

The evidence for Allee effects

Andrew M. Kramer · Brian Dennis ·
Andrew M. Liebhold · John M. Drake

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Abstract Allee effects are an important dynamic phenomenon believed to be manifested in several population processes, notably extinction and invasion. Though widely cited in these contexts, the evidence for their strength and prevalence has not been critically evaluated. We review results from 91 studies on Allee effects in natural animal populations. We focus on empirical signatures that are used or might be used to detect Allee effects, the types of data in which Allee effects are evident, the empirical support for the occurrence of critical densities in natural populations, and differences among taxa both in the presence of Allee effects and primary causal mechanisms. We find that conclusive examples are known from Mollusca, Arthropoda, and Chordata, including three classes of vertebrates, and are most commonly documented to result from mate limitation in invertebrates and from predator–prey interactions in vertebrates. More than half of studies failed to distinguish component and demographic Allee effects in data, although the distinction is crucial to most of the population-level dynamic implications associated with

Allee effects (e.g., the existence of an unstable critical density associated with strong Allee effects). Thus, although we find conclusive evidence for Allee effects due to a variety of mechanisms in natural populations of 59 animal species, we also find that existing data addressing the strength and commonness of Allee effects across species and populations is limited; evidence for a critical density for most populations is lacking. We suggest that current studies, mainly observational in nature, should be supplemented by population-scale experiments and approaches connecting component and demographic effects.

Keywords Critical density · Depensation · Inverse density dependence · Mate limitation · Predator satiation · Positive density dependence

Introduction

Although Allee effects were first described in the 1930s (Allee 1931), interest has recently surged in tandem with high profile conservation problems (Stoner and Ray-Culp 2000; Courchamp and Macdonald 2001; Wittmer et al. 2005; Angulo et al. 2007). Allee effects, defined as positive effects of increasing density on fitness, are a predicted consequence of multiple mechanisms in small or low-density populations, and are expected to affect many population-level processes, including extinction (Dennis 1989, 2002; Boukal and Berec 2002; Allen et al. 2005), population establishment and biological invasion (Drake and Lodge 2006; Liebhold and Tobin 2006; Ackleh et al. 2007), metapopulation fluctuations (Zhou et al. 2004; Martcheva and Bolker 2007), predator–prey interactions (Gascoigne and Lipcius 2004; Morozov et al. 2004), and parasite transmission (Deredec and Courchamp 2006).

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A. M. Kramer (✉) · J. M. Drake
Odum School of Ecology, University of Georgia,
Athens, GA 30605, USA
e-mail: kramera3@uga.edu

B. Dennis
Department of Fish and Wildlife Resources, University of Idaho,
Moscow, ID 83844, USA

A. M. Liebhold
Northern Research Station, Forestry Sciences Laboratory,
USDA Forest Service, 180 Canfield St.,
Morgantown, WV 26505, USA

The putative variety of mechanisms and affected ecological processes suggest that Allee effects may be widespread, with pervasive effects in nature.

Here we review the evidence for Allee effects in natural animal populations. Our convention for the definition of “natural” populations was to exclude any population reared under controlled conditions (laboratory or greenhouse), domesticated populations (livestock), and cultivated populations (e.g., field crops). Wild populations managed for harvest, however (e.g., fish and game) do fall within the scope of our study. Previous reviews have examined support for theoretical predictions using selected studies (Dennis 1989; Courchamp et al. 1999; Stephens and Sutherland 1999; Stephens et al. 1999; Berec et al. 2007; Gascoigne et al. 2009), but only indirectly addressed the strength of empirical support for key theoretical assumptions and the commonness of Allee effects across natural systems. Determining the pervasiveness of Allee effects has been attempted using meta-analyses of abundance time series for fish (Myers et al. 1995; Liermann and Hilborn 1997; Walters and Kitchell 2001; Barrowman et al. 2003), birds (Sæther et al. 1996), marine mammals (Gerber and Hilborn 2001), and insects (Hopper and Roush 1993). Several of these analyses showed that Allee effects occur, and can be detected, in natural populations. However, they were limited by the type of data available for each taxonomic group and were unable to assess the mechanisms causing Allee effects (but see Walters and Kitchell 2001). The recent increase in documented examples now provides sufficient data to address the following questions:

- What is the evidence for Allee effects in natural populations?
- What mechanisms cause Allee effects?
- Do these mechanisms give rise to hypothesized strong Allee effects, or are most observed Allee effects weak (see below for the distinction between strong and weak Allee effects)?
- How common are Allee effects?

To answer these questions we follow Stephens et al. (1999) and distinguish between *component* Allee effects and *demographic* Allee effects. All mechanisms giving rise to an Allee effect, for example difficulty finding mates or cooperative feeding, result in component Allee effects (Stephens et al. 1999), i.e., a positive relationship between a component of individual fitness, e.g., survivorship or per capita reproduction, and population size or density. If these component Allee effects are not offset by negative density dependence in other components of fitness they may cause demographic Allee effects (Stephens et al. 1999), i.e., positive density dependence manifested at the population level. The population-level consequences of demographic Allee effects are classified as either weak or strong, where

a strong Allee effect results in a critical density (Fig. 1a) below which per capita population growth rate is negative (Wang and Kot 2001; Deredec and Courchamp 2006; the concepts were previously called “depensation” and “critical depensation” by Clark 1976). Detection and discrimination of weak and strong Allee effects may be achieved by comparing density and per capita growth rate (Fig. 1a) or density and the probability of establishment or extinction (Fig. 1b, Dennis 2002; Drake 2004).

Using these distinctions as a guide, in this paper we survey evidence for Allee effects in animals. Focusing on natural populations, we quantify emerging patterns in which populations or species exhibit Allee effects, what causes them, and whether they are strong or weak. We identify links between study design and the propensity of studies to detect demographic Allee effects and critically evaluate the existing evidence for strong Allee effects in natural populations. We also examine whether existing evidence enables assessment of the rarity or ubiquity of Allee effects in natural populations. To provide context, we include a discussion of evidence for Allee effects in natural plant populations. Our results showed both similarities and differences among taxonomic groups in mechanisms

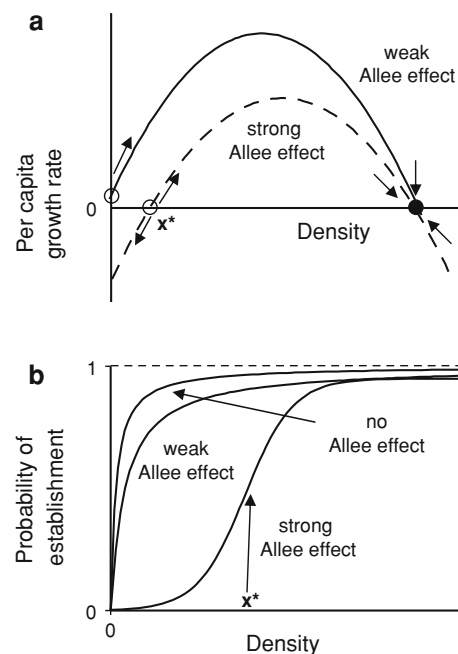


Fig. 1 Definition of the demographic Allee effect (as in Boukal and Berec 2002 or Taylor and Hastings 2005). The positive relationship between per-capita growth rate and density when density is low defines an Allee effect as in **a** Weak vs. Strong Allee effect. When per-capita growth rate is negative below a threshold density, x^* , this is a strong or critical Allee effect. This critical density is an unstable equilibrium. These differences are also seen in **b** Allee effect and probability of persistence. When probability of establishment (or extinction) is compared with population density. Here the threshold density, x^* , creates an inflection point in the probability of persistence

causing Allee effects, and suggest that detection of Allee effects and the ability to link component and demographic Allee effects was influenced by study design. Overall, there is substantial and increasing evidence that Allee effects play an important role in numerous, diverse systems. However, we find existing studies provided only limited direct evidence for strong Allee effects. The pervasiveness of Allee effects in natural populations remains unknown.

Methods

Published studies on Allee effects were identified as follows. We first conducted a search of the ISI Web of Science database with each of the search terms “Allee”, “depensation”, and “inverse density dependence”, examining all references available through August 2008. We enlarged the sample of studies by searching references of review papers (Stephens and Sutherland 1999; Gascoigne and Lipcius 2004; Berec et al. 2007) and examining other papers known to the authors. These approaches identified 492 studies. Our goal was not to include all studies considering low-density populations, but rather to assemble a thorough collection of studies which focused on the dynamics of low population densities and the role of Allee effects, a collection that we believe is more complete than any previously assembled.

To understand further the role of Allee effects in natural animal populations and their importance relative to the other population processes occurring in nature, we selected studies including data from field populations (manipulated or unmanipulated), and excluded purely laboratory experiments, reviews, and strictly theoretical papers; 91 studies met this criterion. For context, we discuss an additional 28 studies on Allee effects in plant populations. Our search on “inverse density dependence” also revealed a group of studies that focus on parasitoid attack rate as a function of host density. These 24 papers are distinct from the main body of literature on animal populations, because they differ in their focus on parasitoid behavior and their lack of explicit consideration of overall fitness or population dynamics of the host species. We considered these separately.

Each study was classified by study design, type of evidence, the classes of phenomena in which Allee effects were present, and taxonomic group (S1 in Electronic Supplementary Material (ESM)). We defined the study design as either experimental manipulation (i.e., treatment imposed by researchers), natural experiment (i.e., observations following a known, uncontrolled perturbation, such as species introduction), or observational study. We categorized evidence according to whether it addressed component Allee effects, demographic Allee effects or both. Those studies presenting evidence for or against

demographic Allee effects were further classified according to the type of phenomenon in which Allee effects were identified: changes in population size and growth rate (“population dynamics”), population persistence (“colonization/extinction”) or rate of spread (note that individual studies occasionally provided more than one type of data).

Studies were categorized into six taxonomic groups based on the study species: terrestrial arthropods, aquatic invertebrates, mammals, birds, fish, and reptiles. No study included more than one taxonomic group, although 16 tested for Allee effects in more than one species. Papers that compared several species were classified on the basis of the overall finding, i.e., if evidence for Allee effects in some subset of populations was conclusive, the study was counted as evidence for an Allee effect in that taxonomic group as a whole. Of special note are seven meta-analyses which examined data on many populations (11–330) of related species (S1, see “Results and discussion”). They were excluded from analyses which considered the number of species rather than the number of studies exhibiting Allee effects, because of the often specialized methods that these studies used to test for Allee effects and the diluting effect that their large number of species would have on the other studies examined. There were also two studies that used retrospective analysis to argue for Allee effects by examining the current distribution (Jordal et al. 2001) or persistence (Munoz-Duran 2002) of beetles and carnivores respectively, and relating it to species characteristics. We considered this indirect evidence to be inconclusive and classified it as such. The remaining papers considered comparable data on only two or three species, each of which was categorized as described below when the analytical unit was species rather than study.

We critically assessed the support for Allee effects in each study according to the following criteria. If the authors presented no evidence for an Allee effect or evidence contrary to an Allee effect, these were labeled as “No Allee effect.” Studies were labeled “Allee effect” when a positive relationship was demonstrated between population density and any component of individual fitness, population growth rate, the probability of persistence or colonization, or spread rate. The remaining papers were labeled “Unclear” because the data did not conclusively demonstrate such a relationship. Many “Unclear” studies were presented by the authors as evidence for an Allee effect, and were suggestive of Allee effects, but relied on circumstantial evidence or contradictory results.

When data supported an Allee effect, the mechanism(s) causing the component or demographic Allee effect, as represented by the authors, were noted. In some cases the mechanism(s) were directly supported by data, in other studies the conclusion was based on expert knowledge. In a few cases the mechanism was not addressed. Although

authors used a variety of terminology, all the mechanisms cited fit into eight broad categories (reviewed in Dennis 1989; Courchamp et al. 1999; Stephens and Sutherland 1999; Boukal and Berec 2002, unless otherwise cited): cooperative breeding, cooperative defense, cooperative feeding, dispersal (Kuussaari et al. 1998), habitat alteration, mate limitation (Gascoigne et al. 2009), predator satiation (Gascoigne and Lipcius 2004), and somatic growth (McCormick 2006).

Each study presenting demographic evidence for an Allee effect was examined for strong vs. weak Allee effects. Because a goal of this review was to assess the evidence for strong Allee effects in nature, we were stringent in our assessment. Strong Allee effects were only recognized if authors reported quantitative support for a critical density in the population (as in Fig. 1a, b for example; see “Results and discussion”). Cases where a critical density was not indicated by the data were

classified as weak, and the remaining studies, classified as “uncertain”, lacked the data necessary to address the strength of the Allee effect.

Results and discussion

What are the patterns in the empirical evidence for Allee effects in natural populations?

The evidence for Allee effects in animal populations is substantial and increasing (Fig. 2). In 63 out of 91 studies (69%), there was conclusive evidence for a component Allee effect, demographic Allee effect, or both. Six studies found no evidence for an Allee effect and 22 presented data which were ambiguous. Research on Allee effects has recently increased, with 62 studies published after 1997 (Fig. 2a). This trend was mirrored by studies on plants, but not in

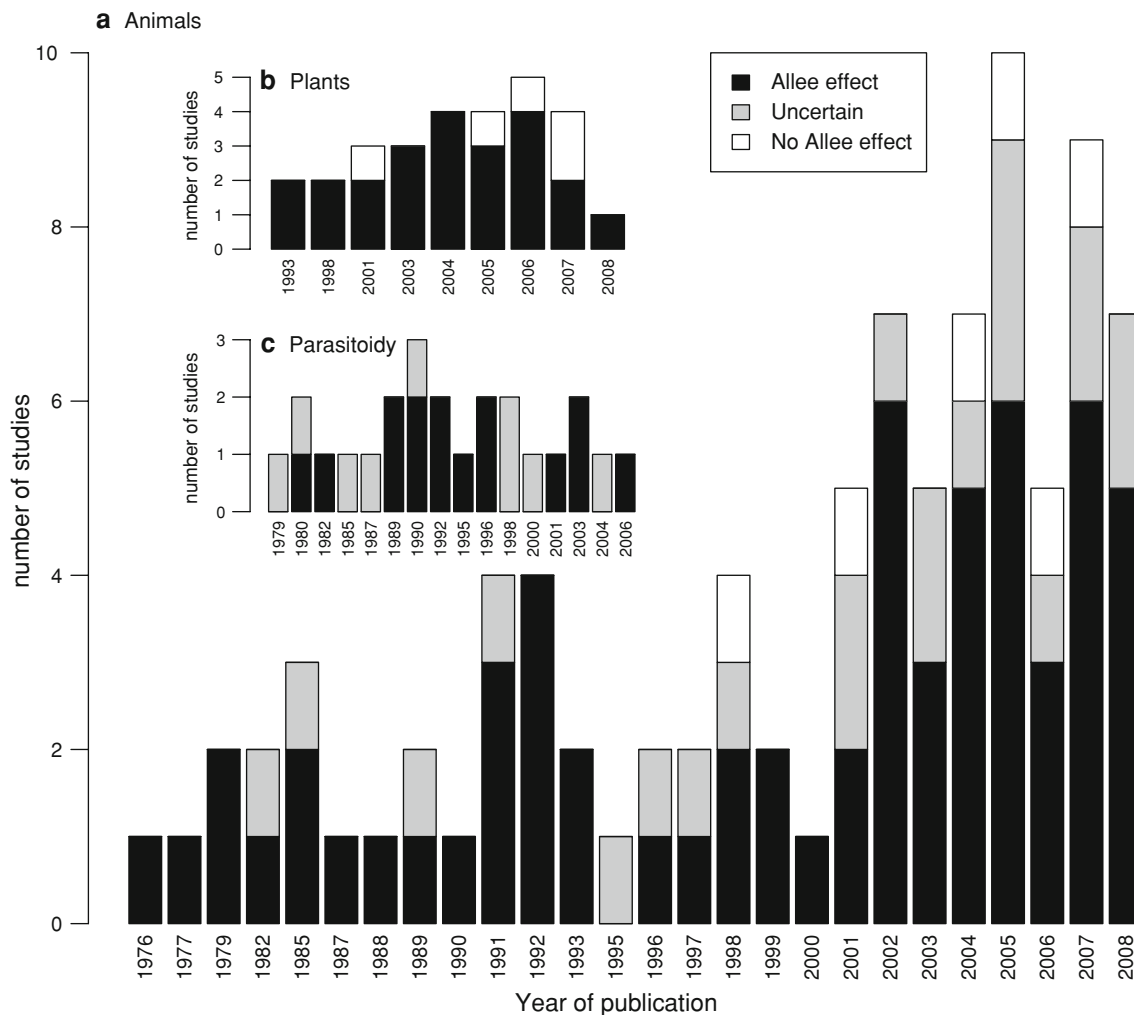


Fig. 2 a The number of empirical studies on Allee effects in natural animal populations per year. Studies are categorized as “No Allee effect”, “Allee effect”, and “Ambiguous” (see “Methods”). **b** The

number of plant studies on Allee effects in natural populations. **c** Studies investigating inverse density dependence in the attack rate of parasitoids on their hosts

studies of parasitoidy (Fig. 2b, c). Five of the six studies that conclusively failed to detect Allee effects were published after the publication of the two influential review papers mentioned in the introduction (Courchamp et al. 1999; Stephens et al. 1999). This trend may have resulted from the tendency of researchers in early studies to have mentioned Allee effects only when they were detected, with a subsequent shift to searching for the Allee effect based on the expectation of their importance in low-density populations. The recent increase in studies resulted largely from an increase in studies relating the Allee effect to species of conservation concern and to invasive species (Fig. 3).

Taxonomic groups and detection of Allee effects

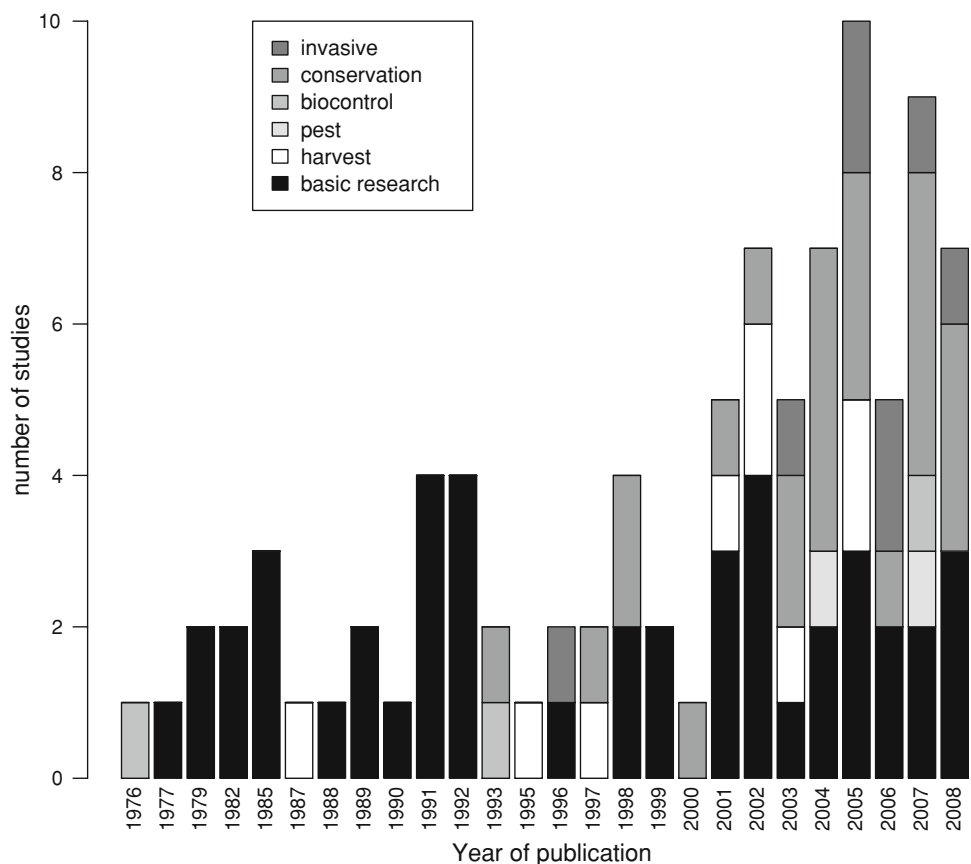
The largest number of studies and the highest proportion detecting Allee effects were for terrestrial arthropods (Fig. 4). The number of studies on vertebrates and invertebrates were similar, with Allee effects detected in all taxonomic groups other than reptiles. There was no difference in the proportion of studies conclusively detecting Allee effects across taxonomic groups or between vertebrates and invertebrates (Fisher’s exact test, $P = 0.48$, $P = 0.67$, respectively). The lack of studies of and evidence for Allee effects in amphibians and reptiles is

notable and the single study which concluded there was no evidence of an Allee effect in sea turtles (Hays 2004) was a brief account offering limited specific data. The number of studies on each taxonomic group is probably related to a combination of theoretical expectations about the likelihood of Allee effects, observed patterns suggesting Allee effects, and research emphases within taxonomic groups.

Study design and detection of Allee effects

The studies (meta-analyses excluded) provided data on 80 species (S1). In more than half of these species, evidence for an Allee effect came from observational data (Table 1). Observational studies typically included both measurements of individual fitness on natural populations (Mooring et al. 2004) and examination of population size across multiple generations (Angulo et al. 2007), and the popularity of this study design can likely be attributed to the availability of population time series from natural populations (Walters and Kitchell 2001). The proportion of species found to have an Allee effect was significantly higher for observational studies than for manipulations and natural experiments (81 vs. 60%, Fisher’s exact’s test, $P = 0.007$). For this analysis, we pooled natural experiments with experimental manipulations because, in both

Fig. 3 The number of empirical studies on Allee effects in natural animal populations per year. The studies are categorized by the author’s purpose for conducting the study. Categories were determined from background presented in the “Introduction”, with studies not citing relevance to an applied problem categorized as “basic research”



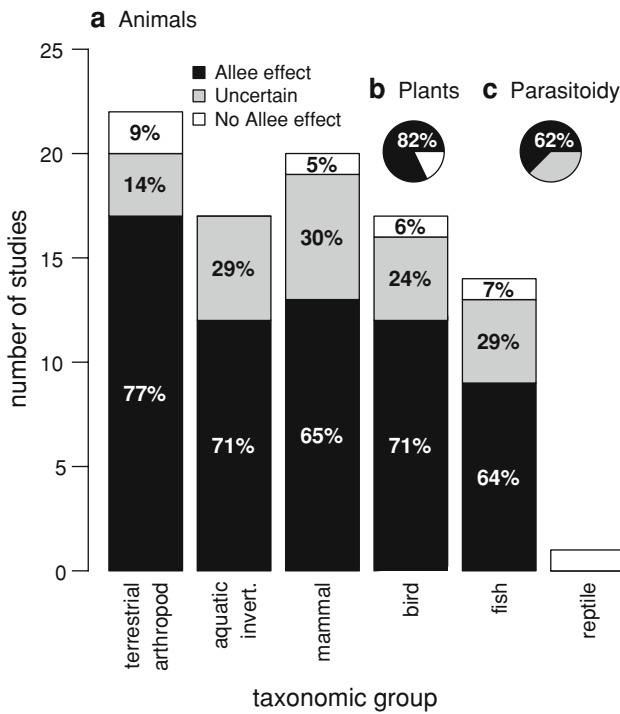


Fig. 4 The percentage of studies which detected Allee effects in **a** animals, grouped by taxonomic group; **b** plants; and **c** parasitoids

Table 1 Number of species where Allee effects were detected, and type of study design

Type of study	Allee effect present?		
	Yes	Ambiguous	No
Observational	38 (81%)	9 (19%)	0
Experimental manipulation	16 (70%)	4 (17%)	3 (13%)
Natural experiment	5 (42%)	4 (33%)	3 (25%)

Gypsy moth and queen conch appear under both observational and experimental manipulation because the Allee effect was assessed by independent studies using each approach. All other species are represented once, and meta-analyses were excluded

cases, fitness and population growth were measured relative to a known treatment/event and there was no statistically significant difference in the detection of Allee effects between these two study designs (Fisher’s exact’s test, $P = 0.28$). There are several possible causes for the higher detection rate in observational studies. First, experimental manipulations and natural experiments may be more successful in rejecting Allee effects when they are not present, because of increased power and fewer ambiguous findings. Second, observational studies often produce and/or analyze larger quantities of data and extend over longer periods, which may be necessary to confirm the presence of Allee effects. (Conversely, one might argue that observational data will under-detect Allee effects, because sampling error is typically high in data on very low

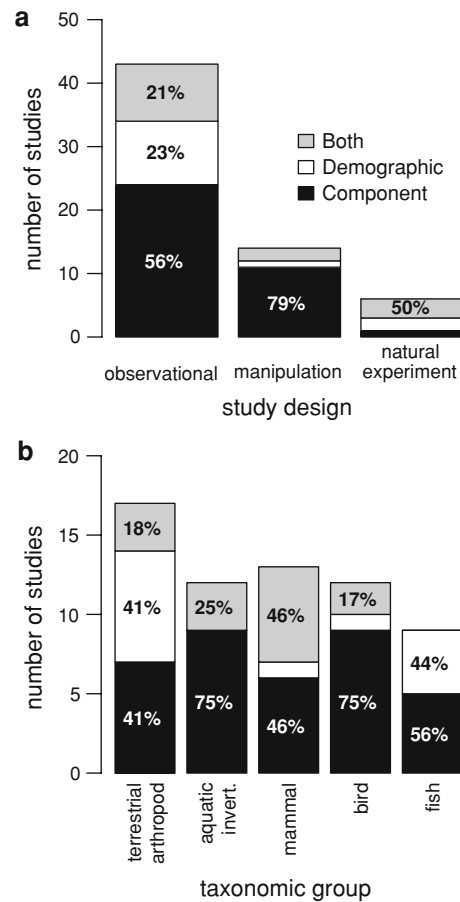


Fig. 5 The percentage of studies detecting the Allee effect which measured component, demographic, or both types of data for **a** different study designs and **b** different taxonomic groups

population densities.) Finally, observational data examined for Allee effects might concern species with low growth rates or low densities for which there is already reason to suspect Allee effects, and which are less amenable to manipulation (see below).

In addition to these possible causes our analysis suggests differences in the types of data resulting from experimental manipulations, natural experiments, and observational studies could explain the differences in the chance of detecting Allee effects, and perhaps offer guidance on when to use alternative study designs. In terms of the type of Allee effect detected, there was a large contrast between experimental manipulations and the other two designs (Fig. 5a). Experimental manipulations were more likely to rely on data about component Allee effects and have few data on demographic Allee effects, including whether the component Allee effects result in demographic Allee effects. Conversely, observational studies and natural experiments that detected Allee effects generally produced data on demographic Allee effects, and were often able to examine both component and demographic Allee effects at

the same time. Ecologists and managers will most often want to know both that a demographic Allee effect is present or possible and what mechanism(s) is causing it, making studies examining both particularly valuable. Ideally, experimental manipulations that detect mechanisms of Allee effects by revealing the component of fitness affected would also be combined with data collected on the demographic consequences of Allee effects. However, collecting demographic data in experimental studies may be inhibited by logistical and ethical or legal problems of manipulating natural populations with very few individuals, especially for vertebrates. Alternatively, it may be that better experimental designs could provide both types of data on the same populations, and enable direct tests of theoretical predictions. Two experimental studies provided data on component and demographic Allee effects (Wallin and Raffa 2004; Kramer et al. 2008) by combining field experiments, highly replicated experiments (mesocosm or laboratory), and simultaneous monitoring of relevant fitness components. More studies like these would enable better verification and/or development of mechanistic models of Allee effects.

The type of data collected varied significantly among taxonomic groups (Fig. 5b, Fisher’s exact test, $P = 0.02$) with aquatic invertebrates and birds having relatively little information on demographic Allee effects, and a substantial majority of studies on other taxonomic groups addressing demographic Allee effects. Many studies of fish and terrestrial arthropods considered demographic data exclusively and, as a result, determination of the mechanisms underlying Allee effects relied on circumstantial evidence or expert knowledge. Studies of both birds and aquatic insects usually lacked empirical evidence for demographic Allee effects, but for different reasons. For aquatic invertebrates most studies were experimental manipulations that rarely provided demographic evidence (see above). For birds, studies that detected Allee effects were primarily observational, documenting components of fitness such as mortality and hatching success, but not population dynamics (Cuthbert 2002). Thus, the lack of evidence for demographic Allee effects probably does not suggest a lower incidence in these taxonomic groups but rather indicates that additional studies are needed that collect the type of data necessary to assess demographic Allee effects in these groups. On the other hand, the substantial number of studies based only on demographic evidence in terrestrial invertebrates and fish was largely because of the use of existing large datasets on long-term dynamics (Myers et al. 1995; Tobin et al. 2007) for detecting Allee effects. Studies on mammals came closest to the ideal balance of understanding both the mechanism and the population dynamic implications, with six studies

(46%) assessing both component and demographic Allee effects (Wittmer et al. 2005; Angulo et al. 2007).

The types of evidence considered in studies which detected demographic Allee effects differed among the taxonomic groups (Fig. 6a, Fisher’s exact test, $P = 0.02$). Evidence from population dynamics revealed demographic Allee effects in all five taxonomic groups. Studies on terrestrial arthropods have relied less on population dynamics, with more focus on the presence/absence of populations (“colonization/extinction”). This may reflect the greater difficulty of accurately estimating insect population size or density rather than simply detecting the presence or absence of a species. In general, it may be particularly difficult to detect the presence of low-density populations, requiring substantial effort (Kramer et al. 2008) and/or creative techniques, such as the use of pheromone traps to detect gypsy moth populations (Liebhold and Bascombe

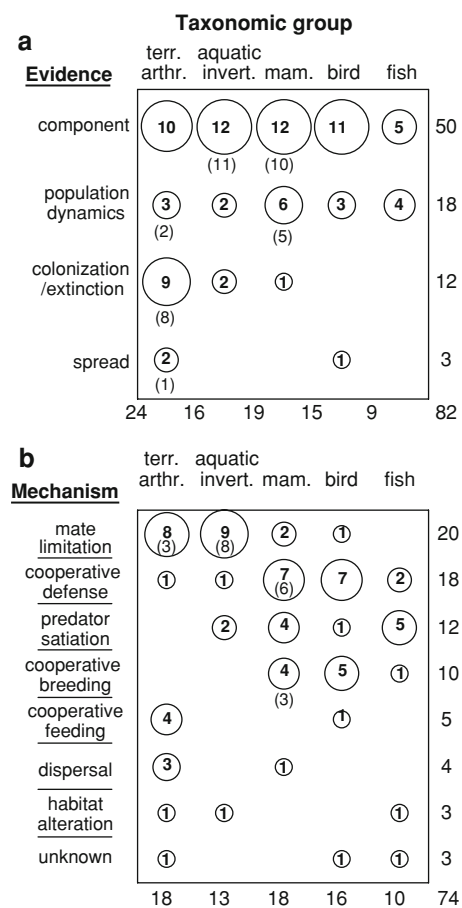


Fig. 6 The number of studies detecting the Allee effect from each taxonomic group which **a** used a given evidence type or **b** attributed the Allee effect to a given mechanism. Single studies can be represented by multiple evidence types and mechanisms (see “Methods”). The area of each circle illustrates the relative number of species; the number of distinct species represented by each circle is in parentheses

2003, see others in S1). Data on colonization and extinction rates are especially relevant to understanding the role of the Allee effect in conserving threatened species and preventing/predicting invasions. More effort should therefore be given to determining the rates of colonization and extinction for vertebrates. Additionally, theory predicts that Allee effects are important in influencing spatial expansion of populations (Lewis and Kareiva 1993; Hastings 1996). Yet evidence in support of this theory exists for only two species, gypsy moths (Johnson et al. 2006; Tobin et al. 2007) and house finches (Veit and Lewis 1996), with indirect evidence for the Montagu harrier (Soutullo et al. 2006).

What causes Allee effects?

The collected studies presented empirical evidence that Allee effects in natural populations are caused by six mechanisms: mate limitation, cooperative defense, predator satiation, cooperative feeding, dispersal, and habitat alteration. For each, at least one study provided evidence for a component Allee effect and for a demographic Allee effect (S1). The four most commonly identified mechanisms (Fig. 6b) occurred in studies containing direct evidence for both the component and demographic Allee effect. An additional process, somatic growth, caused a component Allee effect in one study (Hoddle 1991), but was not implicated at the demographic scale.

The contribution of these mechanisms to Allee effects differed among taxonomic groups (Fisher's exact test, $P < 0.0001$). Two-thirds of detected Allee effects were caused by mate limitation, cooperative defense, or predator satiation (Fig. 6b). Mate limitation was the most common mechanism, occurring mostly in aquatic invertebrates where it is the dominant cause of detected Allee effects (Fig. 6b). This is expected, given the challenges of fertilization in aquatic environments (Gerritsen 1980; Quinn et al. 1993). In general, one expects that species with limited mobility or passive reproduction, for example plankton, plants, and broadcast spawners, are more susceptible to mate limitation (Gascoigne et al. 2009). Mate limitation was less common—or more unexpected and therefore less studied—in vertebrates. Another mechanism used as a classic example of Allee effects, cooperative defense, seems to be important only for vertebrate species. Predator satiation, whereby an Allee effect results from a Type II functional response by a predator (Dennis and Patil 1984; Gascoigne and Lipcius 2004), was also dominant in vertebrates. Further investigation into whether the smaller amount evidence for predator-mediated Allee effects in invertebrates is merely a result of study bias or suggests a real difference between taxonomic groups is important given the ubiquity of predator-prey interactions.

Terrestrial arthropods were subject to the most different mechanisms, but at least four mechanisms were implicated in all taxa. At the same time, each mechanism occurred in multiple taxonomic groups. Dispersal and habitat alteration, the least frequently examined mechanisms, are also less commonly discussed in the theoretical literature (A. Kramer, unpublished data). An Allee effect caused by dispersal occurs when animals are more likely to emigrate from a low-density population than a high density population, or when animals are more likely to colonize already-occupied habitats, thus reducing population growth rate at low abundances (Menendez et al. 2002). Habitat alteration can cause an Allee effect when the presence of conspecifics increases recruitment to the population by altering the biotic or abiotic conditions in a way that increases fitness of recruits (Kent et al. 2003; Gascoigne et al. 2005).

Six studies implicated two mechanisms as contributing to a demographic Allee effect (S1). In four of these studies, component Allee effects were directly documented, with low-density populations subject to reduced fitness from more than one fitness component—for example, reproduction and survival (Angulo et al. 2007). The population-level implications of multiple Allee effects on a single population have recently been explored theoretically (Berec et al. 2007), and these empirical studies confirm the occurrence of multiple Allee effects in natural populations. However, as argued by Berec et al. (2007), existing data do not directly assess the interaction between multiple Allee effects or the population-level consequences. This problem requires studies measuring component and demographic Allee effects simultaneously in addition to experimental manipulations to isolate the influence of each component Allee effect.

Are Allee effects common?

Given the increasing number of studies presenting evidence for Allee effects, it remains to ask two questions:

1. What proportion of species is subject to Allee effects? and
2. Do the population densities at which Allee effects are measurable often occur?

Concerning the first question, the broad patterns of occurrence and diversity of relevant mechanisms uncovered imply that no taxonomic group is invulnerable to Allee effects and that Allee effects should be considered potentially important in low-density dynamics of many species.

Unfortunately, because the only evidence available is from studies in which researchers have already recognized the relevance of Allee effects, the rate of detection in these

studies is a poor indicator of the relative frequency of Allee effects in nature overall. One approach to assessing the commonness of Allee effects is to look for evidence in a randomly selected set of populations. The seven meta-analyses identified here adopted that approach, using a collection of datasets on the dynamics of populations of multiple species (within a restricted taxonomic group, see “Introduction”). The number of populations examined varied from eleven (Sæther et al. 1996) to 330 (Walters and Kitchell 2001). Of these, five were based on model fitting. One study found no evidence for an Allee effect in fur-bearing seals (Gerber and Hilborn 2001). Three studies on fish (Myers et al. 1995; Liermann and Hilborn 1997; Barrowman et al. 2003) and one on birds (Sæther et al. 1996) found weak support for Allee effects in very few populations, or inconclusive evidence for Allee effects. At the same time, all acknowledged very low power for detecting Allee effects. Again, the difficulty of sampling low-density populations is a factor that limits the detection of Allee effects, even those that are strong (Stephens et al. 2002). The failure of these studies to obtain conclusive evidence for Allee effects could have resulted from uncommonness across populations of these species, a lack of observations at sufficiently low densities, or that very few species are subject to Allee effects at any realistic density. The remaining two reviews found support for Allee effects by very different methods than the model-fitting used in the above studies (Hopper and Roush 1993; Walters and Kitchell 2001). Walters and Kitchell (2001) used visual analysis by experts to identify stock-recruitment patterns consistent with Allee effects in multiple populations and Hopper and Roush (1993) use data on biological control introductions which supported significant limitation of establishment success at small inoculum size across broad groups of parasitoid species. The different approaches and inconclusive or conflicting findings (especially between Myers et al. (1995), Liermann and Hilborn (1997), and Walters and Kitchell (2001)) illustrate the limitations of drawing any general conclusions about the commonness of Allee effects overall from existing meta-analyses.

Weak vs. strong Allee effects

Many theoretical predictions about the role and importance of Allee effects, especially predictions concerning extinction and colonization rates, presume the presence of strong Allee effects. This makes understanding the strength of Allee effects at observed population densities as important to ecological theory and management decisions as the ability to detect their presence. Seven of the 91 studies examining Allee effects found a critical density below which population growth rate was negative. Further, while

seven of twenty-three studies showing evidence for a demographic Allee effect presented support for a strong Allee effect, eleven could not discriminate between weak and strong effects and eight suggested the Allee effect was weak over the densities studied (Fig. 7). The small sample size and number of uncertain studies precludes distinguishing whether strong Allee effects occur relatively often and are difficult to detect or whether they are actually the minority of cases. Determining whether weak or strong Allee effects are more common in natural populations will rely on improved study design and analytical techniques. For example, Friedenbergl et al. (2007) present data on extinction probability vs. population density (Fig. 8a), which have the potential to differentiate between weak and strong Allee effects (Fig. 1b). The authors fit a logistic regression, but the lack of inflection point in the model fit suggests a strong Allee effect is absent (Dennis 2002). To us, however, the residuals suggest there might in fact be an S-shape. Further analysis of these data would be warranted. Also possible is that an Allee effect may appear to be weak

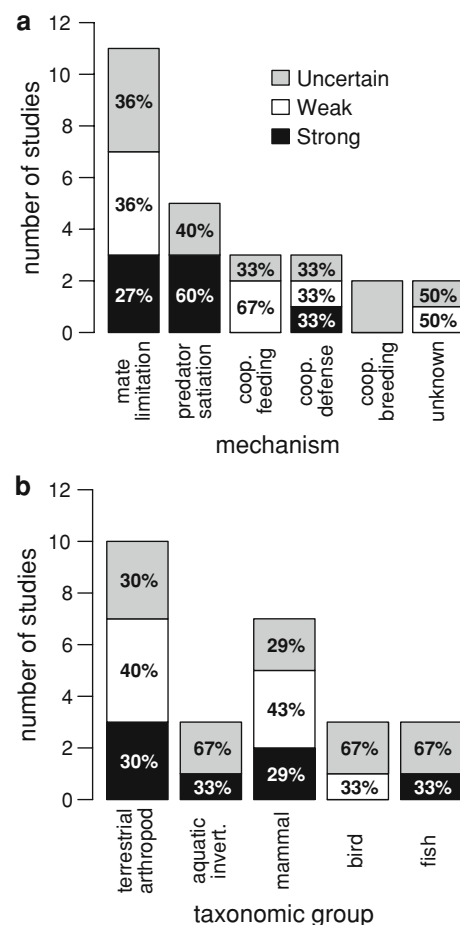


Fig. 7 The percentage of studies detecting demographic Allee effects that are strong, weak, or of unknown strength separated by **a** mechanism and **b** taxonomic group

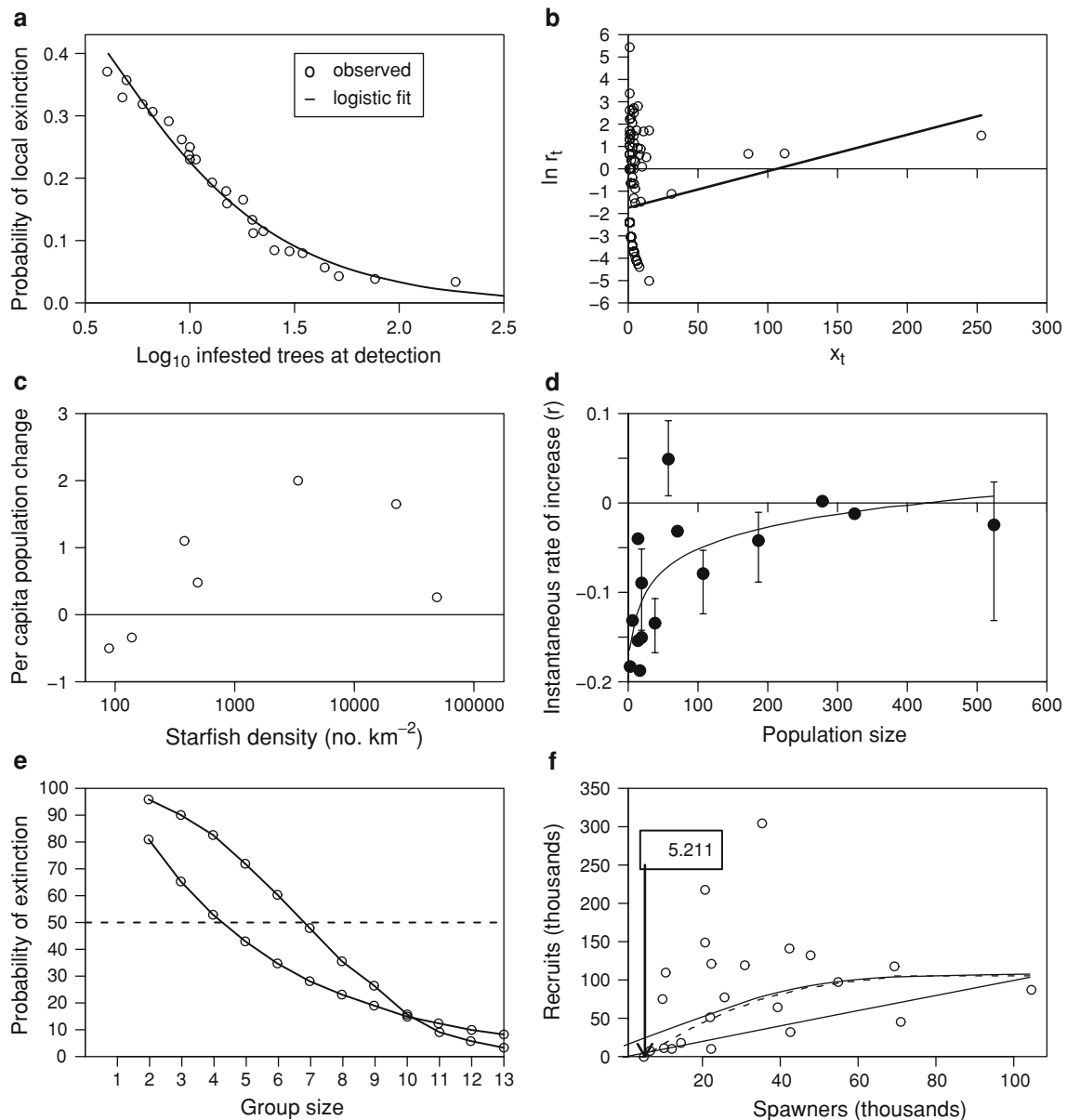


Fig. 8 **a** The probability of local extinction as a function of initial infestation size for southern pine beetles, *Dendroctonus frontalis*, across the south-eastern USA (Friedenberg et al. 2007). It cannot be determined from the analysis whether the Allee effect is strong or weak. **b–f** Results from seven studies which provide quantitative

evidence for a critical density due to the Allee effect: **b** Liebhold and Bascompte 2003 ($\ln r_t = \log$ per capita growth rate, $x_t =$ density), **c** Dulvy et al. 2004, **d** Wittmer et al. 2005, **e** Clutton-Brock et al. 1999, **f** Chen et al. 2002

over a given range of densities, and is only revealed to be strong if observed at sufficiently low population densities. In conclusion, there is relatively limited evidence for strong Allee effects in natural populations, and thus for a key part of the theoretical framework for Allee effects.

Studies finding quantitative support for strong Allee effects show no pattern when grouped by mechanism or taxonomic group (Fig. 7a, b) and both natural experiment and observational study designs provided a variety of types of evidence (S2 in ESM). Strong Allee effects occurred in

multiple taxonomic groups and were caused by mate limitation, predator satiation, and cooperative defense. However, there were some similarities among the seven studies. Three of the studies demonstrated the presence of strong Allee effects in a single species, gypsy moths (Fig. 8b, Liebhold and Bascompte 2003; Johnson et al. 2006; Tobin et al. 2007). In two cases (Johnson et al. 2006; Tobin et al. 2007), the response variable was the replacement rate, or the proportion of populations that replaced themselves. If less than 50% of populations replaced

themselves then the density represented a negative growth rate. A critical density is also revealed by a regression of log-population growth rate on population density (Fig. 8b, Liebhold and Bascompte 2003). The large datasets and the presence of an advancing front of an invasive species resulted in numerous measurements at very low density, enabling statistically significant estimates of the critical densities in various forms. Concurring evidence from multiple datasets and analyses reinforces the potential impact of Allee effects on the spread of invasive species. Notably, Tobin et al. (2007) found evidence for a critical density in some regions of the gypsy moth range but not in others. This extensive work on gypsy moths underscores the potential importance of Allee effects in invasive species, and the feasibility of detecting strong Allee effects in natural populations, while highlighting the large amounts of data that will often be necessary to ensure detection.

Two other studies also compared per capita growth rate to population density. While sample sizes were smaller, population densities were sufficiently low to quantify the critical density (Dulvy et al. 2004, Fig. 8c; Wittmer et al. 2005, Fig. 8d). Clutton-Brock et al. (1999, Fig. 8e) provided evidence for a strong Allee effect by estimating the probability of group loss across various group sizes (an indirect measure of population density), showing that it is lower than expected from a stochastic model and that it extends above 50%, an approach that is similar to the replacement rate for gypsy moths discussed above. Finally, Chen et al. (2002, Fig. 8f) used a modified Ricker model, to argue for a critical density in coho salmon, estimated at 5000 adults (95% CI = (1736, 8686)). All of these studies had data at very low densities, at or below the critical density. Without these data, demonstration that such a density exists must be by extrapolation, severely reducing the power of any statistical test to rule out the null hypothesis that there is no positive critical density. But, the requirement of observing populations below their critical densities is rarely achieved, because a single population that falls below this density is likely to decline to extinction, making detection and monitoring of sufficiently low densities difficult. Accordingly, predicting the critical density for a population of conservation concern before it crosses that density is correspondingly difficult (Lundquist and Botsford 2004).

How do studies on plants compare with those on animals?

Throughout, we have primarily focused on animal populations because they have been studied more thoroughly from both theoretical and empirical perspectives. However, Allee effects can be important in plant populations. Reduced fecundity at low density because of pollen

limitation has been shown for animal-pollinated species of conservation concern (Lamont et al. 1993) and for a wind-pollinated invasive species (Davis et al. 2004a, b). Another invasive species, *Vincetoxicum rossicum* (Asclepiadaceae), attains higher fitness at high density by suppressing background vegetation (Cappuccino 2004). There are clear parallels between these mechanisms and those found in animals, such as between pollen limitation and mate limitation. Are the patterns in empirical evidence for Allee effects in plants similar to the patterns found in animals?

Our ISI search found 28 studies with empirical evidence necessary for examining Allee effects in natural plant populations (S3 in ESM). Of these, twenty-three reported evidence of the Allee effect (Fig. 4b), with twenty focusing on pollen limitation as the mechanism, one on habitat alteration, one on a genetic inbreeding mechanism, and one unknown. The predominance of studies on pollen limitation suggests there may be a more limited set of mechanisms leading to Allee effects in plants. However, the authors often purposely focused on self-incompatible plants as they should be likely to experience pollen limitation (Elam et al. 2007), making it difficult to assess the commonness of Allee effects in plants with other reproduction strategies or the commonness of other mechanisms, a situation which is analogous to mate limitation in aquatic invertebrates. In both cases empirical studies confirm the prior expectation of mate limitation because of passive reproductive behavior, though this expectation probably also biases researchers against investigating other possible mechanisms. The smaller body of research suggests that Allee effects in plants, especially when caused by mechanisms other than pollen limitation, may be less common or less extensively investigated than in animals. Future work should confirm this by looking for additional mechanisms paralleling those found in animals (e.g., Allee effects induced by herbivore satiation) and should take advantage of cases where the sessile nature of plants allows for comprehensive population census, documentation of individual fitness, and replicated manipulation.

Inverse density dependence and parasitoid attack rate

Our bibliographic search revealed a substantial body of work documenting “inverse density dependence” in the attack rate of parasitoids on host insect larvae and eggs (S4 in ESM). These studies included both experimental manipulations and observational data and were often motivated by questions about biological control of pest species. Inverse (positive) density dependence in attack rate should result in an Allee effect on host survival, because a higher proportion of hosts are parasitized at lower host density. Interestingly, these papers did not endeavor to assess fitness or population dynamics of the

host species, reflecting the more limited focus in this literature than in the broader Allee effects literature. Three papers on parasitoids (Campbell 1976; Hopper and Roush 1993; Fauvergue et al. 2007) were included in our broader analysis because they assessed the influence of parasitoid population density on the establishment probabilities of the parasitoids themselves, which was also absent from this group of papers on attack rate. We note that the rate of publication in this area is independent of the recent interest in Allee effects that took place in the plant and animal literature (Fig. 3c), highlighting the distinctiveness of this body of work. Coordinating terminology and linking research on parasitoid attack rate with that on Allee effects has the potential to contribute to both fields by improving understanding of host–parasitoid dynamics and testing theory against a very important class of interspecific interactions.

Conclusions

The number of studies presenting empirical evidence for or against Allee effects in natural animal populations has increased in the past decade, supporting the following conclusions. First, Allee effects have been detected in diverse animal taxa, Mollusca, Arthropoda, and Chordata, including three classes of vertebrates; amphibians and reptiles are notable exceptions. Second, there is evidence of Allee effects caused by at least six mechanisms: mate limitation, cooperative defense, predator satiation, cooperative feeding, dispersal, and habitat alteration. The first three mechanisms constitute 66% of studies on Allee effects in animals, and while the importance of mate limitation is not surprising, the prominence of predator satiation is notable, given its absence from several well-cited definitions of the Allee effect (Myers et al. 1995; Amarasekare 1998). This variety of species and mechanisms suggests that Allee effects may be common, notwithstanding existing meta-analyses that seem to suggest otherwise (Sæther et al. 1996; Gerber and Hilborn 2001). Alternatively, populations may seldom experience densities low enough to produce Allee effects, so that Allee effects are rare among natural populations although they have the potential to affect most species. Current evidence is unable to broadly address this dichotomy. Furthermore, because few studies have directly linked component and demographic Allee effects, and even fewer have demonstrated the existence of critical densities in natural populations, the fact that important theoretical models and assumptions rely primarily on a handful of well-studied examples may be under-appreciated.

Our analysis of the evidence for Allee effects across animal populations has highlighted knowledge gaps and

points to a need for future studies to definitively address the commonness of Allee effects and critical densities. We found that observational studies and natural experiments are generally able to assess demographic Allee effects, but experimental manipulations have primarily focused solely on component Allee effects. We suggest two types of studies have the greatest potential to advance our understanding of the dynamics of low-density populations. First, strong tests of theory and improved understanding of the importance of critical densities in natural populations will need to rely on field-based experimental manipulations that are able to assess population dynamics or rates of colonization and extinctions. Such experiments should allow for larger amounts of data (via replication) from very low population densities and a comparison of the relative strength of positive and negative density-dependent components of fitness. Suitable experiments would also increase our understanding of the interaction among multiple Allee effects. Second, the seven studies successfully detecting critical densities in natural populations depended on long-term/large-scale observational studies and well-chosen analytical methods. While measuring low-density populations is inherently challenging, these studies prove that it can be done effectively, particularly by taking advantage of population response to perturbations such as invasion or harvest. This combination of experiments, increased focus on effective ways to measure very low densities, and approaches connecting component and demographic effects presents the most promise for figuring out the frequency and importance of Allee effects in natural populations.

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