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Allee effects in ecology and evolution

G. Kiran Kumar

Dept. of Mathematics,
Dr. B.R. Ambedkar University, Srikakulam, Etcherla -532 410, AP, India

Abstract: *Allee effects influence the spatial pattern of pest out- breaks through cooperative behaviour. Pine beetles aggregate in order to overwhelm host defences and analyse data from three western U.S. foreststo show how this behaviour leads to a power-law distribution of outbreak patches on the landscape. They provide a mechanistic explanation for spread patterns in west- ernmountainpine beetle out breaks and results in faster spread than would a passively dispersing beetle. In effect, the dispersal behaviour of the beetles overcomes fitness effects of the Allee effect that would slow or stop spread. This pattern may help explain the recent rapid spread of the mountain pine beetle.*

INTRODUCTION

Allee effects are a density-dependent phenomenon in which population growth or individual components of fitness increase as population density increases. They are named after North American animal ecologist W.C. Allee, who studied the benefits of cooperative behaviour in small populations (Allee, 1931; Allee & Bowen, 1932). Allee effects are typically defined demographically as a positive relationship between average individual fitness and population size or density, when population size or density is small (Courchamp, Berec, & Gascoigne, 2008). Research on diverse organisms has documented a range of mechanisms that cause Allee effects, from mate limitation to cooperative feeding to predator satiation (Berec, Angulo, & Courchamp, 2007; Courchamp et al., 2008; Kramer, Dennis, Liebhold, & Drake, 2009). The potential for positive density dependence in small populations to increase extinction risk has led to keen interest in applications, including conservation of small populations (Angulo, Roemer, Berec, Gascoigne, & Courchamp, 2007), fisheries management (Hutchings, 2015) and control of non-native species, such as insect pests (Johnson, Liebhold, Tobin, & Bjornstad, 2006; Tobin, Berec, & Liebhold, 2011).

The substantial increase in research on Allee effects in the 1990s and 2000s has been attributed to these practical implications Kramer et al., 2009), and led to accumulated evidence for potential and realized Allee effects in multiple systems (Courchamp et al., 2008; Kramer et al., 2009). As of August 2017, there have been at least 1,037 published papers on Allee effects (Web of Science). With 701 papers since Courchamp et al.’s (2008) book, the last 9 years has represented a more than doubling of research. Roughly, these post-2008 papers fall into three categories: (1) documenting the presence of (sometimes newly described) demographic mechanisms giving rise to Allee effects, (2) empirical demonstration of earlier theoretical predictions based on the presence of an Allee effect, and (3) modelling the impact of Allee effects on ecological phenomena such as epidemics, predator–prey interactions, spatial distribution or pest control. In many of these latter papers, Allee effects were either a marginal element, or a major element modelled only phenomenologically (without no specific mechanism in mind), and the focus often was on comparing dynamics with and without the Allee effect.

In this period, several groups also built on earlier work in fisheries (Liermann & Hilborn, 1997; Myers, Barrowman, Hutchings, & Rosenberg, 1995) by looking for signatures of Allee effects in time-series data from large numbers of populations (Gregory, Bradshaw, Brook, & Courchamp, 2010; Perälä & Kuparinen, 2017). The data from various fisheries provide a particularly rich dataset in which severely depleted populations have been managed in order to encourage recovery, often without success, for which Allee effects have appeared to be one of the main suspects (Kuparinen, Keith, & Hutchings, 2014). In spite of similar Allee effect mechanisms, aquatic systems can differ from terrestrial ones in which habitat destruction is more likely to be confounded with population decline, and may thus provide important insights on causes and consequences of Allee effects for population and community dynamics.

Despite this fruitful period of research, some areas related to Allee effects theory have been virtually untouched. This special feature emerged from an organized session at the Ecological Society of America meeting in 2015 that focused on new areas, particularly how genetics and evolution relate to Allee effects and how mating behaviour influences population dynamics. The link between Allee effects and population genetics is expected to be strong due to the effect of small population sizes in ecological and evolutionary dynamics, and has led to discussions about whether inbreeding depression constitutes an Allee effect. Luque et al. (2016) recently defined how genetic processes contribute to Allee effects, and here Wittmann, Stuis, and Metzler (2016) use an individual-based odel to quantify how these population genetic processes can increase fitness costs in small populations. Berec, Kramer, Bernhauerová, and Drake (2017) also use an individual-based model to understand when selection weakens Allee effects and when density-dependent selection acts to strengthen Allee effects in high-density populations. In their contribution, Shaw, Kokko, and Neubert (2017) similarly develop a mechanistic model of mating to understand the role of sexual reproduction in the spatial spread of an invading population. Angulo et al. (2017) provide new insight on another key Allee effect mechanism, predicting when social structure causing Allee effects in small animal groups may lead to population scale demographic Allee effects. Blackwood, Vargas, and Fauvergue (2017) then present work on how Wolbachia infection and Allee effects may interact to facilitate the extirpation of targeted insect pests, following a long tradition leveraging Allee effects to improve pest management (e.g. Blackwood et al., 2012; Liebhold & Bascompte, 2003). Powell, Garlick, Bentz, and Friedenberg (2017) are also interested in insect pests and use a large set of forest surveys to show that Allee effects drive the pattern of pine beetle outbreaks. They find that the active dispersal which promotes densities high enough for successful infestation, results in a “pulled” invasion, verifying a prediction of earlier theory (Powell et al., 2017). This has been moved to the appropriate position earlier in the paragraph. See inserted text there.

Of course, prior to this issue there already existed a large body of theoretical work on how thresholds for population growth influence dynamics of populations and communities subject to Allee effects (Courchamp et al., 2008; Dennis, 2002; Taylor & Hastings, 2005). As the contributions in this special feature show, there is still much room to develop theory, and there has been an important shift in the focus of the models from past work. As seen here, current theory is often focused on the intricacies of component Allee effects that act in the context and complexity of real ecological situations. As a result, individual-based models are being increasingly used in order to accurately capture the mechanistic processes underlying positive density dependence and the stochasticity inherent in low-density populations (Berec et al., 2017; Shaw et al., 2017; Wittmann et al., 2016). The work on insect dynamics also shows that close interaction between theory and empiricism is fuelling continued advances in the understanding of Allee effects, which is a necessary prerequisite for any meaningful application to be pursued.

GENETIC AND EVOLUTIONARY ASPECTS OF ALLEE EFFECTS

Allee effects cause decreased fitness in small populations. Becauseof that, inbreeding depression has long been discussed as a poten- tial mechanismfor Allee effects. This has led to some disagreement, as inbreeding itself is not directly dependent on population size. However, there is a connection, which has been recently formalized asatwo-stepprocess: (1)a decrease inpopulationsizechangesge- netic structure, (2) individual fitness decreases due to that changein structure (Luque et al., 2016). Here Wittmann et al. (2016) pro- vide the first model to try to understand how inbreeding depression may lead to, and interact with ecological Allee effects. In particular, inbreeding can cause a strong genetic Allee effect in the presence of deleteriousmutations,whichisusuallyadditivewithe cologi- cal Allee effects if also present. The authors also find support fortheimportanceofgeneticstructureincontrollingth estrengthof the genetic Allee effect and for common occurrence of transient dynamics, including short-term population increases even when declines due to inbreeding are inevitable.

Decreased fitness at small population sizes is likelyto lead to se- lection for improved mate-finding abilities via adaptations like pher- omones, auditory signals or behavioural aggregation (Gascoigne, Berec, Gregory, & Courchamp, 2009). When a population is larger, thesetraitsmayconfercostsorservedifferentpurpose s.Berec et al. (2017) consider this potential for density-dependent selection on mate-finding ability with the first mechanistic, eco-evolutionary model of an Allee effect.Theyfindthatboththeformofthetrade-off between mate-finding and otherfitness components and the mating structure of the population strongly determine selective pressure. Outcomesvaryfrom evolutionarysuicidewhen males search and do not experience a fecundity trade-off to density-dependent selection under manyforms of female mate search.The potential for density- dependent selection on traits influencing Allee effects provides an explanation for the tendency to observe Allee effects in anthropo- genically rare organisms.

MECHANISMS GENERA TING ALLEE EFFECTS

Mate-finding Allee effects are also afocus of Shawet al. (2017) who consider the case of sex-structure dinvasions. By combining an individual based model of mating and integro difference model of spatial spread, Shaw etal. (2017) show that sex-based asym- metrie samplify the effects of mate limitation, slowing invasions. On the other hand, multiple matings are found to ameliorate these effects, which imply that polygynandrous populations may be ableto invade under conditions where monogamous populations would collapse. Shaw et al. (2017) also propose a stricter formal definition of the mate-finding Allee effect which allows a better distinction between mating functions that can or fail to capture Allee dynam-ics arising from difficulty finding mates in low-density populations. In any case, linking individual- and population-level models holds promise for addressing other questions of how Allee effects alter spatial spread. While the mechanisms and implications of Allee effects are better understood now than a decade ago, papers here and elsewhere offering conceptual developments are still needed to understand how and when positive density dependence should be important in natu- ralsystems (Berecetal., 2017; Luqueetal., 2016; Shawetal., 2017; Wittmannetal.,2016). In their contribution, Anguloetal. (2017) consider apuzzle arising in Allee effects in social species, namely that demographic Allee effects and extinctions seem to be rareeventhough Allee effects are expected to be inherent in group living animals. They show that group size, hetero geneity in group size and inter group interactions combine to determine whether “group scale” Allee effects are propagated to the population scale. Specifically, they show that population-level demographic Allee effects are weakened by group size heterogeneity and between-group cooperation. The paper pro- vides a conceptual framework for understanding these relationships and considering how the strength of Allee effects may differ depending on the form of sociality.

APPLICATIONS OF ALLEE EFFECT THEORY

The tendency for mate limitation to lead to population collapse has been often studied in the context of controlling insect invasions (Black woodetal., 2012; Boukal & Berec, 2009; Liebhold & Bascompte, 2003), and Black woodetal. (2017) add to this tradition by considering the interactive effects of amating-related control mechanism currently being proposed for pest control. Males infected with *Wolbachia* bacteria tend to experience mating failure when pairing with unin- fected females, reducing population growth and size while the bac- teria spread. Blackwood etal. (2017) use models to show that while *Wolbachia* -induced cytoplasmic incompatibility and the mate-finding Allee effect act more or less independently, by combining these two processes, it may be possible to achieve pest population collapse even in established populations. In particular, a cascade of transient destabilizations occurs which may bring the population density under the Allee threshold. The importance of transient populations mir-rorsthatin Wittmannetal.(2016), and suggests this is an interesting area for further exploration for both conservation and management applications.

Allee effects can also influence the spatial pattern of pest out- breaks through cooperative behaviour. Pine beetles aggregate in order to overwhelm host defences and Powell etal. (2017) analyse data from three western U.S. foreststo show how this behaviour leads to a power-law distribution of outbreak patches on the landscape. They provide a mechanistic explanation for spread patterns in west- ernmountainpine beetle out breaks and results in faster spread than would a passively dispersing beetle. In effect, the dispersal behaviour of the beetles overcomes fitness effects of the Allee effect that would slow or stop spread. This pattern may help explain the recent rapid spread of the mountain pine beetle.

MOVING FORWARD

Because quantifying the presence and magnitude of Allee effects in natural systems has been impeded by the difficulty of sampling low-density populations (Gregory etal., 2010; Perälä & Kuparinen, 2017), there have been persistent questions about their relevance to observe decological dynamics. Inotherwords, are demographic Allee effects rarely detected because of the difficulty of sampling small populations or because the mechanisms are often overwhelmed by other aspects of species ecology? Our experience suggests that a combination of (1) testing mechanisms in systems amenable to experimentation with replicate populations, (2) continuing to leverage data from manage dandcontroll edpopulations and(3) improvement in statistical analysis will be most effective in answering this set of questions. While the issue of detection in natural populations is a very challenging one, we think the sepapers provide across-section of the exciting work that is showing how Allee effects can have wide-ranging influence on ecological dynamics. This influence may not always be observable as collapse of small populations, but has nevertheless shaped population genetics, trait evolution and spatial patterns. To pinpoint just a single insight in this respect from this special feature, models revealed that despite negatively affecting individual fitness in small or low-density populations, Allee effects might not be selected against in large or high-density populations, providing an explanation for the tendency to observe Alleeeffects in anthropogenically rare organisms. Generally, combining this understanding with explicit models for how various mechanisms give rise to Allee effects points a way towards improved application to conservation and management of particular species. The relevance of these concernsis under scored by the pursuit of the setopics in multiple systems and our goal here was to help continue these advances.

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