effect in invading populations, we present here a special issue entitled “Mate-location failure, the Allee effect, and the establishment of invading populations”. We invited nine papers that encompass a range of approaches, including reviews of precedent works, empirical investigations of natural systems, theoretical inquiries of new scientific hypotheses, and practical explorations of strategies for managing invasions. Two papers provide overviews of the ubiquity of the Allee effect among populations of various types of organisms. Kramer et al. (2009) address the prevalence of the effect among different animal taxa by comparing empirical results provided in 75 papers. They find evidence for demographic Allee effects in nearly all taxa for which data are available. Furthermore, they find that these demographic Allee effects arise most frequently from mate limitation in invertebrate populations, and from predator–prey interactions in vertebrate populations. Another overview of the prevalence of the Allee effect is provided by Gascoigne et al. (2009) who approach their synthesis from an evolutionary standpoint. They conclude that evolution may act to diminish the frequency of mate-location failure through selection either for more efficient mate-finding mechanisms or for behaviors, such as aggregation, that avoid low densities. They hypothesize that, as a result of this evolutionary pressure, component Allee effects due to mate-location failure may not be common in natural systems.

Three groups contribute empirical evidence of component and demographic Allee effects in specific populations. Tobin et al. (2009) review the literature on the Allee effect arising from mate-location failure in gypsy moth populations. This is a system in which the population biology is understood relatively well and which has been extensively monitored for decades in North America. As such it provides an exceptional opportunity for observing the Allee effect in field populations and understanding the effect on invasion success. Fauvergue and Hopper (2009) took a novel approach to investigate the existence of the Allee effect caused by mate-location failure by observing the consequences of intentional introductions of a parasitoid wasp, *Aphelinus asychis*, as a biological control. Contrasting two population sizes, high and low densities, they concluded that there was a significant demographic Allee effect in wasp populations. However, they also found that

wasps did not suffer from a mate-finding Allee effect. They proposed that a number of behavioral and life-history features of many parasitoids (e.g., a haplo-diploid sex determination mechanism) could protect them from mate-finding Allee effects. Though his study was not based on observation of a natural system, Takasu (2009) gained considerable insight into the system of pine wilt disease in Japan by applying an individual-based model. The disease is caused by a nematode, which is vectored by the Japanese pine sawyer beetle. He showed that an Allee effect can arise in beetle dynamics as a result of the necessity of beetles to make contact with a pine tree at least twice in order to successfully reproduce.

Two theoretical studies make important contributions to rather general aspects of the Allee effect. Sato (2009) constructs a spatially explicit metapopulation model in which immigrants only colonize from the nearest neighboring patches. His ecologically meaningful model indicates that the entire metapopulation does not have an Allee threshold for initial population size even if each local population is influenced by the Allee effect. In addition, he finds that the metapopulation extinction threshold becomes lower than that estimated by the standard and classic metapopulation model of Levins (1969). As many invasive species characteristically colonize patchy host resources in the field, his findings have important implications for managing such species. Takimoto (2009) constructs a stochastic differential equation of an invasive species with the Allee effect. Using this tractable but biologically realistic model, he explores which indicator will have the most diagnostic value for a sudden shift from low to high population levels. He finds that the standard deviation of population abundance during a period of low abundance is a useful predictor of an impending demographic upsurge.

To elucidate direct countermeasures against invasive species, Yamanaka and Liebhold (2009) utilized a spatially implicit modeling approach which they applied to three different eradication strategies: mass-trapping, mating-disruption, and sterile male release. Using their generalized mechanistic approach, it was possible for them to quantify the impact of these strategies on the mate-finding Allee effect and to compare the effectiveness of the different approaches for eradication of insects with varying life history traits. Boukal and Berec (2009) also explored implications of the interaction between the Allee effect and anthropogenic intervention (i.e., pest-control) using a series of simple differential equations. They concluded that, in many situations, by combining two or more management strategies, invasive species can be more easily eliminated than by applying only a single strategy.

By facilitating this special issue, we aim to improve the general understanding of process operating during the early

establishment phase of biological invasions. Some pessimistic ecologists may complain that there has been little progress in our ability to identify general ‘rules’ that govern the processes of invasion that have practical predictive value, despite 40 years of study (Bright 1998). We, however, feel that current theories on the Allee effect provide useful insight into practical strategies for managing invasions, but applied information also provides some insight into basic theories. We intend for this special issue to not only promote a deeper understanding of the mechanisms operating during biological invasions, but also to evoke new ideas for future theoretical efforts and empirical investigations of invasions and their management.

Cover photo descriptions

1 (upper left): a gypsy moth male. Tobin et al. (2009) review the invasion of gypsy moth in North America. Photo by Louis-Michel Nageleisen, Département de la Santé des Forêts, Bugwood.org. 2 (upper right): The first fabled Allee effect: the fate of humanity hangs in the balance as Adam and Eve search for each other in the sparsest of populations. Illustration credit: Mike Blackburn. 3 (lower left): the photo shows the parasitoid wasp *Aphelinus asychis* Walker (Hymenoptera: Aphelinidae) ovipositing in the Russian wheat aphid *Diuraphis noxia* (Modvilko) (Hemiptera: Aphididae). *Aphelinus asychis* was introduced during the 1990s in the United States for the biological control of *D. noxia*, a major pest on small grains (wheat, barley, etc.). Fauvergue and Hopper (2009) analyzed these introductions, mate-finding behavior, and the dynamics of small introduced populations. 4 (lower right): the green anole (*Anolis carolinensis*) preying on an endemic cicada (*Meimuna boninensis*) of the Ogasawara Islands, Japan. Photo courtesy of Mitsuhiro Toda, Japan Wildlife Research Center.

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