Introduction

The gypsy moth in North America (Elkinton and Liebhold 1990) is one example of a much larger problem, namely, ever increasing biological invasions. Over the last 50 years, the forests of Eastern North America have been particularly afflicted by a multitude of alien insects and diseases. Many of these have substantially altered ecosystem properties and processes (Liebhold et al. 1995). Given the magnitude of this problem we need to understand the population processes operating during biological invasions. The development of such an understanding is a prerequisite for developing strategies for managing current and future invasions.

Biological invasions can be divided into three distinct population processes: arrival (the process by which individuals are transported from their native to an exotic habitat); establishment (the process by which populations grow to sufficient levels that extinction no longer is likely); and spread (the expansion of a population’s range in the exotic region) (Dobson and May 1986, Liebhold et al. 1995, Shigesada and Kawasaki 1997, Natl. Res. Counc. 2002). Corresponding to each of these invasion phases is a management activity: 1) international quarantines and inspections are strategies for preventing arrival, 2) detection and eradication are activities for preventing establishment, and 3) domestic quarantines and barrier zones are strategies for limiting the spread of alien species.

The gypsy moth is an excellent species for illustrating the population processes operating during biological invasions. The first arrival of the gypsy moth occurred many years ago; the accidental release of gypsy moth occurred in 1868 or 1869 in the Boston suburb of Medford by an amateur entomologist, Etienne Léopold Trouvelot (see Chapter 1). Despite early efforts to eradicate the gypsy moth, the insect was firmly established in the Boston area by 1900. Due to the limited dispersal capability of the European gypsy moth strain (Trouvelot is thought to have released a European strain in which females are incapable of flight), gypsy moth spread in North America has been slow. Over the last century it has invaded less than a third of its potential range (Sharov and Liebhold 1998b, Morin et al. 2004). This prolonged period of spread has provided considerable
time to study gypsy moth spread and the vast quantity of data collected on gypsy moth dynamics at the expanding population front has led to an extensive understanding of the spread of this insect, perhaps better than any other alien species.

Introduction to the Population Ecology of Biological Invasions

Not every seed that falls to the ground becomes a tree. Similarly, of the many insect invaders that arrive in a new habitat, few become established. Founder populations typically are small and consequently are at great risk of extinction from both direct effects such as disturbance and indirect effects such as the highly restricted genetic variability in founding populations. Generally, the smaller the founder population, the less likely the insect will become established (MacArthur and Wilson 1967, Mollison et al. 1986). This relationship is clearly illustrated by historical records of introductions of natural enemies as part of biological control programs; establishment frequencies are consistently higher from releases of large numbers of individuals (Beirne 1975, Fagan et al. 2002).

Much of what we know about the population biology of low-density invading populations is extracted from a rich literature on the population ecology of rare species, i.e., conservation biology. All populations are affected by stochastic abiotic influences, e.g., weather, but low-density populations are particularly sensitive to perturbation. We can mathematically represent the generational change, from \( t \) to \( t+1 \), in population density as

\[
N_{t+1} = f(N_t) + \epsilon_t, \quad (2.1)
\]

where \( N_t \) is population density in year \( t \), \( f(N_t) \) is a function that encompasses birth and death processes, and \( \epsilon_t \) is variation due to environmental stochasticity. The important result of demographic and environmental stochasticity is that low-density populations, e.g., newly founded invading populations, are particularly prone to extinction as a result of this random variation. However, another factor contributing to extinction of low-density populations must be considered: Allee dynamics.

Warder Allee (1932) studied animal population ecology and generally is recognized as the first worker to recognize a phenomenon in low-density populations of most species, that is, certain processes may lead to decreasing net population growth with decreasing density. As a result of this relationship, there sometimes is a threshold below which low-density populations are driven toward extinction (Fig. 2.1). This phenomenon, called the Allee effect, can result from one of many biological mechanisms, for example, an Allee effect could be due to insufficient cooperative feeding or a failure to find mates at low densities (Courchamp et al. 1999). The Allee effect has been identified as critical
in understanding patterns of extinction from the perspective of conservation biology (Stephens and Sutherland 1999), and there is growing recognition of its important role during the establishment phase of biological invasions (Drake 2004, Leung et al. 2004, Johnson et al. 2006, Tobin et al. 2007b). The magnitude of the Allee effect varies greatly among species due to variation in life history traits. However, virtually every sexually reproducing species can be expected to exhibit an Allee effect at low densities. As such, Allee dynamics may be of critical importance in understanding why some species establish more easily than others.

Understanding the establishment process has important implications for management. The activity we call “eradication” is aimed at reversing the process of establishment; eradication is forced extinction (Myers et al. 2000). It follows from the previous description that eradication is likely to succeed only in situations in which the target population is both low in density and highly restricted in its spatial distribution. Liebhold and Bascompte (2003) used an Allee effect model to illustrate the numerical relationships between initial numbers of individuals, the strength of an eradication treatment (percent killed), and the probability of population persistence.

![Figure 2.1.— Schematic of the Allee effect. Change in population density, $N_{t+1}/N_t$ is plotted as a function of density at the beginning of the generation, $N_t$. This relationship determines change in population density $f(N_t)$ shown in equation 2.1. Note that when density is greater than the minimum population density, it will increase or decrease toward the stable equilibrium, but when it is below this threshold, density will decrease toward extinction.](image)
Once a population is established, its density typically will increase and individuals will disperse into adjoining areas of suitable habitat. Three phases to the range expansion process are generally recognized (Shigesada and Kawasaki 1997) (Fig. 2.2). Following establishment of the alien population, there is an initial period during which spread accelerates. In the early stages of this phase, populations may remain at extremely low densities and, therefore, remain undetected for several years (Kean and Barlow 2000). The bulk of range expansion occurs during the expansion phase. During this phase, the radial rate of spread often increases linearly, but in other cases it may accelerate in a nonlinear fashion (Andow et al. 1990). Finally, as the expanding range begins to saturate the geographic extent of suitable habitat, spread declines and ultimately stops.

The spread of a population is driven by two processes: population growth and dispersal. As a result, most models of population spread have focused on these processes. The simplest and probably the most widely applied model of population spread was developed by Skellam (1951). This model combined random (Gaussian) dispersal with exponential (Malthusian) population growth to model expansion following an initial introduction of $N$ individuals at time $t=0$, and at location $x=0$ and $y=0$, denoted as $N_{0,0,0}$. The number of individuals at a distance $x$ and $y$, and time $t$, from the initial site of introduction is given by

$$N_{x,y,t} = \frac{N_{0,0,0}}{4\pi Dt} e^{-\frac{x^2+y^2}{4Dt}},$$

Figure 2.2.—Generalized range expansion of invading species. Radial distance refers to the distance from the site of introduction to the expanding population front.
where $D$ is the “diffusion coefficient” (a measure of the amount of movement) and $r$ is the intrinsic rate of increase from the exponential growth model and is a measure of population growth under ideal conditions. The assumption of random movement in this model implies that the population will spread radially at an equal rate in all directions (Fig. 2.3A). Skellam (1951) showed that for any detection threshold, $T$, such that the infested area at any time $t$ is restricted to points where $N_{x,t} > T$, the expansion velocity of the infested front (radial rate of spread), $V$, is constant and can be described:

$$V = 2\sqrt{rD}.$$  \hfill (2.3)

This model assumes that $r$ and $D$ are constant through time and space during the period of range expansion of the invading organism, an assumption that intuitively seems unlikely, e.g., spatial variation in the habitat may profoundly affect birth/death functions as well as dispersal rates. Nevertheless, there has generally been some (but not total) congruence between predictions of this model and observed rates of spread of most exotic organisms (Andow et al. 1990, Shigesada and Kawasaki 1997).

Fisher (1937) advanced a nearly identical model to that of Skellam (1951) except that he assumed population growth had finite limits represented by a logistic growth model versus the exponential model. Interestingly, the asymptotic wave speed in the Fisher model is identical to that of the Skellam model (eq. 2.3). This similarity of spread behavior reflects the fact that range expansion in both models is driven by population growth near the expanding population front; population growth in areas that have been infested for many years has little effect on spread. A mathematical exploration of general conditions leading to constant rates of spread is found in Weinberger et al. (2002).

Skellam’s model assumes a single, continuous form of dispersal and predicts that range expansion should be a smooth, continuous process (Fig. 2.3a). However some species may be able to disperse in at least two ways. The existence of two forms of dispersal is referred to as “stratified dispersal” (Hengeveld 1989); in those situations, range expansion will proceed through the formation of multiple discrete, isolated colonies established ahead of the infested front (Shigesada et al. 1995, Shigesada and Kawasaki 1997). These colonies, in turn, will expand their range and ultimately coalesce. The result of this phenomenon is that range expansion may occur much faster than would occur under a more simple diffusion model. This pattern of spread through coalescing colonies also has been represented mathematically by applying spread models that incorporate dispersal kernels with “fat tails” (Clark et al. 2001), that is, there is an increased chance of relatively long-distance dispersal events.

There are many examples of invasive species that spread according to a coalescing colony model (Shigesada and Kawasaki 1997). Interesting aspects of this type of spread
are that establishment is an important component, isolated colonies are formed ahead of the expanding population front due to dispersal of propagules (Fig. 2.3b), and the ability of these propagules to successfully initiate new populations that spread and coalesce is entirely dependent on their ability to establish successfully. Therefore, all of the population processes that are important to establishment, namely, stochasticity and Allee dynamics, may be of critical importance to the spread process. For example, the existence of a strong Allee effect will reduce probabilities of establishment, which, in turn, may reduce rates of spread (Lewis and Kareiva 1993). Studying the historical spread of the house finch in North America, Veit and Lewis (1996) found that mating success in isolated, low-density populations is low, and that this results in a strong Allee effect. Veit and Lewis (1996) modeled this effect and showed that Allee dynamics was of critical importance in explaining observed rates of spread.

Gypsy Moth Spread: The “Big Picture”

As stated in Chapter 1, efforts to eradicate gypsy moth from Boston, Massachusetts, were abandoned by 1900; at that time, populations existed in parts of three counties in the greater Boston area. Over the next 100 years, the intensity of efforts to retard the spread of gypsy moth in North America varied. Through most of this period, there were considerable efforts to delimit the geographical extent of invading populations. As early as 1896, the production of chemical attractants by females was recognized and traps baited with live females were being utilized as powerful tools for detecting low-density, newly invaded populations (Forbush and Fernald 1896). By the 1940’s, state and Federal
agencies had discovered that the pheromone could be extracted from adult females and used as lures in traps. In 1970, the compound disparlure was isolated and ultimately synthesized for use as lures in thousands of traps (Bierl et al. 1970).

The continual use of pheromone-baited traps for detecting new gypsy moth infestations provides some historical consistency in records of gypsy moth range expansion. Unfortunately, records from most traps deployed prior to 1980 were not archived. Thus, our only source of historical information on the range expansion of gypsy moth over long periods (prior to 1980) and over the entire expanding population front (except perhaps excluding Canada) are records of when individual counties first became infested. Beginning with the enactment of the Domestic Plant Quarantine act of 1912, the U.S. Department of Agriculture (USDA) has listed (in the annual Code of Federal Regulations Title 7, chapter 301.45-2a) all counties that comprise the generally infested area (Weber 1930).

County-level maps of gypsy moth spread illustrate historical spread over the last 100 years (Fig. 2.4). While initial spread from 1900 to 1915 was primarily to the north, most of the spread since that time has been to the west and south. At the county level, spread appears as a continuous process; with the exception of Michigan, the range has always expanded into adjacent counties rather than “jumping” to outlying locations. The lone exception to this pattern is the population that apparently started in Midland, Michigan; populations were first detected there in the 1950’s, but six counties were
infested by 1981 due to failed eradication efforts. This secondary focus has accelerated gypsy moth spread into much of the Midwest and spread from this focus now comprises a large proportion of the area infested (Fig. 2.5).

Liebhold et al. (1992) analyzed the historical spread of the gypsy moth in North America (both the United States and Canada) from 1900 to 1989 using historical county-level records of the advancing quarantine. By plotting the year of first establishment (quarantine) over the minimum distance from the point of introduction (Medford; calculated in a GIS), they were able to estimate the radial rate of range expansion as the slope of the linear model fit to this relationship using linear regression. Exploration of the data indicated that the rate of range expansion had varied through time and space (Table 2.1). Liebhold et al. (1992) speculated that the extremely slow rate of spread from 1916 to 1965 most likely was due to the implementation of a barrier zone in and around the Hudson River Valley during that time (see Chapter 1). Although this program apparently failed to stop the spread, it appears to have succeeded in slowing it. Liebhold et al. (1992) also found that from 1966 to 1989, spread rates in cold, northern climates were less than half those in the more temperate areas to the south. They attributed these lower rates of spread to lower population growth rates caused by severe overwintering mortality that is known to occur in extremely cold winter temperatures (e.g., Madrid and Stewart 1981).
Table 2.1.—Radial rates of gypsy moth range expansion, 1900-1989, reported in Liebhold et al. (1992) and estimated from historical county-level quarantine records

<table>
<thead>
<tr>
<th>Interval</th>
<th>County subset</th>
<th>Number of counties</th>
<th>Radial rate of range expansion (km/yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1900–1915</td>
<td>All</td>
<td>52</td>
<td>9.45 ± 0.76</td>
</tr>
<tr>
<td>1916–1965</td>
<td>All</td>
<td>48</td>
<td>2.82 ± 0.19</td>
</tr>
<tr>
<td>1966–1989, T &lt; 7 °C</td>
<td>All</td>
<td>225</td>
<td>7.61 ± 0.49</td>
</tr>
<tr>
<td>1966–1989, T ≥ 7 °C</td>
<td>All</td>
<td>98</td>
<td>20.78 ± 0.33</td>
</tr>
</tbody>
</table>

*Mean minimum January temperature.

Liebhold et al. (1992) compared these empirically derived estimates of spread rate with rates predicted from gypsy moth life-history traits. They used Skellam’s (1951) equation (eq. 3.3) to estimate the expected spread rate under natural dispersal. Their estimates of $r$ and $D$ were derived from previously published demographic studies of population growth and dispersal (through windborne movement of first instars) and yielded an expected spread rate of ca. 2.5 km/yr. Since this rate falls far below the ca. 21 km/yr spread rate observed from 1966 to 1989 along most of the expanding gypsy moth population front, they concluded that the higher rates of spread must be due to the enhanced movement of gypsy moth through the accidental movement of life stages. Indeed, the behavior of late-instar gypsy moth, in which they seek cryptic resting places, frequently results in the inadvertent transport of life stages on vehicles and other manmade objects (McFadden and McManus 1991, Liebhold et al. 1994).

Gypsy Moth Spread: The “Close-up Picture”

Although the historical quarantine records described are the only data available for examining gypsy moth spread over long periods, they are problematic in that designations of quarantines are not always based on objective biological data, and county-level records do not provide very detailed spatial information about spread. As early as the 1890’s (Forbush and Fernald 1896), pheromone-baited traps were used to monitor the spread of gypsy moth populations. In early efforts, traps were baited with live females; later, extracts of pheromone glands were used. The chemical structure of the attractant disparlure was identified in 1970 (Bierl et al. 1970) and the enhanced activity of the (+) enantiomer was not recognized until later (Iwaki et al. 1974, Mori et al. 1976). The standardization of trap designs (see Chapter 3) did not occur until the mid-1970’s, and the concept of deploying large numbers of traps in a grid to characterize the advancing population front was not implemented until the early 1980’s (see Chapter 1) (Reardon et al. 1987, 1993). As part of various intensified programs to manage gypsy moth along the expanding population front, grids of traps have been deployed along the transition...
zone since the mid-1980’s and the data obtained are a useful resource for furthering our understanding of gypsy moth spread. The central Appalachian region has the longest history of intensified trapping but since the STS Program became a multistate effort, trapping has been extended along the entire population front. Currently, 70,000 to 90,000 traps are deployed annually as part of the program (see Table 3.1).

The United States can be divided into a generally infested area, i.e., gypsy moth populations are established, an uninfested area, i.e., populations are not established, or a “transition zone” between the two (Fig. 2.6). Male gypsy moths can sense small concentrations of disparlure (Leonhardt et al. 1996) and traps baited with (+) disparlure can detect newly established populations at low densities. Grids of traps deployed over large landscapes in the transition zone are powerful tools for characterizing the shape and dynamics of the advancing population front.

The development and use of mathematical algorithms to interpret male moth counts from trapping grids and estimate the boundaries of advancing populations is a critical component of the STS Decision Algorithm. See Chapter 5 as well as Sharov et al. (1996b, 1997b), and Tobin et al. (2004). This method can be used to identify boundaries

![Figure 2.6](image_url)  
**Figure 2.6.**—From the perspective of gypsy moth range expansion, the United States can be divided into the generally infested area (red), uninfested area (gray), and transition zone (yellow) as of 2000.
corresponding to various gypsy moth population levels measured in spatially referenced traps, e.g., 1, 3, 10, ..., and 300 moths per trap, populations measured using standard egg mass sampling procedures, e.g., 1, 3, 10, ..., and 100 egg masses/1-ha plot, and populations evaluated based on aerial surveys for the presence of defoliation (Fig. 2.7). These results indicate that there is a type of gradation in gypsy moth abundance in the transition area. At the most distal portion, gypsy moth populations are absent as there were no captures in the majority of traps. But as one moves proximally toward the generally infested area, there is a zone of increasing numbers of positive trap catches. The point at which populations are present in nearly every location (one moth/trap line reaches unity in figure 2.7b) roughly corresponds with the 50th percentile of the 10 moths/trap line. For this reason, and because it is the most stable boundary (Sharov et al. 1997b), the 10 moths/trap line is a useful definition of the advancing population front. However, one still must move even more toward the infested region before reaching an area at which egg masses can be detected by standard sampling methods (Fig. 2.7b). It is for this reason that egg mass sampling is not considered effective for assessing populations in the transition area even though it is the primary method for evaluating populations in

Figure 2.7.—Population boundaries estimated from trapping grids located in the Appalachian Integrated Pest Management Program area in the central Appalachians, 1988-92: (a) maps of boundaries, and (b) distribution of boundary locations perpendicular to the general boundary direction (modified from figures 2 and 3 in Sharov et al. 1996b).
suppression programs. Finally, located even deeper into the infested region is the area in which outbreak populations (detected through aerial surveys for defoliation) occur.

An important use of population boundaries is the estimation of spread rates based on the distance between boundaries in successive years (see Chapter 5) (Sharov et al. 1997b). Estimation of spread rates from trap data in this manner provides much more precision in space and time than estimates of spread rates from the county-level quarantine information described earlier (Tobin et al. 2007a). Yearly estimates of spread from trap data indicate that spread rates can vary considerably from year to year (Sharov et al. 1997b). Analysis of spread from trapping data collected in the central Appalachian region from 1984 through 1995 indicated that from 1984 to 1989, spread rates ranged from 17 to 30 km/yr. This is in approximate agreement with the 21 km/yr spread rate estimated from 1966 to 1989 by Liebhold et al. (1992) from county-level data. According to Sharov et al. (1997b), spread rates in this region after 1989 fell to an average of about 9 km/yr. They concluded that this decrease in spread resulted from containment activities conducted as part of the AIPM and STS Programs (see Chapter 1).

Another important characteristic of populations in the transition zone is their characteristic spatial aggregation. Sharov et al. (1996a) found that trap captures in the transition zone (defined as the area between the 1 and 300 moths/trap boundaries) were highly spatially autocorrelated, indicating the existence of “clumps” of elevated trap capture. The existence of these clumps in the transition area can be seen in Figure 2.8. Most of these clumps are thought to represent isolated populations that are formed ahead of the advancing population front. Thus, the spread of the gypsy moth appears to be an example of stratified dispersal as described previously. Isolated colonies are formed when propagules occasionally disperse well beyond the infested front. Populations in these colonies grow and eventually coalesce (Fig. 2.9a). Presumably, the mechanism of short-range, continuous dispersal that causes the growth of isolated populations is windborne dispersal of first instars (Mason and McManus 1981), and the mechanism behind the stochastic, long-range colony formation is accidental movement of life stages by humans (McFadden and McManus 1991). The potential role of long-range movement of gypsy moth life stages through meteorological events such as wind is still unknown. Sharov and Liebhold (1998a) used trap-grid data collected over several years from the transition area in the central Appalachians and were able to objectively identify isolated colonies and thereby estimate their rate of formation (Fig. 2.9b). They found that the rate of colony formation was around 70 per km$^2$ at a distance of 100 km from the defoliating front and then declined linearly to near zero at a distance of 250 km from the front. However, low levels of colony formation continued distally as far as their data extended. Indeed, isolated colonies are detected every year well beyond the expanding population front, even as far as Washington State (Liebhold and Bascompte 2003),
though state and Federal eradication efforts generally are successful in eliminating them. The formation of these isolated colonies in the transition area is a possible explanation for spread rates that historically have greatly exceeded the predictions (Liebhold et al. 1992) of spread based on first-instar dispersal in Skellam’s equation.

Figure 2.8.—Trap capture of male moths interpolated from grids in the central Appalachians in 2004. Note the isolated colonies in the transition zone and ahead of the generally infested area.

Figure 2.9.—Colonization of isolated populations as a function of the distance (x) from the population front: (a) Colonization rates, c(x), decline over distance; (b) Colonization rates estimated from trap grids in the central Appalachians (modified from figure 9 in Sharov and Liebhold 1998a).
Sharov and Liebhold (1998a) used the linear approximation of colony formation (Fig. 2.9) to model range expansion of the gypsy moth and predict the effectiveness of containment efforts. The model was inspired by the coalescing colony model (Shigesada and Kawasaki 1997), but instead of assuming a constant “jump distance” for colony formation, the model simulated variable jump distances. The rate of colony formation declined linearly with distance from the infested front (Fig. 2.9). The model of Sharov and Liebhold (1998a) combined colony formation in the transition area with colony growth and ultimate coalescence. They then used this model to predict the effect of various barrier-zone management activities. Specifically, they assumed that over some band of a specific width in the transition zone, all isolated colonies would be detected and eradicated. The model predicted that a barrier zone that was 100 km wide would result in a reduction in the radial rate of spread by about 50 percent. In the STS Program, there is no “control” so the actual effectiveness of the program cannot be evaluated directly. Nevertheless, over the last 10 years that the program has been in place in the central Appalachians, the radial rate of spread has averaged well below 10 km/yr, or nearly half of the historical average of 21 km/yr measured by Liebhold et al. (1992) from 1966 to 1989. Thus, the program appears to be exceeding the 50-percent reduction predicted by the model of Sharov and Liebhold (1998a).

We now know that the formation of isolated colonies ahead of the generally infested front is a central mechanism in gypsy moth spread. It is the formation of these colonies that causes spread to greatly exceed the approximate 2.5 km/yr spread rate that would be expected by continuous spread and first-instar dispersal in Skellam’s model (Liebhold et al. 1992). Further, the entire strategy of the STS Program is built on the concept of finding isolated colonies (using grids of traps) and eliminating or retarding their growth. Despite the importance of colony formation, there are many unresolved questions about this process. Foremost among them is what mechanism(s) leads to colony formation? To iterate, life stages are constantly moved ahead of the infested front on objects such as firewood, timber, and motor vehicles, but the relative importance of these various pathways remains unknown. Certain types of long-distance dispersal of life stages, e.g., through wind, could contribute to colony formation but this has not been documented.

Because populations are initially isolated and sparse, it rarely is possible to observe the initial colonization event. Instead, we expect that colonization usually goes unnoticed and that some time must pass for colonies to grow in population size and geographical extent before they are detected in trapping grids. Nevertheless, there is one important characteristic of the early stages of colony formation that seems to be universally true: most isolated colonies go extinct on their own with no intervention. This phenomenon can be seen both in data collected in the transition area (Whitmire and Tobin 2006) and in more distant portions of the uninfested area (Liebhold and Bascompte 2003). Both of
these studies found that most isolated populations went extinct by the year following their detection and that the probability of population persistence increased with increasing abundance (measured by trap capture). This population behavior is indicative of an Allee effect and is a critical aspect of the dynamics of isolated populations.

There are several possible mechanisms that contribute to the observed Allee effect in low-density populations. For example, predation by generalist predators (mostly small mammals) has been recognized to be the major source of mortality affecting low-density gypsy moth populations (Campbell and Sloan 1977, Elkinton et al. 1996); this predation is characterized by a type II functional response (Elkinton et al. 2004) and, therefore, causes inverse density-dependent mortality which can be expected to cause an Allee effect (Courchamp et al. 1999). Failure to find a mate is another major contributor to the existence of an Allee effect in isolated gypsy moth populations. Studies in the transition area in both Virginia and Wisconsin indicate that in sparse, isolated gypsy moth populations, a high proportion of females goes unmated and that this proportion increases as the abundance of males, as measured by trap capture, decreases (Sharov et al. 1995a, Tcheslavskaia et al. 2002).

Females of the European strain of the gypsy moth that is present in North America are incapable of flight while males are much more mobile. However, a mark-recapture experiment with males in small trap grids indicated that few disperse great distances (Elkinton and Carde 1980). Despite these results, there is other evidence that large numbers of males occasionally disperse from high-density populations into trapping grids in the transition area. One piece of evidence is simply the spatial and temporal patterns of trap capture. For example, in Figure 2.10 we see that in 1996 there were

Figure 2.10.—Interpolated moth trap-capture surfaces from Wisconsin in (a) 1995 and (b) 1996.
several “fingers” of elevated trap capture in areas of Wisconsin, where there were no populations previously. There probably are several possible causes for these patterns; one explanation is that large numbers of males dispersed into these areas from elsewhere, e.g., outbreak populations in Michigan’s lower peninsula.

Probably the most definitive piece of evidence for adult male dispersal are historical unpublished records of trap capture in the Upper Peninsula of Michigan in 1993. These records showed two major peaks of trap capture during a single season. The first peak, apparently composed of immigrant moths, was observed from July 22 to August 6, and coincided with the timing of adult development to the south, i.e., the lower peninsula. A second and much smaller peak caused by resident moths was observed from August 18 to September 9, and coincided with the timing of adult emergence in the Upper Peninsula. Positive trap captures over large, continuous areas where none were previously detected have been observed elsewhere along the expanding population front, for example North Carolina in the early 1990’s, along the Ohio/Indiana border in 1998, and in central Ohio in 1999. Unfortunately little is known about the behavior of adult males or meteorological conditions that might explain why these events occur in certain locations in specific years.

Since males alone are not capable of reproducing, a cursory interpretation of these dispersal events is that they have no consequence to gypsy moth spread. However, as stated earlier, most isolated gypsy moth populations in the transition area go extinct with no intervention, and the most likely cause is an Allee effect due to a failure to find mates. However, dispersal of large numbers of males into the transition area could greatly alter this phenomenon. Dispersing males would mate with females and the result would be the persistence of a much larger proportion of isolated colonies, leading to a much higher rate of spread than would exist without male dispersal. However, it remains unclear whether the higher rates of spread observed in Wisconsin, where dispersal episodes appear to have been numerous, could be explained by this effect.

Nevertheless, Whitmire and Tobin (2006) reported that the persistence of isolated populations was much greater in Wisconsin than elsewhere in the transition area and that this elevated persistence can be expected to result in higher spread rates. They also reported that after controlling for population density, persistence was much greater among isolated populations near the continuously infested areas than among more distantly located populations. Presumably, male availability could be expected to be greater for the proximal populations and this could explain their increased persistence.

Since the spread of any invading population is the result of population growth coupled with dispersal, one could expect that any habitat characteristic that causes increases in dispersal or population growth would lead to elevated rates of spread. But despite this intuitively obvious connection between habitat quality and range expansion, there is little evidence of a strong interaction between characteristics of the habitat and...
spread rates. For example, in figure 1 from Liebhold et al. (1992), the expanding population front (excluding the secondary Michigan population) in 1989 was largely equidistant from the original site of introduction in Medford, Massachusetts. This indicated that historical spread had been spatially constant—except for decreased rates of spread to the north—despite considerable geographical variation in land use and forest types in the area through which the gypsy moth had expanded its range. In a more detailed analysis, Sharov et al. (1997a) examined relationships between habitat characteristics and trap capture in the central Appalachians. They found that in the uninfested area, trap captures were highest in the lower elevations, but in the transition area, trap captures were highest in the upper elevations. This suggested that these patterns may reflect higher colonization rates in low elevations (due to higher human population activity) but higher population growth at higher elevations (due to higher densities of forests).

Cold winter temperatures cause considerable mortality in overwintering gypsy moth populations. Liebhold et al. (1992) concluded that slower rates of gypsy moth spread to the north were due to this phenomenon, though the high rates of spread observed over the last 10 years in Wisconsin do not support this conclusion. Sharov et al. (1999) examined historical gypsy moth spread in Michigan and concluded that spatial and temporal variation in spread rates there were more closely associated with variation in forest composition (relative densities of gypsy moth host tree species) than with winter temperatures, though these two factors were confounded. In summary, there seems to be a weak relationship between gypsy moth spread rate and the quality of the habitat, and populations seem to be able to spread through areas of only moderate habitat quality. It may be that spread is affected both by variation in habitat invasibility for initial colonization (e.g., areas of intense human activity) and by quality for population growth, e.g., forest composition, and, therefore, no single factor alone can explain the variation in spread rates.

Conclusion

Given the enormous amount of data and intensity of research, the gypsy moth is a model system for understanding the population biology of range expansion. Spread is not a continuous expansion process as predicted by Skellam (1951). This discovery provided the basis for the implementation of the STS Program, which focuses on slowing spread by finding and eradicating isolated colonies, or suppressing their growth. The experience with gypsy moth clearly demonstrates that understanding the population biology of an invader can be instrumental in developing effective approaches to managing the invasion.
The literature is rich with information on gypsy moth range expansion, particularly the role played by the formation of colonies ahead of the infested area in gypsy moth spread. The remaining chapters of this report address various aspects of the STS Program, which was fundamentally and conceptually based on our understanding of gypsy moth invasion dynamics. The Slow the Spread approach to monitoring gypsy moth populations and collecting data, keystone aspects of the IPM philosophy, is discussed in Chapter 3.
Literature Cited


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