

Mate-finding failure as an important cause of Allee effects along the leading edge of an invading insect population

Mario Contarini^{1,2}, Ksenia S. Onufrieva³, Kevin W. Thorpe⁴, Kenneth F. Raffa² & Patrick C. Tobin^{5*}

¹Dipartimento di Protezione delle Piante, Università di Sassari, via E. De Nicola, 07100 Sassari, Italy, ²Department of Entomology, University of Wisconsin-Madison, 345 Russell Laboratories, 1630 Linden Drive, Madison, WI 53706, USA, ³Department of Entomology, Virginia Polytechnic Institute and State University Blacksburg, VA 24061, USA, ⁴Agricultural Research Service, US Department of Agriculture, Beltsville, MD 20705, USA, and ⁵Forest Service, US Department of Agriculture, Northern Research Station, 180 Canfield St., Morgantown, WV 26505, USA

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Abstract

The movement of humans and goods has facilitated the arrival of non-native insects, some of which successfully establish and cause negative consequences to the composition, services, and functioning of ecosystems. The gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), is currently invading North American forests at variable rates, spreading by local and long-distance movement in a process known as stratified dispersal. Newly arriving colonizers often occur considerably ahead of the population front, and a key question is the degree to which they successfully establish. Prior research has highlighted mate-finding failures in sparse populations as a cause of an Allee effect (positive density dependence). We explored this mechanism by measuring the relationship between female mating success and background male moth densities along the gypsy moth western front in Northern Wisconsin (USA) over 2 years. The mating results were then compared with analogous previous studies in southern Wisconsin, and the southern front in West Virginia and Virginia (USA). Mate-finding failures in low-density populations were consistently observed to be density-dependent across all years and locations. Mate-finding failures in low-density populations have important ramifications to invasive species management, particularly in predicting species invasiveness, preventing successful establishment by small founder populations, and concentrating eradication efforts where they are most likely to succeed.

Introduction

The arrival of non-native insect species has accelerated considerably in recent years as a result of increased human mobility, modification of natural avenues of movement, and disturbances to natural habitats that change their suitability (Di Castri, 1989; Niemelä & Mattson, 1996; Langor et al., 2009). Subsequent establishment of non-native species has increasingly altered the composition and functioning of the earth's ecosystems (Dukes & Mooney, 1999; Parker et al., 1999; Mack et al., 2000; Mooney & Cleland,

2001), leading to the displacement of native species, decline of natural resources, and increased costs associated with their management and damage (Pimentel, 2002; Pimentel et al., 2005). Although there are a number of pathways through which invasive insect species may arrive to a new habitat, not all species successfully establish (Ludsin & Wolfe, 2001; Simberloff & Gibbons, 2004). Invasion success can be complex (Starfinger, 1998), in part because the ultimate success of an introduced species is the integrated product of a multistage process, commonly divided into five main stages: initial arrival into a new region, release or escape into the wild, establishing a population, spreading from an established population, and causing adverse effects (Kolar & Lodge, 2001, 2002; Torchin & Mitchell, 2004; Williamson, 2006; Lockwood

*Correspondence: Patrick C. Tobin, Forest Service, US Department of Agriculture, Northern Research Station, 180 Canfield St., Morgantown, WV 26505, USA. E-mail: ptobin@fs.fed.us

et al., 2007). The probability of going from one stage to the next is often small (Williamson, 2006).

One important aspect of invasion success is the role that Allee effects play in the establishment and spread phase of introduced organisms (Lewis & Kareiva, 1993; Drake & Lodge, 2004; Leung et al., 2004; Taylor & Hastings, 2005; Johnson et al., 2006). Allee effects refer to a positive relationship between individual fitness and population density (Allee, 1932; Dennis, 1989; Courchamp et al., 1999, 2008; Stephens et al., 1999; Berec et al., 2007). A decrease in a component of fitness with a decrease in population density is known as a component Allee effect (e.g., the failure of an individual to locate a mate in sparse populations), whereas a demographic Allee effect refers to a decline in the per capita population growth rate with population density. A consequence of demographic Allee effects is that populations could require a minimum number of individuals to remain viable (Allee, 1932; Stephens et al., 1999). Allee effects have been recognized as a common cause of extinction in low-density populations, and their causes include the inability to locate mates, overcome host defense, inbreeding depression, and the failure to satiate or evade natural enemies (Dennis, 1989; Courchamp et al., 1999, 2008; Taylor & Hastings, 2005). An increasing body of evidence suggests that a better understanding of Allee effects, and incorporating them into establishment and spread models, will greatly improve our ability to predict and counter the threats posed by invasive species (Courchamp et al., 1999; Drake, 2004; Tobin et al., 2007b).

The gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), is one of the most economically important insect pests of hardwood forests in North America (Doane & McManus, 1981). It accidentally escaped from captivity near Boston (MA, USA) in 1869 following deliberate transport from Europe (Liebhold et al., 1989). Since its escape, it has invaded >1 000 000 km² of the eastern United States of America, causing large-scale defoliation (700–50 000 km² annually) and occasionally extensive tree mortality during outbreaks (Montgomery & Wallner, 1988; Liebhold et al., 1992; Johnson et al., 2006). Its current North American range extends from Nova Scotia to Wisconsin, and Ontario to North Carolina (Tobin et al., 2007a). In many parts of its established range, populations of gypsy moth intermittently erupt to outbreak densities causing defoliation in stands dominated by its primary hosts (e.g., *Quercus*, *Populus*, and *Larix* species) (Liebhold et al., 1997; Davidson et al., 2001). The mechanisms that drive low-density populations to outbreak levels are only partially understood. During outbreaks, early instars may be transported by wind when source populations are dense and hatch periodicity and optimal meteorological conditions are synchronized (Mason & McManus, 1981; Taylor & Reling, 1986). How-

ever, larval dispersal generally occurs over relatively short distances (McFadden & McManus, 1991). Long-range movement is primarily a result of anthropogenic transportation of immature life stages (Mason & McManus, 1981; Schwalbe, 1981; Hajek & Tobin, 2009).

In the United States, the gypsy moth is currently spreading south through North Carolina and west through Wisconsin at a variable rate of ca. 6–18 km year⁻¹ (Tobin et al., 2007a). Populations do not spread uniformly along the population front; rather, gypsy moth spread occurs through stratified dispersal in which long-distance dispersal is coupled with short-range dispersal and local population growth (Hengeveld, 1989; Shigesada et al., 1995; Sharov & Liebhold, 1998). The rate of spread in Wisconsin has been consistently greater than in other regions into which gypsy moth is spreading (Tobin & Whitmire, 2005; Tobin et al., 2007a; Tobin & Blackburn, 2008). Recent studies suggested that Allee effects may be important contributors to the establishment failure of gypsy moth at low-population densities (Liebhold & Bascompte, 2003; Whitmire & Tobin, 2006) with a consequent effect on its rate of spread (Johnson et al., 2006; Tobin et al., 2007b). Knowledge of how these processes affect both establishment and spread is essential to the development of strategies for managing this and other invasive pests (Taylor & Hastings, 2005; Liebhold & Tobin, 2008). In contrast, there is no evidence for demographic Allee effects at moderate population densities during the post-establishment, pre-erupting stage (Gray et al., 2008).

A potential source of an Allee effect in low-density gypsy moth populations is mate-finding failure (Sharov et al., 1995; Tcheslavskaja et al., 2002; Tobin et al., 2009). We tested the relationship of mate-finding failure to population density in newly establishing populations in northern Wisconsin in 2003 and 2008. We also compared rates of female mating success from this study with results from previous studies along the western front in southern Wisconsin (Tcheslavskaja et al., 2002) and along the southern front in West Virginia and Virginia (Sharov et al., 1995) to highlight the importance of mate-finding failure as a cause of an Allee effect in invading gypsy moth populations.

Materials and methods

We established 6 and 12 plots in 2003 and 2008, respectively. The 2003 plots were in the Chequamegon-Nicolet National Forest and nearby forested sites in Forest and Florence counties (WI; 45°40'N, 88°49'W), and were located along the leading edge of the gypsy moth invasion front. The 2008 plots were on Oak, Stockton, Basswood and Hermit Islands of the Apostle Islands National Lakeshore (Ashland County), Madeline Island (Ashland

County), and adjacent mainland in Bayfield County (WI). The 2008 sites were located slightly ahead of the general gypsy moth invasion front, and represented an area into which gypsy moth spread through stratified dispersal was occurring.

The sites in Forest and Florence counties are classified as the *Acer/Viburnum* habitat type in oak-dominated northern hardwood stands. The climate is characterized by an annual average high temperature of 11 °C, a low of -3 °C, and annual precipitation of 772 mm (Wisconsin State Climatology Office, 2009). The sites in and adjacent to the Apostle Islands are located at the contact zone between the hemlock-white pine-northern hardwood forest and the boreal forest. Common tree species include northern red oak (*Quercus rubra* L.), sugar maple (*Acer saccharum* L.), red maple (*Acer rubrum* L.), ironwood [*Ostrya virginiana* (Miller) K. Kock], paper birch (*Betula papyrifera* Marshall), and balsam fir (*Abies balsamea* L.) (Beals & Cottam, 1960). Annual high and low temperatures are 10 and 0 °C, respectively, with an average precipitation of 850 mm (Wisconsin State Climatology Office, 2009).

Gypsy moth females were reared from pupae obtained from USDA Animal and Plant Health Inspection Service (Pest Survey Detection and Exclusion Laboratory, OTIS Air National Guard Base, MA, USA). We maintained female pupae separate from males to prevent mating until they were deployed in the field. Virgin females of <2 days were tethered with a 15-cm length of cotton thread tied to the base of the forewing and attached to the stem of a tree 1.5 m above the ground level by a pushpin, using the method of Sharov et al. (1995). In 2003, a circle of 15 tethered females placed 21 m apart was established in each plot. In 2008, 16 females were deployed in each plot in two rows, 8 females per row. There was 20 m between rows and between females. Females were deployed daily over 1–7 days depending on the site and year. Additional details of the sampling intervals for each site and year are presented in Table 1. Females were left on trees for 24 h during peak male flight, which was estimated by the gypsy moth phenology model GMPHEN (Sheehan, 1992) implemented using BioSIM software (Régnière & Sharov, 1998). After 24 h, females and any egg masses they had oviposited were collected and returned to the laboratory to determine fertilization by examining embryonation (Sharov et al., 1995; Gray et al., 2008).

The density of male moths was estimated using two 1.9-l milk carton pheromone-baited traps per plot (Sharov et al., 1995). The traps were baited with 500 mg of (+)disparlure in twine dispensers, and contained a Vapona kill strip (10% 2,2-dichlorovinyl dimethyl phosphate; Hercon Environmental, Emigsville, PA, USA). The traps were placed ca. 250 m apart at 100 m from the circle of females

in 2003, and ca. 200 m from the nearest row of females in 2008. Any males trapped by the pheromone-baited traps prior to the placement of tethered females were removed and counted, and males were also counted at the end of the 24-h period during which females were deployed. Male density was expressed as the number per trap per plot over the 24-h period. Logistic regression (SAS Institute, 2003) was used to test the effects of background male moth density on female mating success, and significance was based on the likelihood ratio chi-squared test (Agresti, 1990).

Because we designed our current mating success experiments in a manner consistent with those previously reported (Sharov et al., 1995; Tcheslavskaja et al., 2002), we were able to conduct a spatial and temporal comparison of the role of gypsy moth male density on female mating success. One prior study focused on the role of mate-finding failures within small density populations but also within the gypsy moth established area (Sharov et al., 1995), whereas the other, like our current study, examined this effect at various distances from the leading edge (Tcheslavskaja et al., 2002). Overall, the similar experimental design allowed for a broad comparison to determine the consistency of the effect of female mating success as a function of background male moth densities. Logistic regression (SAS Institute, 2003) was used to test the main effects of background male moth density and study location (West Virginia and Virginia in 1993 and 1994, southern Wisconsin in 2000, and our current studies in northern Wisconsin in 2003 and 2008), and their interaction, on female mating success. The significance of main and interaction effects was based upon the likelihood ratio chi-squared test, and post-hoc comparisons among studies were conducted by partitioning chi-squared into non-significant components (Agresti, 1990).

Results

Trap catch ranged from 0 to 871 males per trap per day, with the highest number in 2008 in both plots on Stockton Island (871 and 532.5 males; Table 1). The percentage of mated females ranged from 0 to 100. There was a strong effect of background male moth densities on female mating success in both 2003 ($\chi^2 = 74.4$, d.f. = 1, $P < 0.0001$) and 2008 ($\chi^2 = 121.9$, d.f. = 1, $P < 0.0001$), suggesting a density-dependent effect (Figure 1). Total female mating failure was observed in only two plots, one in each year, with daily male trap catches of 0 and 0.5. Interestingly, at least some females were successfully mated in seven of the eight plots in which no males were recorded from either trap, with a range of 7–50% (Table 1).

When comparing our two studies with those previously published, we observed a consistent density-

Year	Plot no.	Date of female deployment ¹	Males/trap/day	Females/plot	Females analyzed	Proportion of mated females
2003	1	14	0	14	12	0.08
		15	0	15	15	0.07
		16	1.5	15	12	0.08
		17	0	15	11	0.09
		18	1	15	11	0.64
		19	2.5	15	9	0.56
		20	0	15	14	0.50
	2	15	36	15	13	1.00
		16	52.5	15	9	1.00
		17	49.5	15	11	0.91
	3	15	0.5	15	14	0.00
		16	1.5	15	13	0.15
		17	1.5	15	12	0.17
		18	1.5	15	13	0.38
		19	2	15	14	0.71
	4	20	0	15	14	0.43
		15	0	15	13	0.31
		16	7	15	12	0.83
		17	3.5	15	10	0.90
		18	8	15	11	0.73
19		3.5	15	11	0.82	
5	16	5	15	9	1.00	
	17	2.5	15	13	0.85	
	18	12	15	12	0.92	
	19	6	15	11	0.82	
6	20	6	15	11	0.36	
2008	1	19	0	26	21	0.00
	2	19	1.5	16	15	0.14
	3	19	0	16	12	0.17
	4	19	2.5	16	16	0.25
	5	21	202.5	16	15	0.93
	6	21	402.5	16	14	1.00
	7	21	355	16	15	0.87
	8	21	318	16	15	0.80
	9	21	871	16	14	1.00
	10	21	532.5	16	15	1.00
	11	21	233	16	16	0.94
	12	21	272	16	15	0.80

Table 1 Gypsy moth female mating success and background male moth densities in northern Wisconsin in August 2003 (Forest and Florence counties) and August 2008 (Bayfield and Ashland counties)

¹Date that tethered females were placed in the field.

dependent relationship of mating failure with male moth catch. We also observed a significant difference among study locations ($\chi^2 = 28.2$, d.f. = 4, $P < 0.0001$). When partitioning chi-squared, there was no difference among the studies in West Virginia and Virginia in both 1993 and 1994 ($P = 0.6$), or among any of the studies conducted in Wisconsin in 2000, 2003, and 2008 ($P = 0.75$), whereas the former and latter groups were significantly different from each other ($\chi^2 = 6.2$, d.f. = 2, $P = 0.013$). In both groups, male moth density was a significant predictor of female mating success

($\chi^2 = 65.8$, d.f. = 1, $P < 0.0001$ for the West Virginia and Virginia group, and $\chi^2 = 140.5$, d.f. = 1, $P < 0.0001$ for the Wisconsin group). At densities above five males/trap/day, however, there was no difference among study locations (Figure 2). Indeed, the more consistent observation across all locations and years is gypsy moth female mate-finding failures in sparse male populations. A single logistic regression model fit to all locations and years is presented in Figure 2, which highlights the positive density dependence in gypsy moth female mating success.

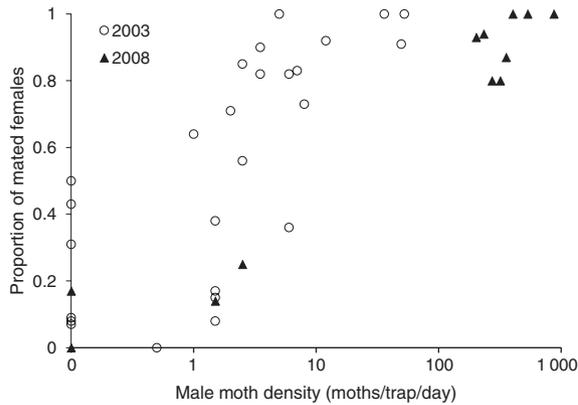


Figure 1 Proportion of mated gypsy moth females in northern Wisconsin in relation to the background population density of male moths in 2003 and 2008.

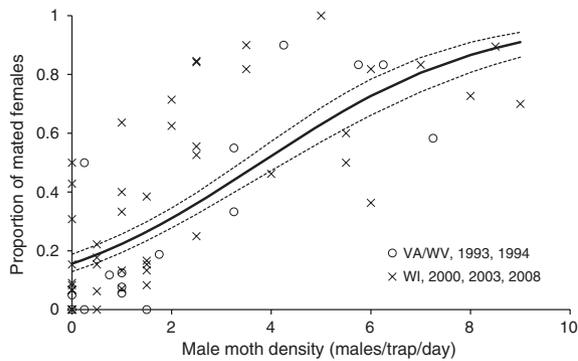


Figure 2 Proportion of mated gypsy moth females in Wisconsin (2000, 2003, and 2008) and in West Virginia and Virginia (1993, 1994) in relation to the background population density of male moths (truncated to ≤ 10 male moths/trap/day for graphical purposes). A common logistic regression fit (solid line) and 95% confidence intervals (dashed lines) are shown.

Discussion

These results support the importance of mate-finding failure as a consistent cause of an Allee effect in newly establishing gypsy moth populations along both the western and southern leading edges of this biological invasion. Because gypsy moth has been shown to spread at variable rates (Tobin & Whitmire, 2005; Tobin et al., 2007a), spatial and temporal variation in the strength of an Allee effect as a result of mate-finding failures could be a contributing factor (Tobin et al., 2007b). Specifically, if females in low-density populations are able to be located by males, then establishment success increases and these populations are eventually able to contribute to range expansion (Shigesada et al., 1995; Sharov & Liebhold, 1998). The statistical differences in female mating success rates between the West Virginia and Virginia sites, and the

Wisconsin sites, are consistent with this idea, but should be interpreted cautiously, because at a regional scale there is only one western and one southern front. Thus, at finer spatial scales there could be important differences in topography, weather, habitat structure, and trap efficacy. However, the current study provides support for future tests of this hypothesis, with particular emphasis on such finer-scale features.

Based on these and prior results, we propose how various life-history processes can interact with an Allee effect to either constrain or release expansion of the gypsy moth, and thus have landscape-scale consequences. Female mating success shows positive density dependence with the resident population of males, and in part with the size and proximity of neighboring populations. The density of resident adults can also be influenced by several factors affecting pre-adult emergence, such as mortality rates in eggs, larvae, and pupae as a result of natural enemies. The degree to which natural enemies cause an Allee effect in low-density gypsy moth populations is not fully known (Tobin et al., 2009). A primary cause of mortality in low-density gypsy moth populations is the result of pupal predation by small mammals (Elkinton & Liebhold, 1990; Elkinton et al., 1996, 2004; Liebhold et al., 2005). However, more work is needed to quantify an Allee effect owing to the failure of low-density gypsy moth populations to satiate predators.

There are several means by which conditions may change to create interactions that favor the likelihood of newly founded gypsy moth colonies surpassing an Allee threshold. For example, reduced precipitation is unfavorable to the gypsy moth fungal pathogen, *Entomophaga maimaiga* Humber, Shimazu et Soper (Zygomycetes: Entomophthorales) (Hajek, 1999), which would lead to decreased larval mortality and consequent increased adult emergence; hence, a higher frequency of mating success. Likewise, factors that decrease the abundance of predators and parasitoids could increase gypsy moth population density to levels that then are released from a mate-finding demographic Allee effect. An abrupt introduction of egg masses by humans or a large-scale immigration of male moths could also allow populations to surpass the Allee threshold. This latter possibility is particularly interesting because the biological significance of male 'moth blow' that commonly occurs with shifts in wind direction (Drake & Farrow, 1988) is often discounted as a dead end because females do not likewise fly. However, if immigrating males are synchronized with the phenology of the resident male population, such events could elevate populations above the point where positive feedback begins to dominate.

A central and ongoing question in invasion ecology is why establishment success in a new environment varies so

markedly among and within species. Many if not most arrivals are thought to result in establishment failure (Ludsin & Wolfe, 2001; Simberloff & Gibbons, 2004). This variability arises in part from details of natural history and demographics of the invader, as well as the susceptibility of the habitat into which the species arrives (Lonsdale, 1999; Davis et al., 2000; Kolar & Lodge, 2001). Moreover, depending on the habitat, the presence of competitors, mutualists, and regulators, and exogenous factors such as climate (D'Antonio, 1993; Marler et al., 1999; Ohlemüller et al., 2006), an invader could experience spatial and temporal variability in its establishment success and invasion speed (Whitmire & Tobin, 2006; Tobin et al., 2007b).

The roles of specific life-history processes in Allee effects are likely system-specific. For example, in some systems, natural enemies with a type II functional response have been observed to induce an Allee effect in their host (Gascoigne & Lipcius, 2004; Berec et al., 2007). In other systems, the failure of small populations to overcome host defense responses when foraging can contribute to an Allee effect (Raffa & Berryman, 1983).

Financial and logistic constraints on cargo inspection necessitate prioritization based on risk assessments, so that more attention is given to those species having the highest potential to establish and cause environmental and economical harm. Arriving species beset by strong demographic Allee effects could thus be less likely to establish. Many assessments are based on propagule pressure, which refers to both the absolute number of arriving individuals (propagule size) and the frequency of introduction events (propagule number; Leung et al., 2004; Lockwood et al., 2007). However, propagule pressure is not always an adequate predictor of establishment success as evidenced by *Ips typographus* (L.), a bark beetle that has been consistently detected outside of its native range, yet seemingly has never become established (Brockerhoff et al., 2006). The continual failure of *I. typographus* to establish could be because of an Allee effect, as this species relies on mass-attacking and mass-foraging behaviors when colonizing host trees, and thus, the required founder population size could be very high (Grégoire et al., 2006). Much of our current inability to predict the invasiveness of various species may reflect a greater attention to the high-density dynamics and eruptive potential of insects in their native regions, rather than the constraints they face at very low densities. Hence, we propose that Allee effects and mechanisms be incorporated into existing factors such as propagule pressure, pathways, and habitat susceptibility, in the development of management strategies, prioritizations, and guidelines to reduce the consequences of non-indigenous species.

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