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Abstract

The successful establishment of non-native species in new areas can be affected by many factors including the initial size of the founder population. Populations comprised of fewer individuals tend to be subject to stochastic forces and Allee effects (positive-density dependence), which can challenge the ability of small founder populations to establish in a new area. Although the conceptual relationship between initial colony size and establishment success has been previously documented, it is not trivial to estimate precisely the colony size needed to ensure colony persistence. Over the last 40 years, there have been many studies on the probability of mating success of female *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) in the USA related to background male moth densities. We were motivated by this wealth of data and sought to combine the results from these prior studies with the goal of estimating a robust measure of the male moth density required to achieve varying levels of female mating success. Although the data are specific to *L. dispar*, the pheromone communication system in *L. dispar* is not unique and thus the results of this analysis could be broadly applicable to our general understanding of Lepidoptera mating behavior.

Introduction

The successful establishment of non-native species can often be linked to the initial size of the founder population (Hopper & Roush, 1993; Drake & Lodge, 2005; Lockwood et al., 2005), a phenomenon that has been observed in a variety of taxa (Courchamp et al., 1999, 2008; Kramer et al., 2009; Simberloff, 2009). Populations comprised of a smaller number of individuals could be subject to demographic and environmental stochasticity, as well as Allee effects, which can exacerbate the challenge that small founder populations could face when initially establishing in a new area. The Allee effect refers to positive-density dependence in which individual fitness increases with an increase in population size (Stephens et al., 1999; Taylor &

Hastings, 2005). There are many potential causes of Allee effects, and in some cases, multiple causes of Allee effects can act in a multiplicative rather than an additive manner (Berec et al., 2007). One important cause of Allee effects in sexually reproducing insects is mate-finding failure in sparse populations (Gascoigne et al., 2009; Tobin et al., 2009b; Rhainds, 2010). Although many insect species have evolved efficient mate-location strategies, such as through chemical communication, these strategies may not necessarily be effective when a species is transported to a novel habitat with a limited number of conspecifics (Robinet et al., 2008).

Although the conceptual relationship between initial colony size and establishment success has been previously documented (Liebhold & Bascompte, 2003; Courchamp et al., 2008; Kramer et al., 2009), it can be challenging to estimate the precise colony size needed to ensure colony maintenance. Furthermore, habitat quality can affect the minimum density required for colony maintenance, a concept observed by Allee when describing differences in

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the required herd sizes of elephants depending on the habitat in which they lived (Allee, 1938). Another limitation is simply due to a lack of data; after all, collecting density data in populations that are sparse enough to be subject to Allee dynamics is not a trivial endeavor.

In efforts to manage the *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) invasion in the USA, pheromone traps are deployed along the expanding population front where populations initially arrive and establish (Sharov & Liebhold, 1998; Tobin & Blackburn, 2007). Traps are baited with a synthetic form of the *L. dispar* sex pheromone disparlure (cis-7,8-epoxy-2-methyloctadecane; Bierl et al., 1970), which provides a highly sensitive and host-specific survey tool that is effective at estimating sub-outbreak population densities (Mastro et al., 1977; Doane & McManus, 1981; Elkinton & Childs, 1983; Thorpe et al., 1993). In contrast, there is no reliable sampling procedure for adult females, and sampling egg mass densities is only practical in outbreaking populations where they can correlate to expected levels of defoliation (Liebhold et al., 1995). *Lymantria dispar* is univoltine. Larvae emerge from overwintering eggs in spring and develop through five (male) or six (female) instars. After emerging from pupae in summer, adults are believed to be short-lived (<4 days; Doane & McManus, 1981). Females only mate once after which they no longer produce a sex pheromone (Giebultowicz et al., 1990), whereas males can mate multiple times over their life span. At sub-outbreak densities, an approximate adult male-to-female sex ratio was reported as 1:0.4, although in a sparse population contained within an area-wide outbreak, a male-to-female ratio of 1:1.8 was reported (Campbell, 1969; Doane & McManus, 1981). At larval hatch, the sex ratio is ca. 1:1 (Campbell, 1967).

Under *L. dispar* management programs the number of male moths captured is used to identify newly formed colonies so that they can be eliminated before they grow, spatially expand, and contribute to range expansion through a process known as stratified dispersal. These data have also been used to estimate the initial density, in terms of male moth density per trapping area, required to ensure colony persistence from year to year (Liebhold & Bascompte, 2003; Whitmire & Tobin, 2006), estimate critical patch area required to ensure colony persistence (Vercken et al., 2011), parameterize a model quantifying the role of Allee effects in *L. dispar* range expansion (Johnson et al., 2006), and highlight the spatial and temporal variability in the strength of Allee effects and its effect on the rate of *L. dispar* spread (Tobin et al., 2007). However, these prior estimates of an Allee threshold, defined as the minimum density required for colonies to persist and replace themselves from year to year, were indirect measures of the importance of mate-finding failures as female mating success as a function of male moth density was not directly measured.

Fortunately, there have been several studies on *L. dispar* female mating success under natural conditions (Sharov et al., 1995; Tcheslavskaia et al., 2002; Contarini et al., 2009), which have consistently highlighted the functional relationship between male moth density and female mating success. However, because such mating success studies are labor-intensive and time-sensitive, past efforts have been conducted over limited spatial and temporal scales. There have also been several studies over the past four decades, which have measured this effect as a consequence of refining mating disruption products and strategies (Thorpe et al., 2006). We were motivated by this potential wealth of data, and sought to combine the results from these prior studies with the goal of estimating a robust measure of the male moth density required to achieve varying levels of female mating success. Although the data are specific to *L. dispar*, the pheromone communication system in *L. dispar* is not unique; thus, the results of this analysis could serve as a basis for understanding mating behavior in other non-native Lepidoptera for which analogous data are rare or non-existent.

Materials and methods

Data sources

The data used in this analysis were obtained from 13 references collectively published between 1974 and 2010 (Beroza et al., 1974, 1975; Granett & Doane, 1975; Schwalbe et al., 1983; Webb et al., 1988, 1990; Kolodny-Hirsch et al., 1990; Kolodny-Hirsch & Webb, 1993; Sharov et al., 1995; Tcheslavskaia et al., 2002; Thorpe et al., 2006; Contarini et al., 2009; Onufrieva et al., 2010). The combined data set consisted of 220 plots conducted in the USA between 1972 and 2008 in the following states: Connecticut, Maryland, Massachusetts, West Virginia, Wisconsin, and Virginia (Table 1). In most cases, plots were monitored at several times over the course of the male moth flight period; thus, there were in total 588 unique sampling intervals, defined as intervals (generally 24 h but occasionally up to 48 h) over which the mating success of *L. dispar* females was determined. Because many of these studies were designed to measure the efficiency of mating disruption products and tactics (Cardé & Minks, 1995), some of the plots were treated with synthetic pheromone for mating disruption (e.g., Beroza et al., 1975; Kolodny-Hirsch & Webb, 1993; Onufrieva et al., 2010); however, in all cases, there were also untreated control plots so that the percent mating reduction from mating disruption could be estimated. Other studies were

Table 1 Summary of the sources from which data were used in this analysis

Reference	Year(s) of experiment	State (USA)	No. untreated plots	No. treated plots[1]	Trap catch data available[2]
Beroza et al. (1974)	1973	MA	11	3	S
Beroza et al. (1975)	1974	MA	4	4	S
Granett & Doane (1975)	1974	CT	10	10	D + S
Webb et al. (1988)	1980	MD	4	12	S
Webb et al. (1990)	1981	MD	4	12	S
Tcheslavskaia et al. (2002)	2000	WI	7	0	D + S
Thorpe et al. (2006)	2005	VA	10	0	D + S
Schwalbe et al. (1983)	1978–1979	MA	6	18	D + S
Kolodny-Hirsch et al. (1990)	1984–1988	MD	16	16	D + S
Kolodny-Hirsch & Webb (1993)	1988–1990	WV	8	8	D + S
Sharov et al. (1995)	1993–1994	VA, WV	9	0	D + S
Contarini et al. (2009)	2003, 2008	WI	18	0	D + S
Onufrieva et al. (2010)	2006–2008	VA	15	15	D + S
Total			122	98	

[1]Plots were treated using mating disruption products.
[2]Refers to the availability of reported trap catch data: S, season-long; D, daily.

conducted exclusively under untreated control conditions (e.g., Sharov et al., 1995; Tcheslavskaia et al., 2002; Contarini et al., 2009). Of the 588 unique sampling intervals, 346 were from untreated control plots and 242 from treated plots.

In conjunction with female mating success, these studies also reported the corresponding male moth trap catch during the 24–48 h when females were deployed, which was ascertained through nearby traps baited with disparlure, the synthetic form of the *L. dispar* sex pheromone. This provided a method to estimate a common variable among studies: the number of males per trap, day, and plot, which we could then relate to the percentage of females mated per day per plot (e.g., Sharov et al., 1995). Because female mating success was often measured at multiple time intervals, trap catch data from a plot were also summed over the entire period of the experiment to provide a measure of the season-long (or experiment-long) male trap catch. Although the number of males per trap per day provides the most direct measurement of the background population in the vicinity of deployed females, and hence the most direct measurement of the relationship between male moth density and female mating success, season-long trap catch is generally the only measurement of population density available from *L. dispar* management programs (Thorpe et al., 2006; Tobin & Blackburn, 2007). Under these management programs, pheromone-baited traps are deployed to detect newly founded *L. dispar* populations, which yield the total male moth trap catch per trap. Thus, the ability to relate season-long trap catch to female mating success has immense practical utility.

Basic plot design

The basic plot design for determining *L. dispar* mating success has remained fairly constant throughout the decades, which allows for a collective examination of the combined data. In most studies, *L. dispar* females were tied with thread or dental floss at the base of one of the forewings, and then attached to the trunk of a tree ca. 1.5 m from the ground (females of the European strain of *L. dispar* are not capable of sustained flight). Although this method is labor-intensive, it also tends to provide the highest rate of female mating success relative to other techniques for deploying females in mating studies (Thorpe et al., 2007). In some studies from which we extracted data, females were placed on trunks untethered (e.g., Beroza et al., 1974), or placed in modified traps that prevented female escape but allowed males to enter (e.g., Kolodny-Hirsch & Webb, 1993). Some studies also supplemented deployed females by collecting naturally occurring females from the field to ascertain mating success (e.g., Webb et al., 1990). After 24–48 h, females were returned to the laboratory. Successful fertilization of females was determined through microscopic examination of eggs for evidence of embryonization (e.g., Tcheslavskaia et al., 2002), or in some cases spermathecae were dissected and examined microscopically for the presence of sperm (e.g., Stark et al., 1974). Female deployments varied slightly among studies, but were generally attached to trees separated by 15–30 m.

The background density of male moths was determined by deploying 2–4 pheromone-baited traps 100–200 m from tethered females to avoid interference between synthetic and natural pheromone plumes (Elkinton & Cardé, 1988). Most studies were conducted during the 2- to 3-week period of peak male moth flight during which $\geq 80\%$ of male moths are generally trapped (Tobin et al., 2009a). Some of the more recent studies reported data over a 6- to 8-week period that corresponded to the full extent of the male flight period (e.g., Tcheslavskaia et al., 2002; Thorpe et al., 2006; Onufrieva et al., 2010). We do note that the season-long male trap catch from the studies that were conducted over a 6- to 8-week period resulted in additional male moths relative to those studies conducted over 2–3 weeks; however, we also noticed that the additional male moths were only a small proportion of the total trap catch, and their influence was furthermore reduced when counts were transformed using $\log(x + 1)$. We opted for this approach in lieu of attempting to ascertain the corresponding 2–3 weeks phenological window, which also induces uncertainty, in the studies that were conducted over 6–8 weeks.

Analyses

The relationship between the proportion of females successfully mated from unique sampling intervals, and the number of male moths per trap per day or the total number of males trapped (i.e., season-long trap catch) was first analyzed using a general linear model in R (R Development Core Team, 2011). Male moth trap catch data were $\log(x + 1)$ transformed. We assessed the influence of the main effects plot type (treated or untreated control plot), trap catch (per trap per day or season-long), and their interaction on the arcsine-transformed proportion of successfully mated females.

The quantitative relationship between the proportion of successful female mating, and daily and season-long trap catch, was modeled using locally polynomial quantile regression with the quantreg package (Koenker, 2007) in R (R Development Core Team, 2011). Quantile regression (Koenker & Bassett, 1978; Cade & Noon, 2003) was used in lieu of conventional regression because of our interest in understanding the expected conditional response at different percentiles of its distribution instead of only the conditional mean response. We estimate the probability of successful female mating at the 10th, 25th, 50th (conceptually equivalent to the conditional mean response when using conventional logistic regression), 75th, 90th, and 95th percentiles. An advantage of this approach over other regression techniques, such as least squares or logistic regression, is that the expected conditional responses at different percentiles can provide a more robust measure of

risk because quantile regression tends to be more sensitive to outliers. In the case of monitoring for a non-native species, such as *L. dispar*, the mean male moth density at which female mating is successful could describe adequately the expected mean yet still represent a considerable uncertainty if left unmanaged. Estimating the expected response based upon the upper distribution of a set of observations could thus provide a better threshold to base management decisions, particularly so in eradication programs.

Because many of the plots were monitored at several points in time, we also sought to relate the season-long male moth trap catch to the mean and maximum percentage of females that were mated across all unique sampling intervals within a plot. In addition to estimating the expected conditional response at the previously-stated percentiles, we also estimated the response at the 99th percentile to provide the most conservative estimate of the minimum total male moth trap catch over the course of the season required at different percentages of successful mating of females.

Results

When considering the male moth catch per trap per day, we observed a significant effect of male moth density ($F_{1,584} = 225.9$, P<0.001) and plot type (e.g., treated or untreated; $F_{1,584} = 52.9$, P<0.001) on the proportion of mated females; the interaction between these two main effects was not significant ($F_{1,584} = 2.89$, P = 0.09). Because of the lack of an interaction effect, data from treated and untreated plots were pooled to quantify the relationship between successfully mated females and male moth trap catch (Figure 1A). The estimates from 50th quantile (i.e., the quantile most analogous to conventional regression techniques) indicated that half of females were successfully mated at a male moth density of ca. 4.5 males per trap per day. However, the variability in this relationship (Figure 1A) suggested that half of females could be successfully mated at densities as high as 31.2 males per trap per day (10th quantile) or as low as 1.2 males per trap per day (95th quantile). Of the 588 unique sampling intervals, 193 recorded no male moth trap catch during female deployments, of which 164 also recorded no successful female mating. In the remaining 29 unique sampling intervals with a 0-male moth trap catch, successful mating ranged from 3.8 to 70%, on average 24.3%.

When considering the season-long male moth catch, we also observed a significant effect of male moth density on the proportion of mated females ($F_{1,531} = 245.3$, P<0.001); however, the main effect of plot type ($F_{1,531} = 0.25$, P = 0.61) or its interaction with male moth
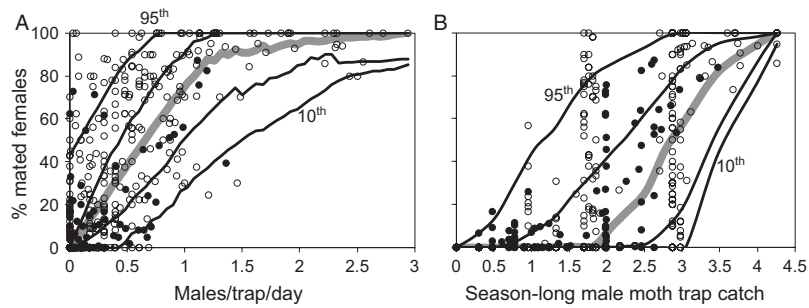
Figure 1 Percentage of female *Lymantria dispar* successfully mated relative to the background male moth density [log(x + 1)] during (A) the period of female deployments and (B) the season-long male moth density. Open and closed circles represent data obtained from untreated control and treated plots, respectively. Lines represent the quantile regression fits (10th, 25th, 50th, 75th, and 95th); the 50th quantile regression fit is shown as the thick gray line.

density ($F_{1,531} = 2.06$, P = 0.15) was not significant. The season-long trap catch at which half of the females were successfully mated was 743.7 when using the 50th quantile, and ranged from 3 691.6 to 15.1 male moths when using the 10th or 95th quantile, respectively (Figure 1B). It is also important to note that there were 30 and 63 plots in which the season-long trap catch was 0 and 1, respectively. In the former plots, none of the females were recorded as successfully mated, whereas in the latter plots, 62 plots recorded no successful mating and one plot indicated that 6.6% of females (9 of 136 females; Webb et al., 1990) were successfully mated.

The relationship between season-long trap catch and the mean and maximum percent of mated females across all periods of female deployments in each plot is shown in Figure 2. Although there was less variability when considering mean as opposed to the maximum percentages, the latter is likely a more conservative measurement, especially for use as a guideline in management programs where the tolerance threshold could be relatively low, such as in eradication efforts. An extreme example of a low tolerance

threshold was the aggressive response to the detection of one male *Lymantria umbrosa* (Butler) from a pheromone-baited trap in New Zealand, which triggered an eradication program consisting of eight weekly aerial applications of the biopesticide *Bacillus thuringiensis* var. *kurstaki* across 12.5 km^2 (Brockerhoff et al., 2010; Kean et al., 2011). Thus, in an effort to develop a comprehensive understanding for use in management decisions, we related the season-long trap catch and the maximum percent of mated females and used the predicted estimates from multiple quantiles to highlight different measures of risk (Figure 3). For comparative purposes, we also show this relationship using the male moth catch per trap per day during the time of female moth deployments (Figure 3). In the case of the maximum percent mating observed at any time across all unique sampling intervals within a plot, the 50th quantile predicted that half of the females were successfully mated at a season-long trap catch of 207.1, whereas the 10th and 99th quantiles predicted that half of the females were successfully mated at a season-long trap catch of 727.4 and 6.7, respectively. Furthermore, the 99th
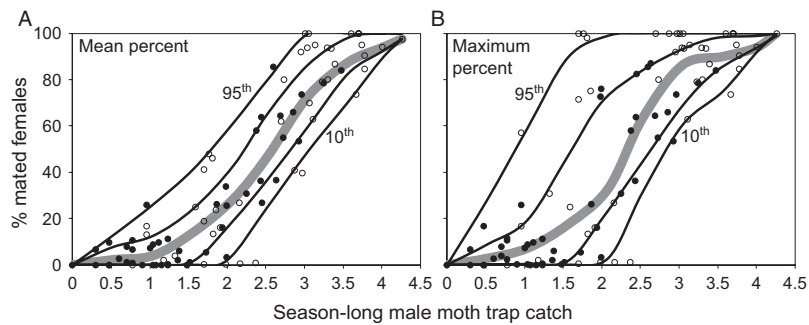

Figure 2 The (A) mean and (B) maximum percentage of female *Lymantria dispar* successfully mated relative to the season-long male moth density [log(x + 1)]. Open and closed circles represent data obtained from untreated control and treated plots, respectively. Lines represent the quantile regression fits (10th, 25th, 50th, 75th, and 95th); the 50th quantile regression fit is shown as the thick gray line.
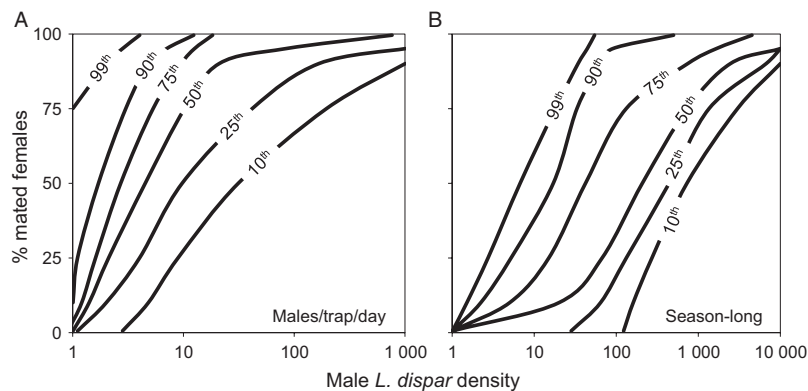
Figure 3 Estimates of the percentage of female *Lymantria dispar* successfully mated based upon (A) male *L. dispar* trap catch per trap per day, and (B) the maximum percentage of successful mating across the season-long trap catch. The contours are the fits from quantile regression and can be used to represent different measures of uncertainty by highlighting the minimum male moth density required to result in different percentages of successful mating in a given percentage of observations.

quantile, the most conservative quantile to use to determine the absolute minimum season-long male trap catch that resulted in successful female mating, predicted that 10, 25, 75, 90, and 99% of females would be mated at season-long trap catches of 1.4, 2.7, 18.3, 33.4, and 51.2, respectively.

Discussion

The data collected on *L. dispar* mating success from several studies over the past four decades provided us with the unique opportunity to develop a comprehensive framework linking male moth trap catch to expected female mating success. These data collectively illustrate that a density of 4.5 males per trap per day during the time of female deployment or a season-long trap catch of 207.1 equates to approximately half of females successfully mated based upon the 50th quantile. It is also important to note that although there were instances of females being successfully mated when the corresponding male moth trap catch during the interval (24–48 h) of female deployment was 0, we did not detect any instance (out of 30 plots) where females were successfully mated when the season-long male moth trap catch was 0, and only 1 instance (out of 63 plots) where females (6.6%) were mated when the season-long male moth trap catch was 1. These observations underscore the sensitivity of *L. dispar* pheromone-baited traps in detecting male moths even when reproducing populations are not present, and confirm past observations as to the reliability of the trap designs currently used (Mastro et al., 1977; Doane & McManus, 1981; Elkinton & Childs, 1983).

Aside from the management implications of these results, these data also lend support to the importance of Allee effects due to mate-finding failures in *L. dispar*

(Tobin et al., 2009b). The failure of low-density populations to persist has been observed in areas in which *L. dispar* is not considered to be established (Liebhold & Bascompte, 2003) and along its invasion front (Whitmire & Tobin, 2006), with the assumption that in low densities, males are unable to locate females. Several past studies that specifically sought to quantify female mating success based upon background male moth densities (Sharov et al., 1995; Tcheslavskaia et al., 2002; Contarini et al., 2009) have furthermore outlined mate-finding failures as a potential source of an Allee effect. Additional studies have likewise demonstrated the importance of mate-finding Allee effects in *L. dispar* (Robinet et al., 2007, 2008) as well as the consequence of Allee effects on its invasion dynamics (Johnson et al., 2006; Tobin et al., 2007; Vercken et al., 2011). This study advances our understanding of the importance of mate-finding failures in *L. dispar* by providing a comprehensive link between male moth trap catch data and female mating success.

Although there are numerous invasion pathways through which new species can arrive to new areas (Hulme et al., 2008; Aukema et al., 2010), the majority of arriving species seem to fail to establish (Williamson & Fitter, 1996; Simberloff & Gibbons, 2004), perhaps due to small founder population size (Lockwood et al., 2005; Courchamp et al., 2008; Simberloff, 2009). It is thus not surprising that smaller density populations of a non-native species distributed over a smaller spatial scale tend to be more amenable to management strategies, such as eradication, than those that are more abundant and spatially widespread (Rejmánek & Pitcairn, 2002; Veitch & Clout, 2002; Liebhold & Bascompte, 2003; Tobin et al., 2011). In this regard, detection tools are paramount for managing non-native invasive species. For many species, including

L. dispar, trapping devices based upon semiochemicals provide a sensitive tool to detect new populations or estimate density in existing populations as a means to implement management strategies (Elkinton & Cardé, 1981; Borden, 1989; Tobin & Blackburn, 2007; El-Sayed, 2011). Secondarily, there is also a need to interpret trapping data so that informed management decisions can be developed. In the case of *L. dispar*, only males are trapped; thus, it is not always apparent if the presence of males equates to a reproductively viable population. This is especially true in areas, such as Western North America and New Zealand, where *L. dispar* is not established but where males are occasionally detected in pheromone-baited traps, often near ports-of-entry (Hajek & Tobin, 2009; Brockerhoff et al., 2010). The ability to relate comprehensively trap catch data, which are generally collected over the season, to expected levels of female mating has immediate application in *L. dispar* management programs. This information also could serve as a basis for understanding the role of mate-finding failure at low densities in other non-native insect pests, especially for other Lepidoptera that also rely upon mate-location through sex pheromones.

Acknowledgements

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