Long-Distance Dispersal of the Gypsy Moth (Lepidoptera: Lymantriidae) Facilitated Its Initial Invasion of Wisconsin

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ABSTRACT Gypsy moth (*Lymantria dispar* L.) spread is dominated by stratified dispersal, and, although spread rates are variable in space and time, the gypsy moth has invaded Wisconsin at a consistently higher rate than in other regions. Allee effects, which act on low-density populations ahead of the moving population that contribute to gypsy moth spread, have also been observed to be consistently weaker in Wisconsin. Because a major cause of an Allee effect in the gypsy moth is mate-finding failure at low densities, supplementing low-density populations with immigrants that arrive through dispersal may facilitate establishment and consequent spread. We used local indicator of spatial autocorrelation methods to examine space-time gypsy moth monitoring data from 1996 to 2006 and identify isolated, low-density colonies that arrived through dispersal. We measured the distance of these colonies from the moving population front to show that long-distance dispersal was markedly present in earlier years when Wisconsin was still mainly uninfested. Recently, however, immigrants arriving through long-distance dispersal may no longer be detected because instead of invading uninfested areas, they are now supplementing high-density colonies. In contrast, we observed no temporal pattern in the distance between low-density colonies and the population front in West Virginia and Virginia. We submit that long-distance dispersal, perhaps facilitated through meteorological mechanisms, played an important role in the spread dynamics of the initial Wisconsin gypsy moth invasion, but it currently plays a lesser role because the portion of Wisconsin most susceptible to long-distance immigrants from alternate sources is now heavily infested.

KEY WORDS *Lymantria dispar*, biological invasions, aerobiology, local indicator of spatial autocorrelation, quantile regression

Biological invasions are major threats to native ecosystems (Parker et al. 1999, Mack et al. 2000, Pimentel et al. 2000, Mooney and Cleland 2001). After the arrival and successful establishment of nonindigenous species, invaders begin to spread, and for many biological invasions, spread is the result of a combination of short-range and long-range movement known as stratified dispersal (Hengeveld 1988, Andow et al. 1990, Shigesada et al. 1995, Shigesada and Kawasaki 1997). Such dynamics have important ramifications because colonies established through long-distant jumps increase in both abundance and in their spatial extent, eventually coalescing with the established range of the organism. This results in a more rapid overall rate of spread than what would be expected under diffusive spread (Skellam 1951).

The movement of the gypsy moth, *Lymantria dispar* L., throughout North America is a well-documented example of spread being dominated by stratified diffusion (Sharov and Liebhold 1998). The gypsy moth was introduced outside of Boston, MA, in 1869 (Elkinton and Liebhold 1990), and now is distributed from Wisconsin to North Carolina (Fig. 1) but continues to spread into new areas. Its long-range dispersal most frequently occurs through anthropogenic movement of life stages to areas outside of its distribution (Schwalbe 1981, Mason and McManus 1981). Long-range dispersers do not always become successfully established in new environments, and their establishment can be influenced by habitat susceptibility and Allee effects, which refer to a decrease in population growth rates with a decrease in population abundance (Courchamp et al. 1999). Although the historical (dating back to 1900) and current rate of gypsy moth spread has been highly variable in space and time, its spread in Wisconsin since the mid-1990s (mean spread rate, ≈16 km/yr), when the gypsy moth first invaded Wisconsin, has been consistently higher than in other regions (mean spread rate, ≈6 km/yr) (Tobin et al. 2007a). Furthermore, the strength of Allee effects, which is inversely correlated to the rate of gypsy moth spread, has been consistently weaker in Wisconsin than in other regions (Tobin et al. 2007b).

Low-density gypsy moth populations are particularly prone to Allee effects, which have been observed to play an important role in its establishment (Lieb-

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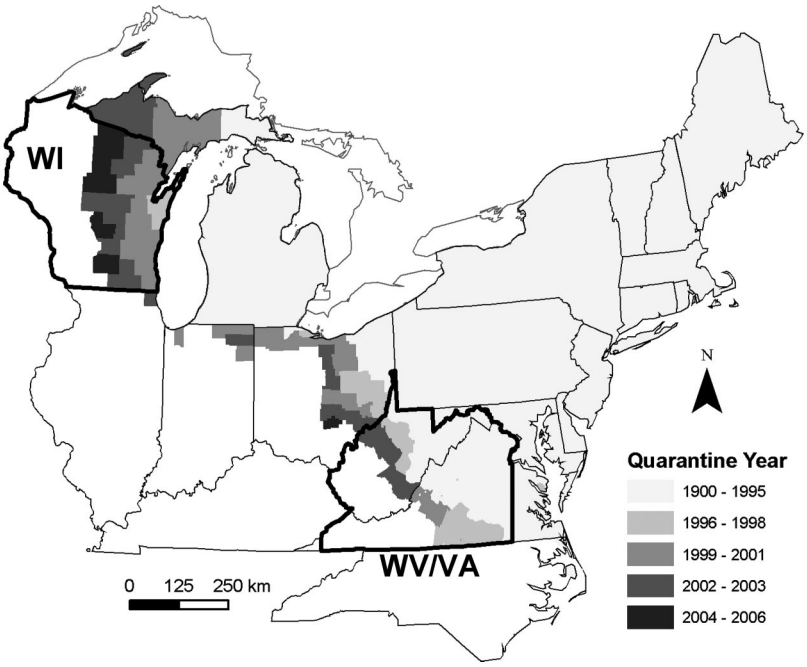

Fig. 1. Distribution of the gypsy moth in the United States, based on county quarantine as maintained by the U.S. Department of Agriculture. Regions (Wisconsin, WI; West Virginia and Virginia, WV/VA) used in this analysis are indicated with thick lines.

hold and Bascompte 2003, Whitmire and Tobin 2006) and spread (Johnson et al. 2006, Tobin et al. 2007b). A primary contributor of an Allee effect in the gypsy moth that has been observed consistently is the challenge of locating mates at low population densities (Sharov et al. 1995a, Tcheslavskaia et al. 2002, Robinet et al. 2007). In field studies, tethered females, which are each capable of ovipositing 250 or more eggs per egg mass (Campbell 1969) were significantly more likely to be mated with increasing male moth density (Sharov et al. 1995a, Tcheslavskaia et al. 2002). Under gypsy moth stratified dispersal, isolated colonies, usually of low density, form ahead of the endemic area. Their successful establishment is strongly determined by their initial size; hence, the concept of the Allee threshold. Higher-density colonies are more likely than lower density colonies to establish (Liebhold and Bascompte 2003, Whitmire and Tobin 2006), after which they increase in size, coalesce with the endemic area, and thus enhance the rate of spread. Supplementing low-density populations with additional males allows the colony to overcome the Allee threshold and become established.

One mechanism of supplementing low-density colonies so that they exceed the Allee threshold is through emigration, such as through the anthropogenic movement of life stages. However, human-mediated movement of gypsy moth is spatially and temporally stochastic and not unique to Wisconsin; rather, it occurs throughout the United States through household moves or commerce (McFadden and McManus 1991). Thus, anthropogenic movement of life stages that can supplement low-density colonies ahead of the population front would not seem to provide an explanation to the consistently higher rates of gypsy moth spread in Wisconsin. Another source of emigration is dispersal by life stages (early instars and adults) from source populations, but this too would seemingly not be unique to Wisconsin. However, enhanced gypsy moth dispersal, such as when facilitated by meteorological events, may be more likely to occur in certain areas, such as the Great Lakes region of the United States. We used robust space-time monitoring data on the gypsy moth in Wisconsin to show that long-distance dispersal, perhaps facilitated through meteorological mechanisms, may have greatly enhanced the ability of the gypsy moth to rapidly invade this region. We also provide a comparable analysis using space-time data from West Virginia and Virginia to furthermore support the notion of enhanced movement of the gypsy moth in Wisconsin.

Materials and Methods

The identification and quantification of isolated low-density colonies ahead of the endemic area, which could be indicative of short and long range dispersal, required a systematic, spatially explicit approach. One such method is the local indicator of spatial autocorrelation (Anselin 1995, Getis and Ord 1996, Boots 2002), which can be used to identify local spatial anomalies within a larger region of interest. These anomalies can be "low-high" or "high-low" associations, and both occur when data from one area

Table 1. Total no. 5 by 5-km grid cells and the no. identified by the local Moran as high-low associations with their respective mean population density

Year	Wisconsin			West Virginia/Virginia		
	Total no. of cells	*N* (%) high-low cells	Mean (SE) density	Total no. of cells	*N* (%) high-low cells	Mean (SE) density
1996	2,855	238 (8.3)	2.14 (0.05)	3,977	203 (5.1)	2.63 (0.50)
1997	3,191	279 (8.7)	2.54 (0.05)	3,708	225 (6.1)	2.22 (0.26)
1998	3,257	373 (11.5)	2.58 (0.10)	3,854	195 (5.1)	1.65 (0.13)
1999	3,264	334 (10.2)	2.82 (0.10)	3,498	207 (5.9)	2.32 (0.26)
2000	3,366	293 (8.7)	6.00 (1.50)	3,126	225 (7.2)	2.10 (0.19)
2001	3,572	235 (6.6)	4.22 (0.36)	3,992	256 (6.4)	1.78 (0.15)
2002	3,694	255 (6.9)	4.05 (0.21)	3,749	236 (6.3)	0.71 (0.05)
2003	3,869	205 (5.3)	2.92 (0.13)	4,097	264 (6.4)	1.30 (0.09)
2004	3,874	173 (4.5)	1.92 (0.13)	4,039	243 (6.0)	1.21 (0.13)
2005	3,876	217 (5.6)	2.47 (0.74)	4,127	175 (4.2)	3.96 (0.35)
2006	3,625	180 (5.0)	2.52 (0.36)	4,345	170 (3.9)	2.98 (0.24)

are different than data from adjacent areas. "Low-high" associations refer to localized depressions, in which data from one area are low in value while data from neighboring areas are high in value. High-low associations refer to the inverse and can be used to objectively identify isolated gypsy moth colonies (cf. Whitmire and Tobin 2006). This method also has the advantage of only considering localized spatial structure, particularly important here because established populations tend to be spatially structured (e.g., high-high associations) and hence have a vastly different spatial signature than isolated colonies, which tend to exhibit little spatial structure as defined by classical geostatistics (Deutsch and Journel 1998).

We used the local indicator of spatial autocorrelation with counts of male moths recorded from pheromone-baited traps placed from 1996 to 2006 in Wisconsin and in West Virginia and Virginia (Fig. 1). Traps are placed 0.25–3 km apart along the leading edge of the advancing gypsy moth population front under a U.S. Department of Agriculture gypsy moth management program, which has existed in both regions since at least 1996 (Sharov et al. 2002, Tobin et al. 2004, Tobin and Blackburn 2007). Under this program, the leading endemic edge and adjacent uninfested areas, extending to ≈200 km from the leading edge, are monitored. Because we were interested in the dynamics of newly establishing populations, we excluded data from areas in which the gypsy moth is already established. This was done by estimating a population isocline, for each year, that delineated a 10-moth population boundary (i.e., a spatial boundary at which 10 or more moths per trapping area are captured on one side and <10 on the other; Sharov et al. 1995b) and omitting data from those areas recording ≥10 moths. Because some newly established colonies of high density are targeted for eradication under this gypsy moth management program, we excluded data that were within 1.5 km of an area treated against gypsy moth (<3% of the total trapping area). The final set of data for each year in Wisconsin comprised ≈18,000–36,000 traps and ≈14,000–25,000 traps in West Virginia and Virginia, over an approximate area of 140,000–150,000 km^2 (for both regions).

Next, for each year, we divided the entire trapping area into a series of 5 by 5-km grid cells. In each cell (number of cells reported in Table 1), we calculated the average number of male moths per 5 by 5-km trapping area and extracted the spatial coordinates from the center of each cell. In Wisconsin and West Virginia and Virginia, the mean number of traps per 5 by 5-km cell was 6.3 (SE = 0.1) and 4.9 (SE = 0.1), respectively. We estimated the local Moran statistic (Anselin 1995, Getis and Ord 1996, Boots 2002) for each cell in R (R Development Core Team 2007) using the spdep package (Bivand 2007)

$$\text{local Moran} = \frac{(z_i - \bar{Z})}{\text{var}(Z)} \sum_{j=1}^{N} W_{ij}(z_j - \bar{Z}), \quad [1]$$

where z_i is the average moth count in the cell, z_j is the average moth count in a cell within a local neighborhood around z_i, and $\bar{Z}$ and var (Z) refer to the year-specific mean and variance, respectively. The weight function, W_{ij}, is binary and equal to one when a neighboring cell (i.e., z_j) was located within 7.5 km (which captured the eight nearest neighboring cells) of z_i. Negative values of the local Moran represent localized anomalies (high-low or low-high associations), and we used only high-low associations in subsequent analyses.

For each cell characterized by a high-low association, we measured the distance between it and the endemic area, defined by the 10-moth population boundary, which is dynamic in space and time (Fig. 2). These distances were regressed over the year using quantile regression with the quantreg package (Koenker 2007) in R (R Development Core Team 2007). Quantile regression (Koenker and Hallock 2001, Cade and Noon 2003) was used in lieu of conventional regression because of our interest in understanding the expected conditional response at different quantiles instead of only the conditional mean response. Within each year, consider the distribution of these distances at the 10th, 50th, or 90th percentiles to represent the distance between local anomalies that are close (10th), of the median distance (50th), or far

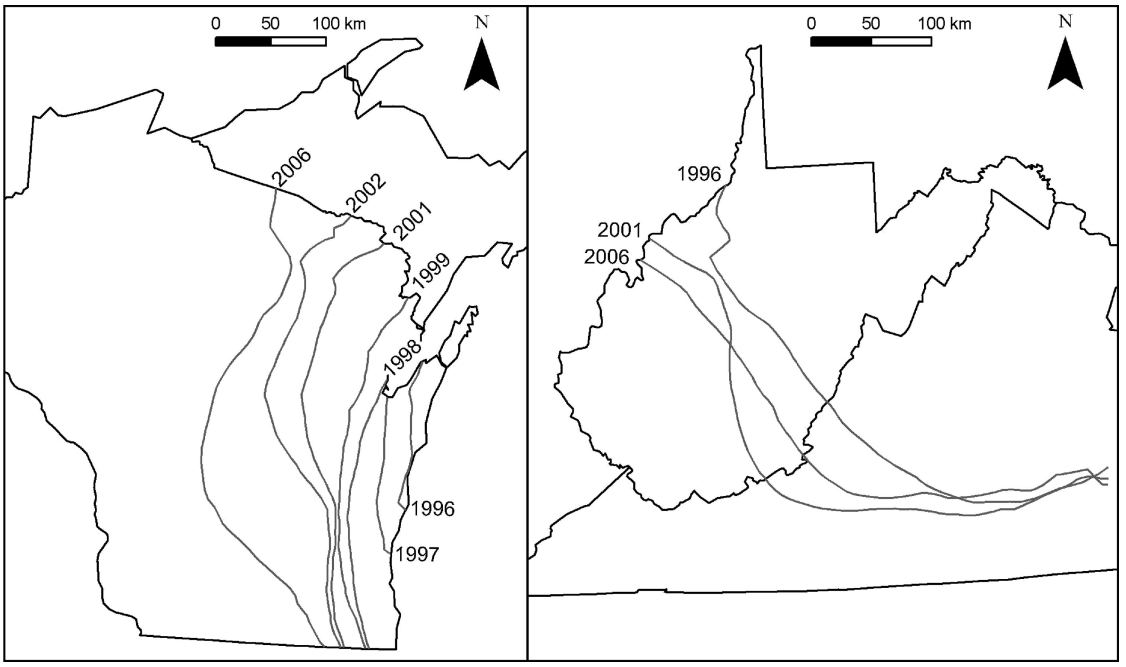

Fig. 2. The 10-moth population boundaries, for selected years, which were used as reference boundaries.

(90th) from the 10-moth population boundary. Assuming spread through stratified dispersal in the absence of enhanced dispersal, we hypothesized that the distance between anomalies and the endemic area should not follow a temporal gradient and should furthermore not be different between the regions of Wisconsin, and West Virginia and Virginia. Significance of slope estimates for each quantile response and tests of slope heterogeneity (within a region) were conducted using the quantreg package (Koenker 2007).

Results and Discussion

The number of cells identified by the local Moran as a high-low association is listed in Table 1 with their corresponding mean population density. In both regions of study, these anomalies were of low male moth abundance (<3 moths/trapping area) but adjacent to cells generally recording 0 moths. There were no overt patterns in density through time, although there was a noticeable increase in density in Wisconsin from 2000 to 2002. There was, however, a tendency in Wisconsin for the proportion of high-low associations to decline through time that was not detected in West Virginia and Virginia (Table 1), indicating that as the gypsy moth moved through Wisconsin, fewer areas over the entire area were characterized as localized high-low anomalies.

The temporal dynamics of the distance between high-low cells and the 10-moth population boundary is shown in Fig. 3. In Wisconsin, this distance sharply declined through time at all three quantiles, and the slope estimates (±SE) for the 10th (slope = -2.45 ± 0.20; t = -12.2; df = 2780; $P < 0.001$), 50th (slope = -6.22 ± 0.23; t = -26.4; df = 2780; $P < 0.001$), and 90th (slope = -9.39 ± 0.37; t = -25.5; df = 2780; $P < 0.001$) percentiles were all significantly negative. Further-

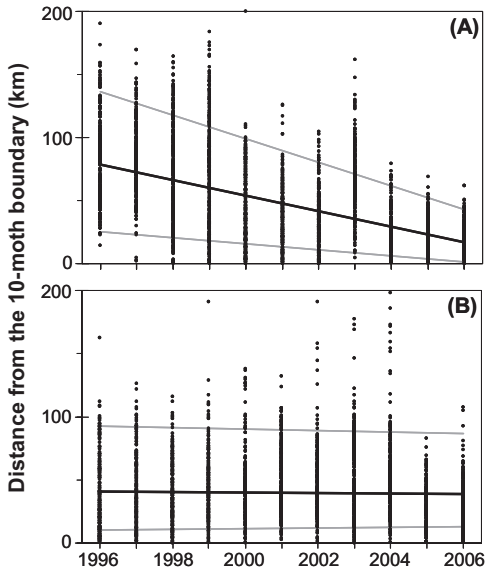

Fig. 3. Distance between cells recording high-low association (identified by the Local Moran, equation 1, and the dynamic 10-moth population boundary in Wisconsin [A], and West Virginia and Virginia [B], 1996–2006). Dots are observed distances, and the three lines are the predictions from the quantile regression fit to the 90th percentile (top gray line), the 50th percentile (middle black line), and the 10th percentile (bottom gray line). Note how the distance in A sharply declines through time although not in B.

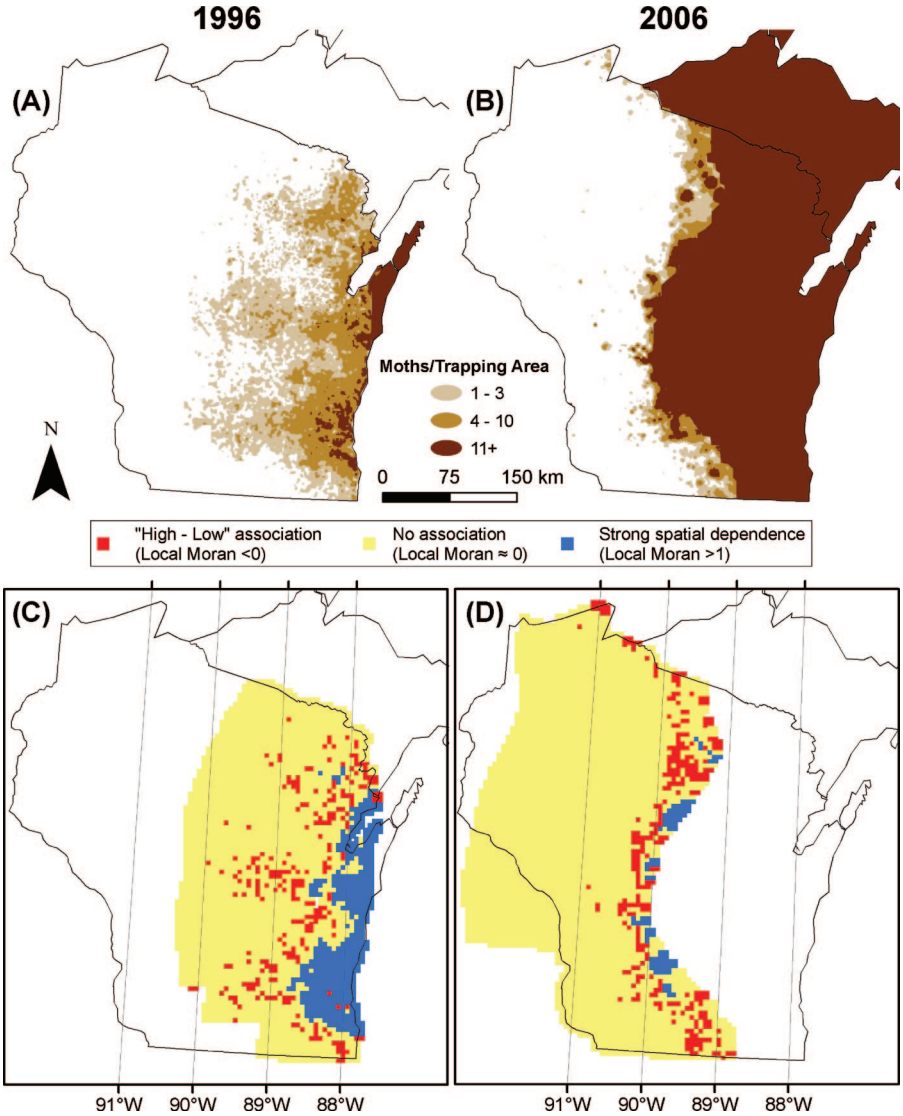

Fig. 4. Interpolated surfaces (using indicator kriging; Deutsch and Journel 1998) of trap catch data in 1996 and 2006 (A and B, respectively). 1996 (C) and 2006 (D) show cells identified as a high-low association (red) or cells with or without spatial autocorrelation. In 1996, the distribution of high-low cells extended to roughly the middle of the state, which by 2006 is infested by the gypsy moth.

more, they each were significantly different from each other, with the 0.9 response decreasing more rapidly than the 0.5 response ($F = 75.4$; df = 1,5563; $P < 0.001$), which in turn decreased more rapidly than the 0.1 response ($F = 220.5$; df = 1,5563; $P < 0.001$). For example, in 1996, the predicted distance of the 90th percentile (indicative of long-range dispersal) was 136.6 km from source populations, yet by 2006 this distance had declined to 42.7. At the 10th percentile (indicative of short-range dispersal), the distance declined from 25.6 km in 1996, to 1.05 km in 2006, which is particularly interesting given historical work on gypsy moth spread by Liebhold et al. (1992) who used a Skellam model parameterized from field data to predict gypsy moth spread as 2.5 km/yr. Because their model did not incorporate long-distance movement but instead was based on local population dynamics (i.e., the intrinsic rate of population growth coupled with short distance larval dispersal), it provides an estimate of local gypsy moth spread. Thus, short-range dispersal in Wisconsin in recent years, using the 10th percentile of dispersers as a surrogate, seems to coincide with local spread predictions by Liebhold et al. (1992).

In contrast, in West Virginia and Virginia, there was no significant change in the predicted responses through time (Fig. 3), and the slope estimates (±SE) for the 10th (slope = −0.24 ± 0.18; t = 1.3; df = 2397; $P = 0.183$), 50th (slope = −0.23 ± 0.23; t = −1.0; df = 2397; $P = 0.325$), and 90th (slope = −0.58 ± 0.39; t =

-1.5; df = 2397; $P = 0.139$) were each not significantly different from 0. Across all years, the predicted distance of the 90th percentile (indicative of long-range dispersal) from source populations was 89.8 km, whereas the predicted distance at the 10th percentile (indicative of short-range dispersal) was 11.7 km, which is slightly higher than the spread predictions by Liebhold et al. (1992).

Collectively and comparably, the dynamics presented in Fig. 3 suggest that gypsy moth long-range dispersal may have played a particularly strong role in the early years of the Wisconsin invasion by supplementing low-density populations with immigrants and thus allowing some proportion of low-density populations ahead of the endemic area to surpass the Allee threshold, successfully establish, and contribute to gypsy moth spread. This is not to say that long-range distance dispersal is no longer occurring in Wisconsin; rather, one limitation could be the distance of the current uninfested area in Wisconsin from alternative source populations, such as those in Michigan. In 1996, most of Wisconsin was uninfested, so if life stages were, for example, aerially transported from source populations and over the Great Lakes, most of these immigrants would have found themselves in uninfested habitats where their detection could be noticed. However, in later years, in which the eastern half of Wisconsin is now infested, long-range immigrants would more likely be supplementing high-density populations. It is far more likely to notice low moth densities (<3 moths/trapping area; Table 1) in areas in which the population is generally 0 (such as in 1996) than to distinguish immigrants from resident populations when the latter exceeds 100 moths/trapping area (such as in 2006). This dynamic is supported by Fig. 4, which highlights the distribution of distances in 1996 and 2006 (as examples) and reveals that despite tremendous differences in the spatial extent of the endemic area between these 2 yr, that the distance of dispersers in Wisconsin, particularly those at the farthest distances, does not greatly differ between these 2 yr.

The rapid rate at which the gypsy moth is spreading (Tobin et al. 2007a), the enhanced rate of low-density colony persistence (Whitmire and Tobin 2006) and the reduced strength of Allee effects (Tobin et al. 2007b) in Wisconsin relative to other regions currently under invasion suggest the occurrence of mechanisms possibly unique to or at least of greater importance in Wisconsin. Although low-density gypsy moth populations are affected by predation from small mammals (Elkinton and Liebhold 1990, Elkinton et al. 1996; Elkinton et al. 2004), the effects of small mammal predation have not been observed to differ among different regions in the United States, including Wisconsin (Liebhold et al. 2005). Instead, we propose that long-distance dispersal, perhaps facilitated by meteorological mechanisms, of the gypsy moth during the early stages of the Wisconsin invasion played an important role in facilitating the establishment of low-density populations ahead of the population front, with the consequence of enhanced spread. We also propose that long-distance dispersal plays a lesser role now—at least in terms of the dynamics of newly established populations and their effect on spread—because the portion of Wisconsin most susceptible to long-distance immigrants from alternate sources is now generally infested. It remains uncertain how long-distance dispersal could affect outbreak dynamics in Wisconsin, which has not yet experienced major gypsy moth outbreaks.

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