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SPECIAL ISSUE: FEMALE MATING FAILURES

A review of mate-finding Allee effects in insects: from individual behavior to population management

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Abstract

Like other animals and plants, insects may find it difficult to survive and reproduce in small populations, to the extent that their long-term persistence may be jeopardized. The Allee effect is a theoretical framework that formalizes this decrease in survival or reproduction in small populations, and the resulting decrease in population growth and persistence. Mating failure in low-density populations is likely to generate an Allee effect and, therefore, has a major effect on the functioning of small populations. Here, I review mate-finding Allee effects in insect species, and their consequences for individual mating success, population dynamics, and population management. I focus, in particular, on the comparison of theoretical expectations with observational data. Several studies have reported some degree of mating failure at low density. However, almost none of the datasets available allow comparison with the predictions of classical mate-searching models. A few studies at the population level have reported the co-occurrence of mating failure at low density and a demographic Allee effect, but no study has yet clearly demonstrated a causal relationship between mating failure and lower rates of population growth. Thus, although the theoretical development of management tactics based on Allee effects is considered promising, the current lack of evidence supporting this strategy limits its potential relevance. I call here for a more rigorous approach to the study of mate-finding Allee effects and propose new approaches for this purpose.

Introduction

In most plants and animals, each new individual results from the fusion of a male and a female gamete. It is therefore a prerequisite for reproduction that individuals of opposite sexes encounter each other and mate. Males produce smaller gametes than females – a basic asymmetry referred to as anisogamy and defining the essential nature of males and females (e.g., Dawkins, 1976). Anisogamy leads to the production of larger numbers of male than of female gametes, with the obvious consequence that not all male gametes will be able to find female gametes. Male gametes therefore compete for access to limited resources (female gametes) and, as a result, male traits are expected to evolve such that males are good at finding and obtaining these resources. Female mating may therefore be considered a certainty.

Echoing this evolutionary view of sex, theoretical population dynamic models are generally developed with an asexual representation of population size, N. It is implicitly assumed that if females always mate successfully and are therefore able to reproduce, there is no need to take sex into account.

So why bother with sex? The principal reason is that the scenario described above is a caricature that does not hold true in a number of situations, the diversity of which is well illustrated in this special issue on female mating failure (Rhainds, 2013). I focus here on one such situation, small population size, building on the hypothesis that males and females are rare in small populations and may not always encounter one another successfully. Small population size may refer to the total number of individuals (census size) or the density of the population, with a small number of

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individuals per unit area (Stephens et al., 1999). I will use population size and population density interchangeably here, but with a preference for the latter, which is a better determinant of the dynamics of mate encounters. The Allee effect concept will be used as a heuristic guide to approach mating failure at low population density. Allee effects have been well described in a number of landmark publications (Courchamp et al., 1999, 2008; Stephens et al., 1999; Taylor & Hastings, 2005), but I nonetheless provide formal definitions just after this introduction. Here, I highlight the value of the Allee effect concept to studies of mating failure.

A decrease in the probability of mating with decreasing density is referred to as a 'mate-finding Allee effect' (Boukal & Berec, 2009; Gascoigne et al., 2009). It is a particular type of component Allee effect (Stephens et al., 1999), the probability of mating considered here being the component of fitness under scrutiny. Other types of component Allee effects result from decreases in reproduction or survival at low density and are triggered by various mechanisms (e.g., cooperative breeding in African wild dogs, thermal regulation in marmots, cooperative antipredator behaviors in meerkats, predator dilution in colonial seabirds; Berec et al., 2007). A component Allee effect may cause a decrease in the per capita growth rate with decreasing population density (a demographic Allee effect; Courchamp et al., 1999; Stephens et al., 1999). Ultimately, if the growth rate becomes negative, or if stochastic and genetic processes occur alongside Allee effects, this process may doom small populations to extinction (Lande, 1988; Caughley, 1994; Courchamp et al., 1999; Grevstad, 1999b; Stephens & Sutherland, 1999; Dennis, 2002; Fauvergue et al., 2012). Hence, thinking in terms of Allee effects makes it possible to capitalize on the known duality of component and demographic Allee effects, thereby bridging the gap between individual behavior and population phenomena and, further, population management. The Allee effect can thus be used to decipher the links between mating failure at low density and crucial population phenomena, such as decline and extinction.

The number of review articles on the Allee effect has increased exponentially (before 2002: n = 3; 2003–2007: n = 11; 2008–2012: n = 25), and the first textbook dedicated to this subject was published recently (Courchamp et al., 2008). These efforts have improved the definition of theoretical concepts (Courchamp et al., 1999; Stephens et al., 1999), have brought together fragmentary information (Taylor & Hastings, 2005; Gascoigne et al., 2009; Kramer et al., 2009), and have led to the emergence of new ideas (Berec et al., 2007; Tobin et al., 2011). They have also driven the emergence of the Allee effect as a strong scientific theory, with clear hypotheses and predictions, numerous second-generation models, an increasing body of data, and major consequences for conservation biology, invasion biology, and biological control. So why do we really need another review article on this subject? There are several good reasons for reviewing the relationship between population density and mating success:

1. This review, unlike those that have preceded it, focuses on insects. This restriction to a particular taxonomic group may provide a novel view of previous publications and yield new insight. Furthermore, several of the features of insects, described below, are specific to this group, justifying a specific review.
2. Hexapoda is the largest class of living organisms. With about one million species described, insects account for more than half of all known living organisms. They also dominate animal life on Earth in terms of total biomass (Price et al., 2011). However, Hexapoda is also characterized by impressive adaptive radiation, with an extraordinarily rich fauna and astonishing diversity of lifestyles (Price et al., 2011). For these reasons, focusing on insects in investigations of mate-finding Allee effects should bring to light interesting findings.
3. In a recent meta-analysis, Kramer et al. (2009) showed that terrestrial arthropods (mostly insects) were the group of organisms for which the largest number of studies on Allee effects had been published and for which the largest proportion of studies suggested the existence of Allee effects. One third reported strong demographic Allee effects (with negative growth rates at low density), with mate finding the most frequently identified underlying mechanism. This suggests that the mate-finding Allee effect is a relevant process in insects, at both the individual and population levels.
4. Insects are key organisms in agroecosystems, and their response to small population size is a central question for applied ecologists. First, as pollinators, the ecosystem services provided by this group are so crucial that their decline is alarming (Potts et al., 2010). The Allee effect can provide us with a framework for understanding the functioning of declining populations and for developing conservation policies (Wells et al., 1998; Stephens & Sutherland, 1999; Armstrong & Wittmer, 2011). Second, phytophagous insects cause considerable losses on vegetable crops and the manipulation of mate-finding success is at the core of several pest management strategies (Liebhold & Tobin, 2008; Tobin et al., 2011). Third, many insects are predators or parasitoids of other insects and, as such, they form the cornerstone of biological control. When introduced into target environments, natural enemies may be subject to severe bottlenecks, preventing their establishment (Shea &

Possingham, 2000; Fauvergue et al., 2012). Mate-finding Allee effects have been identified as a possible mechanism underlying the failure of populations to become established (Hopper & Roush, 1993; Grevstad, 1999b).

5 Warder Clyde Allee urged ecologists to pay more attention to small populations and positive density dependence, favoring this approach over adding to the already abundant research on large populations and negative density dependence (Allee suggested that doing so could be more 'romantic'; Courchamp et al., 2008). As experiments on insects were at the very heart of the formulation of the Allee effect concept (Figure 1), a review on insects fits to the research avenue envisioned by WC Allee.

This review is structured into four main sections. The first deals with theory and provides general definitions of the Allee effect, followed by a review of the effect of population density on mating success and the expected effects of mate-finding Allee effects on population dynamics. The second section consists of a review of the evidence, or lack thereof, for relationships between population density, mating success, and the dynamics of small populations. The third section addresses the implications of mate-finding Allee effects for population management, focusing on three issues: the disruption of mating with sex pheromones, the release of sterile males, and classical biological control. In the final section, I bring together the results and propose important perspectives for future research.

I will focus on the relationship between population density and mating success reflecting the difficulty of finding a mate at low population density. Hence, mating success will be considered as a binary variable, with a female either mating or not mating. Small populations may also constrain the availability of compatible mates for both sexes (Kokko & Rankin, 2006), but this aspect will not be dealt with in this article.

Theory

What are Allee effects?

A formal definition of Allee effects is required for a clear understanding of the following sections, so that although Allee effects have been well defined elsewhere (Courchamp et al., 1999, 2008; Stephens et al., 1999; Taylor & Hastings, 2005), it is worth defining them again here. A component Allee effect is defined as a decrease in any component of fitness with decreasing population size or density. A decrease in the probability of a female mating with decreasing male density is therefore a component Allee effect, and is generally referred to as a 'mate-finding Allee effect' (Figure 1A provides an illustration for weevils). A component Allee effect is a form of positive density dependence: the component of fitness considered is positively affected by population size or density. Population size may affect one or more fitness components positively and others negatively. Depending on the respective strengths of these opposing influences, a component Allee effect may or may not yield a decrease in 'total individual fitness' (and in turn, population growth rate) with

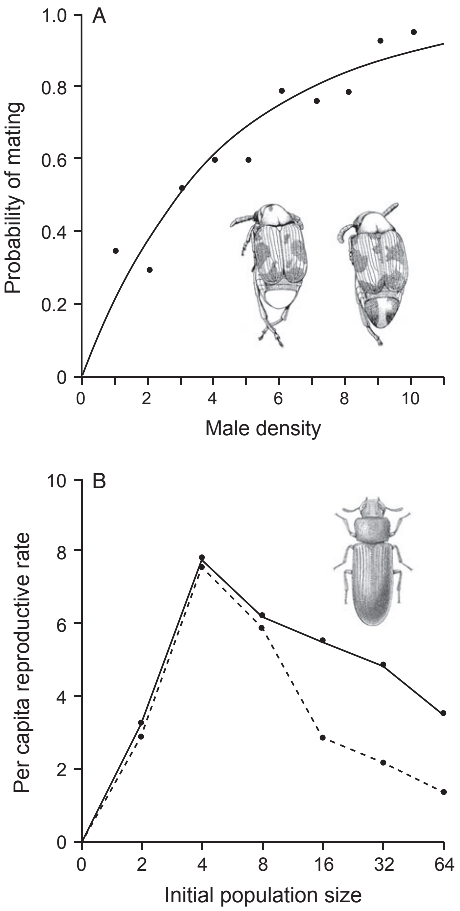

Figure 1 Examples of component and demographic Allee effects in insects. (A) Mate-finding Allee effect in the Azuki bean weevil, *Callosobruchus chinensis*; male density is the number of males per 100 cm^2. Data are from Nishigaki (1963) and the fit of a negative exponential model is from Dennis (1989). (B) Demographic Allee effect in *Tribolium confusum*: at small population sizes, the per capita rate of reproduction decreases with decreasing population size; for larger populations (>4 individuals) negative density dependence is observed and the rate of reproduction decreases with increasing population size. Population size is the initial number of adults per 32 mg of flour. Rates of reproduction were assessed at 11 days (solid line) and 25 days (dashed line). Data were obtained by Chapman (1928) and further analyzed and interpreted by Allee (1931).

decreasing population size or density. A demographic Allee effect is observed if negative density dependence does not outweigh component Allee effects; it is defined as a decrease in per capita growth rate with decreasing population size (Figure 1B provides an illustration for flour beetles). An important detail is the sign of population growth, which may remain positive even for the smallest populations (in the case of a weak demographic Allee effect) or may become negative when population size decreases below a given level referred to as the 'Allee threshold' (in the case of strong demographic Allee effects). The Allee threshold is an unstable demographic equilibrium occurring in the presence of strong Allee effects only: any population with a size below the Allee threshold is deterministically driven to extinction. In summary, a demographic Allee effect at the population level is always produced by one or more component Allee effects at the individual level. Conversely, a component Allee effect may or may not yield a demographic Allee effect (depending on its strength), and such demographic Allee effects may or may not result in population extinction.

How does population density affect mating success?

Mathematical models of mate finding have formalized a general prediction that can be expressed verbally as follows: mating success should decrease with decreasing population density until there are no more potential mates in the surroundings and the probability of mating is zero (an anecdotic example of this situation, reported in the Herald Tribune of June 20th, 1987, is the North American bald eagle christened Iolar after it had crossed the Atlantic and landed, exhausted, in Ireland; in the absence of members of its own species, the eagle would have died there without reproducing and was therefore sent back home). Conversely, mating success should increase with increasing population density, until the density of mates is high enough for mating to be guaranteed. Between these two extremes, the dependence of mating success on density may vary with the spatial distribution of males and females (the mating system), operational sex ratio, movement, and the types of behavior underpinning mate finding.

Mathematical formulations of these verbal predictions have been derived, focusing on female mating success. Various functions relating the probability of a female mating p(M,F) to the densities of males (M) and females (F) have been proposed [Table 3.2 in Courchamp et al. (2008) provides an extensive list; see also Boukal & Berec (2009)]. These functions have several general features: (1) a female has no chance of mating if there are no males, i.e., $p(0,F) = 0$; (2) female mating probability increases monotonically with male density, i.e., $dp(M,F)/dM>0$ for all values of M; (3) female mating probability converges asymptotically toward 1 when the density of males is high, i.e., $p(M,F)\rightarrow 1$ when $M\rightarrow\infty$.

The negative exponential model displays these general features and has often been used to model mate-finding Allee effects, probably because it is simple and fits the observed data well (Dennis, 1989; McCarthy, 1997). This model assumes that searching for a mate is a random process, such that the probability of a female meeting at least one male by time T can be inferred from the Poisson distribution:

$$P = 1 - e^{-M\theta} \qquad (1)$$

where M is male density and θ is a constant quantifying the relationship between male density and mate finding (the strength of an Allee effect is proportional to the inverse of θ). A mechanistic interpretation of θ has often been proposed, based on the fact that the use of a Poisson model implies that the mean number of mating events per female can be expressed as $M\theta$. θ may reflect the area searched during time T by individual males (e.g., Mosimann, 1958; Dusenbery, 1989; Hopper & Roush, 1993; McCarthy, 1997), and may therefore be expressed as $\theta = 2\nu\delta$, where ν is male velocity (m h^{-1}) and δ is mate-detection distance (m). Figure 2A shows the effect of population density on mating probability under an assumption of random searching (equation 1),with three different mate-detection distances. If the mate-detection distance is low, female mating probability decreases with decreasing population density and there is, therefore, a mate-finding Allee effect. If males detect females very efficiently (high mate-detection distance), the mate-finding Allee effect is included, by definition, in the negative exponential model, but may not be apparent at common population densities (Figure 2A, dotted line).

If search rate varies between individuals, the probability of a female mating may be expressed in an alternative manner, as the rectangular hyperbola:

$$P = \frac{M}{M + \beta^2} \qquad (2)$$

where $\beta = 1/\theta$, with θ being the mean area searched per unit time, rather than a constant as in the negative exponential model (McCarthy, 1997). β is also interpreted as the male density at which half of the females mate. In practice, however, the two models may fit observed data equally well (Dennis, 1989), and the choice of model is thus often a question of personal preference. I tend to prefer the negative exponential model, due to its straightforward assumption that the search for a mate follows a Poisson process, in which a random component is combined with simple mechanisms relating to information use

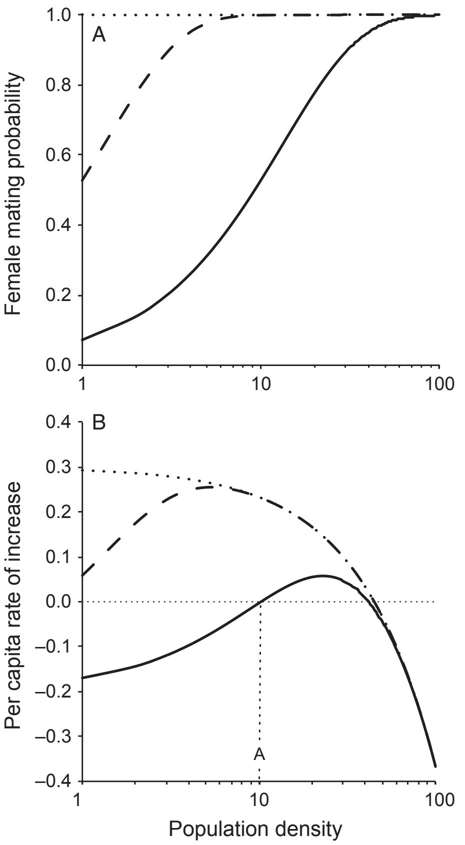

Figure 2 Effect of mate-detection distance on mating success and population growth. Three values are used for mate-detection distance: $\delta = 0.075$ m (dotted lines), 0.75 m (dashed lines), and 7.5 m (solid lines). Other parameter values were velocity ($v = 1\ \text{m h}^{-1}$), time ($T = 1$ h), birth rate ($b = 0.5$), death rate ($d = 0.2$), and carrying capacity ($H = 30$); a balanced sex ratio was assumed ($M = N/2$). (A) Probability of a female meeting a mate and mating vs. population density N, as predicted by the negative exponential model. (B) Density dependence on population growth when mating probability follows the negative exponential model. The smallest mate-detection distance yields no demographic Allee effect (dotted line, representing strict negative density dependence). Higher mate-detection distances produce a weak (dashed line) or a strong Allee effect (solid line). The strong Allee effect is characterized by a threshold population size (A, the Allee threshold), below which the population growth rate is negative. Any population declining below this threshold is deterministically doomed to extinction.

(mate-detection distance) and movement (velocity). The negative exponential model can be used as a general framework for studying various mate-finding behaviors. For instance, it has been used to model mating success when male parasitoids flit from stem to stem in cereal fields, arresting on stems marked by conspecific virgin females (Fauvergue et al., 1995; Fauvergue & Hopper, 2009).

How does mating success affect population growth?

If only a fraction P of the females in the population mate, the birth rate should be lower than that in a population in which all the females mate. If the fraction of females mating depends on population size N, as assumed by mate-finding Allee effect models (equation 1), then population dynamics should be affected by a feedback loop between population size, mating success, and birth rate. Many mathematical approaches to Allee effects have been developed, but some are difficult for non-mathematicians to understand. However, with a basic understanding of the principles outlined above, a good textbook (Hastings, 1997), and minimal experience with population dynamic modeling, the construction of an Allee effect population model is reasonably straightforward. If we assume a simple continuous-time population model in which the instantaneous birth rate (b) and death rate (d) are initially assumed to be constant and immigration/emigration is negligible, the rate of change in the number of individuals is as follows:

$$\frac{dN}{dt} = bN - dN \tag{3}$$

Expressed per individual, this gives the per capita rate of increase:

$$\frac{dN}{Ndt} = b - d \tag{4}$$

A population modeled with equation 4 would continually increase (assuming b>d), so the second step in the modeling process is the addition of at least a minimal level of realism, through the introduction of negative density dependence. This can be achieved by assuming that the death rate increases with increasing N, a relationship that can be expressed by replacing d with $d(1 + N/H)$ (e.g., Berec et al., 2007). The constant H is proportional to the carrying capacity K of classic logistic population growth (Verhulst, 1838; $H = Kd/r$). Finally, positive density dependence can also be introduced in the form of a mate-finding (component) Allee effect. For this, we use the negative exponential model (equation 1) to formalize the assumption that only the females that mate contribute to the birth rate. With the two signs of density dependence, the per capita rate of increase is as follows:

$$\frac{dN}{Ndt} = b\left(1 - e^{-\frac{N}{2}\theta}\right) - d\left(1 + \frac{N}{H}\right) \tag{5}$$

A balanced population sex ratio of 0.5 is assumed, so the male density (M) in equation 1 can be replaced by N/2 in equation 5. Figure 2B shows the relationships between per capita rate of increase and population density predicted by equation 5. High values of θ indicate that a large area is searched by males and, thus, that female mating success is not particularly sensitive to density. At the population level, no demographic Allee effect is observed (Figure 2B, dotted line). Lower values of θ, possibly due to shorter mate-detection distances, produce a weak demographic Allee effect with a rate of increase that remains positive even for the smallest populations (Figure 2B, dashed line), or a strong Allee effect with a negative population growth rate when population size falls below the Allee threshold (Figure 2B, continuous line). Thus, the outcome at the population level (presence or absence of a demographic Allee effect) of a mate-finding Allee effect depends on the ability of males to locate females.

Various population dynamic models incorporating a mate-finding Allee effect have been published (e.g., Dennis, 1989; Hopper & Roush, 1993; Grevstad, 1999b; Berec et al., 2001; Boukal & Berec, 2002, 2009; Pavlova et al., 2010; Gordillo, 2011). In some models, the assumptions of constant sex ratio and equal mortality rates in males and females of equation 5 have been relaxed. This is particularly relevant in haplodiploid organisms, such as insects of the order Hymenoptera. In haplodiploids, females that have not mated can produce some offspring, albeit only (haploid) males, so mating failure results in a sex ratio bias toward males rather than a decrease in birth rate (e.g., Godfray, 1990; Fauvergue et al., 2008; Fauvergue & Hopper, 2009). This unusual feature may decrease mate-finding Allee effects via feedback effects on sex ratio (Fauvergue et al., 2007), but it cannot entirely conceal the influence of these effects on the dynamics of small populations, at least in theory (Hopper & Roush, 1993).

Evidence

How does population density affect mating success?

Several studies have attempted to quantify the effect of population size on mating success in insects. I identified 34 such studies, essentially by cross-reference searching, and have summarized their methods and results in Appendix 1. In 19 of these studies, a positive relationship was found between density and mating success (mating probability increased with increasing population density), no relationship was found in 12 studies, and the remaining three studies reported a negative relationship. Thus, published studies provide similar degrees of support for (56% of the studies) and against (44% of the studies) the existence of a mate-finding Allee effect in insects ($\chi^2 = 0.27$, d.f. = 1, P = 0.60). Most studies suggesting a positive relationship between density and mating success were based on qualitative assessment. A mechanistic model, such as the negative exponential model (equation 1), was fitted to the data for only two species: the gypsy moth *Lymantria dispar* (L.) (Sharov et al., 1995; Tcheslavskaia et al., 2002) and the Azuki bean weevil *Callosobruchus chinensis* (L.) (Nishigaki, 1963; Dennis, 1989).

Insects of the order Lepidoptera were far more frequently studied (17 studies) than those of the other orders of insects (Orthoptera: 5; Diptera: 4; Coleoptera: 3; Hymenoptera: 2; Hemiptera, Odonata, and Phasmoptera: 1 species each). The preponderance of studies on Lepidoptera can be accounted for in part by the extensive research carried out on gypsy moth. Four studies focused solely on the relationship between density and mating success in this species (Sharov et al., 1995; Tcheslavskaia et al., 2002; Contarini et al., 2009; Tobin et al., 2013). This is no surprise, given the status of *L. dispar* as a major invading pest in North America and the key contribution of Allee effects to the development of strategies for controlling its spread. Orthopterans are also well represented, probably because crickets have long served as model organisms for research on mating behavior (Tregenza & Wedell, 2002; Hunt et al., 2004). In this group, males avoid mating failure by adapting their mating tactics to local population density (French & Cade, 1989; Hissmann, 1990; Cade & Cade, 1992; Kindvall et al., 1998). Only two studies of hymenopterans were carried out (Fauvergue et al., 1995; Fauvergue & Hopper, 2009), and this is very little, given the potential consequences of mate-finding Allee effects for the success of organisms introduced for biological control.

Density and mating success are estimated with a panel of methods with different powers for making robust inferences. The detection of a mate-finding Allee effect requires independent estimates of male density and of the proportion of females mating (equation 1). Rhainds (2010) provided a thorough description of various techniques for the assessment of female mating status, and population densities are best estimated by mark–release–recapture approaches – Matter & Roland (2013) provide a recent and beautiful field study where a mate-finding Allee effect was unveiled based on such estimation. However, many alternative methods are listed in Appendix 1. Field observations in Lepidoptera (15 studies) predominated among the 34 studies of the relationship between density and mating success. In many of these species, the number of spermatophores in the mating tract is correlated with mating frequency (Burns, 1968) and may provide some indication of mating success. In bagworms, which are also well represented in publications on mating failure (Appendix 1), mating status can be deduced from the presence/absence of progeny and pheromone scales in the cases built by these moths for protection and from which females do not disperse (Rhainds et al., 1999). An intriguing observation from studies on *L. dispar* and other species is that male density is often assessed by determining the rate of male capture on traps baited with synthetic sexual pheromone (Sharov et al., 1995; Tcheslavskaia et al., 2002; Contarini et al., 2009; Régnières et al., 2013; Tobin et al., 2013). Such a method will be discussed later as it may yield a circular reasoning (females are more frequently mated where they attract more males).

Appendix 1 also highlights various scientific designs. For simplicity, I have used a four-level (2 × 2) classification: field vs. laboratory, and observation vs. experiment, with the term 'experiment' being restricted to manipulative experiments. As mentioned above, field observation (mostly on Lepidoptera) appears to be the most widely used approach (21 studies). However, manipulative field experiments have also been attempted on crickets, or via the diversion of species introductions for biological control. All available laboratory experiments on model insects, such as *Drosophila* and coleopterans, were published before 1975 and involved placing different numbers of mating pairs in mating chambers and recording their behavior. Evidence for a positive relationship between density and mating success was obtained in about half the studies based on observation (13/21) and about half the studies based on experimentation (6/13; these proportions are not significantly different: ($\chi^2 = 0.61$, d.f. = 1, $P = 0.44$).

A compilation of studies on mating success, such as that proposed in Appendix 1, is also of potential historical value. A few seminal studies were published around 1940 [MacLagan & Dunn, 1935; Teesdale, 1940; Utida, 1941; see also Watt 1960 for an ancient review, and Dennis, 1989]. About 20 articles were published between 1960 and 2000 and about 10 during the next decade. This pattern of publication parallels the development of the Allee effect as a concept in population ecology, beginning with the discovery of positive density dependence at low density in laboratory experiments on model insects, such as *Tribolium confusum* Jaquelin Du Val (Chapman, 1928), their reinterpretation by Allee (1931, Figure 1), the development of the concept of the Allee effect (MacLagan, 1932; Park, 1933; Fujita, 1954; Odum & Allee, 1954), and its recent resurgence with the rise of modern invasion biology and conservation biology (Courchamp et al., 1999, 2008; Stephens & Sutherland, 1999; Taylor & Hastings, 2005).

How does mating success affect population growth?

Evidence for demographic Allee effects resulting from mating failure in small populations is rare. In their review of mate-finding Allee effects, Gascoigne et al. (2009) identified only four species for which strong evidence is available: a plant, *Spartina alterniflora* Loisel., a copepod, *Hesperodiaptomus shoshone* (SA Forbes), and the two insects for which the findings are described in detail below.

The Glanville fritillary butterfly, *Melitaea cinxia* L., has a wide geographic distribution, but has been studied mostly as a model species for metapopulation dynamics in the Åland Islands in southwest Finland. The metapopulation occupies a network of dry meadows and persists due to a balance between local extinctions and recolonizations (Hanski et al., 1994). Each local population typically consists of less than 10 groups of mostly full-sib larvae and has a high risk of extinction. Kuussaari et al. (1998) found that the proportion of females mating in local populations increased from 0.7 to 0.9 with an increase in the number of larval groups, suggesting a small, but significant mate-finding Allee effect. The smallest populations had a lower reproductive output and a smaller probability of increasing in size between years than larger populations (0.2 vs. 0.3). This demographic Allee effect may result from mating failure in small populations. However, as carefully discussed by Kuussaari et al. (1998), this interpretation, although attractive, is made less likely by the insignificant effect of the proportion of females mating on population growth rate ($P = 0.1$) and the known occurrence of other deleterious processes in small populations of *M. cinxia* (emigration from small patches: Kuussaari et al., 1998; parasitism: Lei & Hanski, 1997; inbreeding depression: Saccheri et al., 1998).

The gypsy moth, *L. dispar*, is native to the northern hemisphere of the Old World, where it feeds and reproduces mostly on oak trees. Following its introduction into North America, it has become a major invasive pest on this continent (Liebhold et al., 1992). Considerable research efforts are now being devoted to the population biology of *L. dispar* at the invasion front, focusing, in particular, on colonization-extinction dynamics (Johnson et al., 2006; Tobin et al., 2007, 2009; Vercken et al., 2011). As mentioned above, the existence of a mate-finding Allee effect has been documented repeatedly in this species. A strong demographic Allee effect has been demonstrated as an effect of density on the probability of population increase (estimated from paired estimates of density), and a probability of increase below 0.5 has been found below various threshold population densities (Tobin et al., 2007). Most data for gypsy moth suggest that mating failure at low density is the most likely explanation (Liebhold & Bascompte, 2003; Tobin et al., 2009), but other processes, even if less widely studied than mating failure, cannot be entirely discarded.

Similar results have been obtained in studies of the introduced beetles *Galerucella calmariensis* (L.) and *Galerucella pusilla* (Duftschmid), although these findings are less frequently cited in this context. These two species were introduced into North America as biological control agents against the purple loosestrife, *Lythrum salicaria* L.

This introduction made it possible to carry out an experimental test of theoretical predictions relating to initial population size, mate-finding Allee effects, stochasticity, and the probability of establishment (Grevstad, 1999b). In these two species, population growth rates increased with increasing initial population size (Grevstad, 1999a) and mating failure at low density was identified as a putative underlying mechanism for one of the two species (Grevstad, 1998). Hence, small introduced populations of *G. calmariensis* and *G. pusilla* experience a demographic Allee effect, possibly resulting from a mate-finding Allee effect.

By contrast, a few case studies on insects have shown (1) the presence of a mate-finding Allee effect, but no demographic Allee effect, (2) the presence of a demographic Allee effect, but no mate-finding Allee effect, and (3) the complete absence of Allee effects. The first of these situations was reported for the alpine butterfly *Parnassius smintheus* Doubleday. Like the Glanville fritillary butterfly, this species has a metapopulation structure with interconnected populations occurring in alpine meadows along the east slope of the Rocky Mountains of Canada (Roland et al., 2000; Matter & Roland, 2010). In a recent study, Matter & Roland (2013) estimated the proportion of females mating, local density, and population growth across 17 populations and 12 years (more than 10 000 individuals captured). Mating success varied considerably, both within and between populations, but a significant proportion of this variation was accounted for by local population density. Consistent with a negative exponential model (equation 1), the increase in female mating probability was characterized by a sharp increase at the lowest densities and a slow convergence to 1 at higher densities. However, population growth showed clear negative density dependence, with no significant effect of female mating success (Matter & Roland, 2013). The second situation (presence of a demographic Allee effect, but no mate-finding Allee effect) was found in populations of *Aphelinus asychis* Walker, a parasitoid wasp introduced into North America to control the Russian wheat aphid. In an experiment in which initial population size was manipulated to test for the presence of mate-finding Allee effects, Fauvergue & Hopper (2009) found no effect of population density on mating success. Surprisingly, however, they found that populations founded with many wasps grew more rapidly than populations founded with few wasps. This difference persisted over several generations, suggesting that a genetic process, and not mate-finding, was affecting the demographic success of the small introduced populations. The third situation (a simultaneous absence of mate finding and demographic Allee effects) is obvious and certainly widespread, but there the evidence is far from unequivocal. Strong support is again provided by experimental introductions of parasitoid wasps for biological control. *Neodryinus typhlocybae* (Ashmead) was introduced at 45 sites on the French Riviera, to control the flatid planthopper *Metcalfa pruinosa* (Say). Initial population size was manipulated to test for the presence of Allee effects. Intensive sampling across three consecutive reproductive seasons revealed a complete absence of mate-finding Allee effects and of demographic Allee effects, with population growth greatest for populations founded with a single gravid female (Fauvergue et al., 2007).

Mate-finding Allee effects and population management

Several avenues of research into the use of a mate-finding Allee effect for insect population management have been developed. I will analyze here three population management practices: the release of large amounts of sex pheromones to disrupt mate-finding in pest populations, the release of sterile males (which does not strictly disrupt mate finding, but does decrease female fertility and may therefore be useful for the control of insect pests), and the introduction of biological control agents to control unwanted populations, in situations in which the beneficial organism may suffer from an Allee effect before its establishment in the target environment.

Sexual confusion

Models and reviews of sexual confusion approaches have recently been published (Liebhold & Bascompte, 2003; Liebhold & Tobin, 2008; Boukal & Berec, 2009; Tobin et al., 2011; Blackwood et al., 2012). The core reasoning is as follows: if an invasive or otherwise unwanted population experiences an Allee effect, it may be possible to act on underlying processes so as to increase the Allee threshold (i.e., the range of population sizes leading to extinction). This is precisely the purpose of mating disruption tactics based on the release of large amounts of sex pheromones. A simple model was described by Blackwood et al. (2012), which I have modified slightly here to render it consistent with those described above. Let us assume that S false pheromone sources are introduced into the mating pool, each source being as attractive as an individual female. An immediate consequence is that only a fraction F/(F + S) of the M males will be available to mate with true females. Using equation 1, with N/2 replacing F and M, the probability of a female mating becomes:

$$P = 1 - e^{-\left[\frac{N}{2} \cdot \frac{N}{N+2S}\theta\right]} \tag{6}$$

Figure 3A shows the effect of mating disruption on the relationship between female mating probability and population density: the larger the number of false pheromone sources, the more severe the mate-finding Allee effect. The modified expression for the probability of mating (equation 6) can then be inserted into a basic population dynamic model (equation 5), to investigate the consequences of mating disruption for population growth. An increase in the abundance of false pheromone sources yields a lower per capita rate of population increase and the appearance and increase of the Allee threshold (Figure 3B). Hence, populations with a weak demographic Allee effect, which would otherwise have continued to increase naturally in size until they reached the carrying capacity of the environment, may become extinct due to the combination of a weak mate-finding Allee effect with the introduction of mating lures. This theoretical result is particularly promising for population management, especially as formulated by Boukal & Berec (2009): 'as long as the pest population remains under the extinction threshold brought about by difficulties in finding mates, all we need to do is relax, drink mojitos, and wait until the last unfortunate moth expires'. However, it is important to note that in the absence of a mate-finding Allee effect, all females mate (P = 1) and the population dynamics (equation 5) follows the classic logistic growth pattern with a single stable equilibrium at the population carrying capacity.

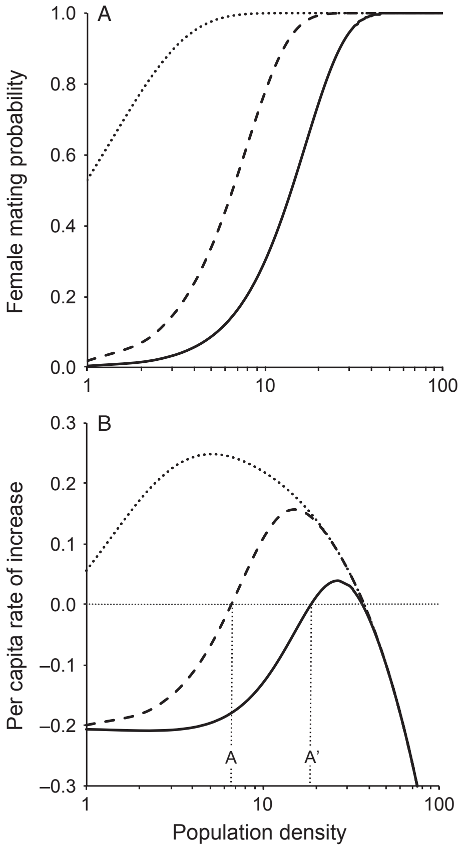

Figure 3 Effect of mating disruption on mating success and population growth. Mating is disrupted by the release of S female-equivalent pheromone sources: S = 0 (dotted lines), 20 (dashed lines), or 100 (solid lines). Other parameter values are the area searched by males ($\theta = 1.5\ \mathrm{m}^2$), birth rate (b = 0.5), death rate (d = 0.2), and carrying capacity (H = 30); a balanced sex ratio was assumed (M = N/2). (A) The mate-finding Allee effect assumed by a negative exponential model occurs in the absence of mating disruption (dotted line) and becomes more intense with increasing densities of pheromone sources (dashed and solid lines). (B) At the population level, the consequence is a decrease in population growth rate at low density and the appearance and increase of the Allee threshold (A→A′), corresponding to an expansion of the range of population sizes for which the population is doomed to extinction.

Sterile males

The release of sterile males can also be used to manage unwanted populations. Again, by adapting the models developed above, we can see how this technique interferes with mate-finding Allee effects and affects the population. We can begin by assuming that the introduction of a number of sterile males into a population of size N results in a proportion U of the N/2 males being sterile. The probability that a female mates with a fertile male is now a function of the probability of encountering and mating with a male, whether sterile or fertile (equation 1), and the probability (1 − U) of this male being fertile, which gives:

$$P = (1 - U)\left(1 - e^{-\frac{N}{2}\theta}\right) \qquad (7)$$

This does not change the severity of the mate-finding Allee effect (the slope of the relationship between female mating probability and population density), but constrains mating success to an upper asymptote dependent on U (Figure 4A). When inserted into a population dynamic model (equation 5) with the assumption that only fertile females contribute to the birth rate of the population, this generates demographic Allee effects, with the per capita rate of increase being lower for higher proportions of sterile males, and an increase in the Allee threshold (Figure 4B).

Introduction of biological control agents

The third line of research concerns classical biological control and the quest for optimal release strategies. The basic problem can be stated as follows: given a fixed total number of exotic natural enemies to be introduced into a target environment, what is the optimal balance between the number of independent introductions and the number of individuals per introduction likely to result in the

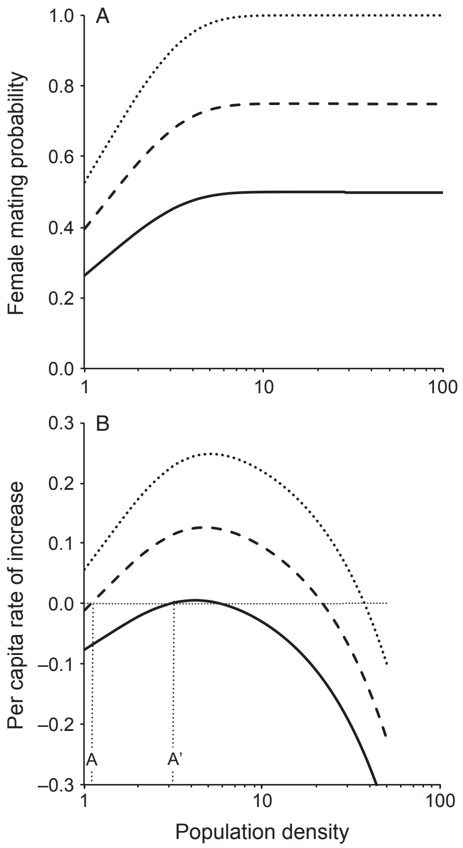

Figure 4 Effect of the release of sterile males on mating success and population growth. Females mate with sterile males with a probability depending solely on their proportion U in the population: U = 0 (dotted line), 0.25 (dashed lines), or 0.5 (solid lines). Other parameter values are the area searched by males ($\theta = 1.5$ m^2), birth rate ($b = 0.5$), death rate ($d = 0.2$), and carrying capacity ($H = 30$); a balanced sex ratio was assumed ($M = N/2$). (A) The mate-finding Allee effect assumed by a negative exponential model occurs in the absence of sterile males (dotted line). With increasing proportions of sterile males, female mating probability converges to a lower asymptote (dashed and solid lines). (B) At the population level, the consequence is a decrease in population growth rate in the presence of sterile males, at all densities, and the appearance and increase of the Allee threshold (A→A′), corresponding to an expansion of the range of population sizes for which the population is doomed to extinction.

maximum number of established populations (Freckleton, 2000; Shea & Possingham, 2000)? This problem is crucial, because the introduction of biological control agents, like all other deliberate or fortuitous species introductions, is likely to be unsuccessful due to the small initial size of the population (Hopper & Roush, 1993; Lockwood et al., 2005; Simberloff, 2009; Fauvergue et al., 2012). One possible reason for this is that introduced populations suffer from mate-finding Allee effects. In a pioneering theoretical approach to Allee effects, Hopper & Roush (1993) developed a reaction-diffusion model with two sexes to investigate the role of mate finding in the dynamics of populations spreading from a single release point. They assumed that the probability of female mating followed a negative exponential model, as in equation 1. Two important predictions relating to mating failure were derived: (1) the frequency of mated females was predicted to decrease with increasing distance from the release point, with a sharp decrease at the invasion front; (2) the critical number of females, above which an introduced population becomes established, is sensitive to the mate-detection distance (a large mate-detection distance decreases the mate-finding Allee effect and allows the introduction of fewer individuals). No formal analysis has yet been carried out, but theoretical relationships between mate-detection distance and critical initial population size, as proposed by Hopper & Roush (1993), could serve as a starting point for predicting optimal release strategies. Other models were then developed in the same vein (Grevstad, 1999b; Berec et al., 2001), confirming the theoretical key role of mate-finding Allee effects in the relationship between initial population size and establishment probability for introduced organisms. Spatial processes have also recently been taken into account and it has been suggested that establishment may be a function not only of the initial number of individuals, as predicted by classical Allee effect models but also of the size of the patches occupied by colonizing populations (Vercken et al., 2011).

Conclusion, criticisms, and perspectives

This review illustrates how, in sexually reproducing insects, individual mate-finding behaviors may affect population dynamics, with possible consequences as dramatic as population extinction. These behaviors can thus serve as a basis for the development of population management strategies. I used the Allee effect concept as a heuristic guide in this review. At the scale of the individual, the mate-finding Allee effect is defined as a decrease in mating success with decreasing population size and can be readily formalized by simple mechanistic models in which individual traits, such as mate-detection distance and velocity, are combined with random walking. Depending on these traits, a mate-finding Allee effect may or may not translate into a demographic Allee effect and may have an impact on several facets of insect population management. I have discussed the use of mating disruption and sterile males, which may facilitate the eradication of invasive or otherwise unwanted species subject to mate-finding Allee effects. Mating failure in small, introduced populations of beneficial insects may also be a major impediment for classical biological control.

Efforts to relate individual behavior to population dynamics and management are not new (Hassell & May, 1985; Lima & Zolner, 1996; Sutherland, 1996). However, with only a few exceptions (Buchholz, 2007; Caro, 2007), these efforts have focused principally on negative density dependence and demographic stability in large populations. In this perspective, the Allee effect provides a well-grounded theoretical framework linking individual behavior to population dynamics. Moreover, the specific focus on positive density dependence in small populations makes this approach more relevant for addressing issues in conservation biology, invasion biology, and biological control (i.e., whenever populations are declining or experiencing severe bottlenecks).

One of my aims in this review was to evaluate the amount of empirical support for mate-finding Allee effects provided by studies of insects. I found some evidence for a higher frequency of mating failure at low population densities (and some evidence against), but it remains unclear in most studies whether female mating probability conforms to theoretical expectations. One of the strongest pieces of evidence for a mate-finding Allee effect was provided by the study by Matter & Roland (2013). The effect identified in this study is quantitatively not very strong, but the use of 17 wild populations over 12 years and the precise estimation of population densities and mating status, based on capture–mark–recapture sampling, is exemplary. The principal advantage of capture–mark–recapture approaches for assessing population density is their complete independence of the variable to be explained, i.e., the proportion of females mating. By contrast, several studies on Lepidoptera have used the recapture rate of males at pheromone-baited traps as a surrogate of male density (Régnières et al., 2013; Tobin et al., 2013). This rate may accurately reflect background male density, but such a method to assess population density may also produce a trivial relationship between male attraction toward sex pheromones (used as a surrogate of male density) and the attraction of males to tethered females, followed by mating (used to assess female mating probability). Indeed, in the same species, male attraction to sex pheromones is sometimes used to infer mating probability rather than male density (Robinet et al., 2008). This proximity between the explained and explanatory variables raises questions about the apparent circularity in studies of component Allee effects. Nevertheless, notwithstanding these methodological twists, this review shows that a mate-finding Allee effect does occur in some insect species.

Unequivocal demonstrations that a mate-finding Allee effect causes a demographic Allee effect are even more challenging to obtain. Some authors have interpreted the co-occurrence of mate-finding and demographic Allee effects as proof of a causal link between the two [reviewed in, e.g., Gascoigne et al. (2009)]. Studies of *L. dispar* fall into this category, with field data suggesting the existence of both a mate-finding Allee effect (Sharov et al., 1995; Tcheslavskaia et al., 2002; Contarini et al., 2009; Tobin et al., 2013) and a demographic Allee effect (Tobin et al., 2007, 2009). This Allee effect may slow the spatial spread of the gypsy moth (Johnson et al., 2006; Vercken et al., 2011) and could therefore be used as a means of eradicating newly founded populations at the invasion front (Liebhold & Bascompte, 2003; Blackwood et al., 2012). However, it remains unclear whether mating failure at low population density is the only cause of the observed demographic Allee effect. Clearly, the invasion of North America by *L. dispar* has produced an unprecedentedly large body of data and generated several novel and important ideas for population biology and management, potentially leading to a halo effect by providing support for the belief that mating failure in low-density populations affect population dynamics and is, therefore, a key element of insect management.

This review, however, highlights the lack of widespread experimental demonstrations of this attractive theory. Field research has tended to reveal either equivocal relationships between mating failure at low density and demographic Allee effects (Grevstad, 1999a), or an unequivocal lack of relationship. For instance, field studies on the butterflies *M. cinxia* and *P. smintheus* have revealed a weak mate-finding Allee effect that has no statistically significant effect on population growth rates (Kuussaari et al., 1998; Matter & Roland, 2013). Of course, the lack of evidence for demographic Allee effects may reflect a true absence of such effects. However, it may, alternatively, reflect the methodological difficulties involved in studies of populations that are small enough to experience a demographic Allee effect.

This critical analysis of the published findings highlights a lack of manipulative field experiments investigating mating failure at low density and formally testing for a causal relationship between mating success and population growth and persistence. Manipulative field experiments would allow more robust conclusions to be drawn than that derived from the simple co-occurrence of mating failure and lower population growth rates at lower population densities. Replicated introductions of exotic insect species for biological control provide an opportunity to manipulate population density and adopt an experimental approach to Allee effects (Grevstad, 1999a;

Memmott et al., 2005; Fauvergue et al., 2007). Such introductions are recognized to be an underused, but promising method for studies of small populations, including Allee effects (Marsico et al., 2010; Fauvergue et al., 2012).

This review highlights a novel approach, inspired by the models developed to relate mating failure to population management. These models express a precise causal relationship between a mate-finding Allee effect and demographic Allee effects, based on the deliberate manipulation of mating success. For instance, increasing the density of sex-pheromone lures increases the severity of mate-finding Allee effects, thereby increasing the strength of a demographic Allee effect (Figure 3). Most of these models were developed with population management in mind, but they also provide an invaluable theoretical framework, giving clear predictions to guide the design of future manipulative experiments. The disruption of mating and assessment of the severity of subsequent mate-finding and demographic Allee effects appears to be an exciting approach that would connect individual and population processes more closely in low-density populations, and improve the dialog between theoretical population biology and population management.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Evidence (or lack thereof) for a relationship between population size and mating success in insects. References are sorted by insect order and family. Only manipulative experiments were classified as 'experiments', natural experiments were considered 'observations'

Appendix 1 Evidence (or lack thereof) for a relationship between population size and mating success in insects. References are sorted by insect order and family. Only manipulative experiments were classified as 'experiments', natural experiments were considered 'observations'

Order; family	Species	Type of study	Method	Effect	Evidence	Reference
Coleoptera: Curculionidae	*Anthonomus grandis*	Lab. exp.	Mating chambers of various sizes for a single pair; daily observation of no. matings per female	+	No. matings per female increased with increasing density	Gilliland & Davich (1968)
	Sitophilus oryzae	Lab. exp.	Proportion of females copulating per hour vs. no. individuals per grain of wheat	+	Proportion of females copulating increased with density at low density, up to an optimum density	MacLagan & Dunn (1935); Watt (1960)
Coleoptera: Nymphalidae	*Callosobruchus chinensis*	Lab. exp.	Unclear	+	Copulation frequency increased with male density	Utida (1941); Watt (1960); Nishigaki (1963); Dennis (1989)
Diptera: Drosophilidae	*Drosophila pseudoobscura*	Lab. exp.	Direct observation of mating vs. no. pairs introduced into mating chambers	0	Proportion of individuals mating unaffected by density	Spiess (1968)
			Various no. pairs per mating chamber and observation of no. matings for three geographic/genetic strains	+	Proportion of individuals mating tended to increase with density but relationship independent of strain	Eckstrand & Seiger (1975)
	Drosophila persimilis	Lab. exp.	Various no. pairs per mating chamber and observation of no. matings	+	Proportion of individuals mating increased with increasing density	Spiess & Spiess (1969)
Diptera: Glossinidae	*Glossina palpalis*	Field obs.	Presence/absence of sperm in spermatheca of captured females	0	Proportion of females mating independent of male density	Teesdale (1940)
Hemiptera: Delphacidae	*Delphacodes scolochloa*	Field obs.	Egg-laying and egg morphology for females captured upon colonization of isolated empty patches and in source populations	0	Proportion of females mating similar in small colonizing populations and large source populations	Cronin (2009)
Hymenoptera: Aphelinidae	*Aphelinus asychis*	Field exp.	Presence/absence of sperm in spermatheca in large and small introduced populations	0	Proportion of females mating not affected by initial population size or subsequent population density	Fauvergue & Hopper (2009)

Hymenoptera: Dryinidae	*Neodryinus typhlocybae*	Field exp.	Proportion of males (proxy for the proportion of virgin females in hymenopterans) in populations introduced with various inoculum sizes	0	Proportion of males (proportion of virgin females) not affected by initial population size and population density	Fauvergue et al. (2007)
Lepidoptera: Hesperiidae, Papilionidae	18 species	Field obs.	Spermatophore counts in wild-captured females	0	High proportion of females mating, not correlated with the number captured (a proxy of population density)	Burns (1968)
Lepidoptera: Gelechiidae	*Pectinophora gossypiella*	Field obs.	Light trapping and presence/absence spermatophores	+	Proportion of females mating lower early and late in the reproductive season – coinciding with lower densities – than during midseason	Ouye et al. (1964)
			Light trapping and presence/absence spermatophores	+	Proportion of females mating lower early and late in the reproductive season – coinciding with lower densities – than during midseason	Graham et al. (1965)
Lepidoptera: Lymantriidae	*Lymantria dispar*	Field obs.	Presence/absence of sperm or embryos in females exposed in the field vs. no. males captured on pheromone traps	+	Proportion of females mating increased with increasing male density along the edge of the invasion front; relationship well described by a negative exponential model	Sharov et al. (1995)
			Presence/absence of sperm or embryos in females exposed in the field vs. no. males captured on pheromone traps	+	Proportion of females mating increased with increasing male density along the edge of the invasion front; relationship well described by a negative exponential model	Tcheslavskaia et al. (2002)
			Presence/absence of sperm or embryos in females exposed in the field vs. no. males captured on pheromone traps	+	Proportion of females mating increased with increasing male density along the edge of the invasion front; relationship well described by a negative exponential model	Contarini et al. (2009)

			Presence/absence of sperm or embryos in females exposed in the field vs. no. males captured on pheromone traps	+	Proportion of females mating increased with increasing male density along the edge of the invasion front; relationship well described by a negative exponential model; pesticide treatment did not change the relationship, although it decreased both density and the proportion of females mating	Tobin et al. (2013)
Lepidoptera: Noctuidae	*Spodoptera litura*	Field-cage exp.	Manipulation of male density and presence/absence spermatophores	+	Proportion of females mating increased with male density (no. males per cage) and no. males per female.	Otake & Oyama (1973)
Lepidoptera: Nymphalidae	*Melitaea cinxia*	Field obs.	Presence/absence of spermatophores and egg-laying and hatching in sampled females vs. no. larval groups per patch	+	Proportion of females mating increased with increasing local population size (population correlated with population density)	Kuussaari et al. (1998)
Lepidoptera: Papilionidae	*Parnassius clodius*	Field obs.	Mark-recapture in a large meadow and presence/absence of a sphragis in captured females	0	Proportion of females mating tended to increase over the reproductive season and best statistical fit to the data obtained with male age	Calabrese et al. (2008)
	Parnassius smintheus	Field obs.	Mark-recapture in 21 meadows and presence/absence of a sphragis in females	-	Proportion of females mating tended to decrease over the reproductive season and best statistical fit to the data obtained with inverse male density as an explanatory variable (fewer mating females at high male density)	Calabrese et al. (2008)
			Mark-recapture in subpopulations and presence/absence of a sphragis in females	+	Proportion of females mating increased with increasing population density; best statistical fit to the data obtained with inverse population density (and a negative parameter estimate)	Matter & Roland (2013)

Lepidoptera: Psychidae	*Metisa plana*	Field obs.	Presence/absence of eggs and pheromone-laden scales in bagworm bags	-	Across generations, highest overall proportion of females mating at lowest overall male densities; within most generations, across sampled trees, proportion of females mating increased with decreasing male density	Rhainds et al. (1999)
	Thyridopteryx ephemeraeformis	Field obs.	Presence/absence of eggs in collected bagworm bags vs. population density	-	Proportion of females mating decreased with increasing population density	Barrows (1974)
			Presence/absence of eggs in collected bagworm bags vs. presence/absence of bagworm bags along a latitudinal gradient	+	Proportion of females mating decreased with decreasing population density at increasing latitude	Rhainds & Fagan (2010)
Lepidoptera: Tortricidae	*Choristoneura fumiferana*	Field obs.	Presence/absence of spermatophores in females exposed in the field vs. no. males captured on pheromone traps	+	Proportion of females mating increased with increasing male density.	Régnières et al. (2013)
			Direct observation of mating of sentinel females placed in populations differing in density	+	No. males attracted per female and per day higher in populations with higher densities	Kipp et al. (1995)
Odonata: Coenagrionidae	*Ischnura graellsii*	Field obs.	Direct observation of marked individuals in two natural populations differing in density	+	Proportion of females mating and no. matings per individual lower in low- than in high-density populations	Cordero (1992)
Orthoptera: Gryllidae	*Gryllus campestris*	Field obs.	No. matings observed per female in a population experiencing a drastic decrease in density	0	No. matings per female similar at low and high population densities	Hissmann (1990)
	Gryllus integer	Field exp.	No. matings observed per male and per night in high- and low-density populations	0	Male (and supposedly female) mating rates were similar at low and high population densities	Cade & Cade (1992)
	Gryllus pennsylvanicus	Field exp.	No. matings observed per male and per night in high- and low-density populations	0	Male (and supposedly female) mating rates were similar at low and high population densities	French & Cade (1989)

	Gryllus veletis	Field exp.	No. matings observed per male and per night in high- and low-density populations	0	Male (and supposedly female) mating rates were similar at low and high population densities	French & Cade (1989)
Orthoptera: Tettigoniidae	*Metrioptera roeseli*	Field exp.	Recapture of marked individuals released at different densities and presence/absence of sperm in spermatheca	0	Proportion of fertilized females (100%) not affected by male density	Kindvall et al. (1998)
Phasmatodea: Timematidae	*Timema* spp. (8 species)	Field obs.	Presence/absence of sperm in spermatheca vs. capture rate	+	Proportion of females mating lower in low- than in high-density populations	Schwander et al. (2010)