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Gypsy moth invasion in North America: a quantitative analysis

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Abstract. The gypsy moth, *Lymantria dispar* (L.), was accidentally introduced to North America in 1868 or 1869. Since that time, the range of this insect has spread to include most of the northeastern states in the US and eastern provinces of Canada. We compiled historical records of gypsy moth invasion in North America and assembled these data in a geographical information system (GIS). Individual US counties and Canadian census districts were used as the smallest spatial unit in this database. Data indicated that three distinct periods occurred during which spread rates differed: a high rate (9.45 km/year) from 1900 to 1915, a low rate (2.82 km/year) from 1916 to 1965, and a very high rate (20.78 km/year) from 1966 to 1990. Furthermore, expansion was slower (7.61

km/year) during the period of 1966–1990 in counties where the mean minimum temperature was less than 7° (C). The rate of range expansion was independently calculated as 2.5 km/year from estimates of r , the intrinsic rate of increase, and D , the diffusion coefficient (dispersal magnitude) and a simple spread model. This estimate was substantially less than the empirically derived expansion rates. The higher observed rates of expansion may be due to human-caused movement of gypsy moth life stages which was not incorporated in estimates of D made here.

Key words. *Lymantria dispar*, Lepidoptera, Lymantriidae, landscape ecology, geographical information systems.

INTRODUCTION

A large proportion of the most devastating pests of agriculture and forestry are species which were introduced from other continents (Sailer, 1983; Simberloff, 1986; Pimentel 1986). Large numbers of exotic organisms are now established on virtually every continent as a result of both intentional and inadvertent introductions. Accidental introductions appear to have accelerated considerably over the last two centuries as a result of increased human mobility, modification of natural avenues of organismal movement (e.g. canals), and disturbances to natural habitats that change their suitability (di Castri, 1989).

The invasion of exotic organisms can be delineated into three processes; (1) arrival, (2) becoming established and (3) spreading (Elton, 1958; Dobson & May, 1986). Because of their economic importance and accelerating frequency, all three stages of biological invasions have recently been the object of increased scrutiny (Mooney & Drake, 1984; Groves & Burdon, 1986; Drake et al., 1989; Hengeveld 1989). This paper is a case study that focuses on the spread process of an extremely damaging forest pest. Because of the high frequency and economic importance of invading organisms, an increased understanding of their spread is important for their future management.

A variety of models, ranging from simple to complex,

have been developed for simulation of the spread of invading species (Skellam, 1951; Mollison, 1977; Okubo, 1982; Kot & Schaffer, 1986; Levin, 1986). The simplest and most widely used approach is a combination of an exponential population growth model and a model of simple Fickian diffusion (Fisher, 1937; Skellam, 1951). Despite its simplicity, there has been remarkable congruence between this model's predictions and actual spread data from a variety of organisms (Levin, 1989). Successful applications of this spread model include studies of human pathogens (Murray, Stanley & Brown, 1986; Cliff et al., 1981; Cliff & Haggett, 1988), mammals (Skellam, 1951; Williamson & Brown, 1986; Lubina & Levin, 1988), plants (Skellam, 1951), and insects (Long, 1977).

The gypsy moth, *Lymantria dispar* L. is one of the most destructive exotic organisms in North America. It is a major forest pest through much of the northern hemisphere; the species is mainly associated with *Quercus* species though it is polyphagous in its feeding habits. In many areas, epidemics are common and resultant defoliation can cause substantial ecological and economic impacts.

The gypsy moth was introduced accidentally from France to Medford, Massachusetts, in either 1868 or 1869 by an amateur entomologist (Liebhold, Mastro & Schaefer, 1989). Eradication was attempted several times but ultimately failed, and the range of the gypsy moth has since

spread through most of northeastern North America. The current distribution of the species includes a large area composed of the north Atlantic states of the US and parts of bordering Canadian provinces (Fig. 1). A second, discrete population exists in Michigan that is due to a secondary introduction and failed eradication efforts. The primary and secondary infested regions continue to spread; there are no current programs underway to stop this spread (though some state and federal programs are aimed at slowing the spread). In contrast, numerous isolated infestations arise sporadically (e.g. recent infestations in California, Oregon and British Columbia); considerable resources are allocated by state and federal agencies to eradicate these populations. These efforts largely have been successful.

The relatively slow rate of spread of the gypsy moth is probably related to its biology. Females in North American populations are unable to fly and thus the primary mechanism for gypsy moth dispersal is thought to be wind-borne passive movement of first instars (Mason & McManus, 1981). The expansion of the generally infested area and the founding of isolated populations may also occur when egg masses or other life stages are accidentally transported on human-made objects (Talerico, 1981).

Because the gypsy moth feeds on a wide variety of tree species, it is likely that gypsy moth populations ultimately will invade most of the US and Canada. However, the rate

of spread is so slow (relative to the historical spread of other exotic organisms) that it may be many years before the full range of the potential habitat becomes infested. A prediction of when various areas will become infested would be useful for planning forest management. Prudent planning would incorporate expected gypsy moth arrival because their populations can cause significant damage to forest resources. The objective of this study was to characterize quantitatively the spread of gypsy moth through North America over the last 90 years. An understanding of the dynamics of gypsy moth spread is valuable both in regard to these management considerations and it is important in improving our general understanding of the ecology of invading organisms.

DESCRIPTION OF THE DATA

Beginning with the enactment of the Domestic Plant Quarantine act of 1912, the US Department of Agriculture (USDA) has regulated the movement of plant material from areas determined to be infested with gypsy moth (Weber, 1930). The methods used to designate the infestation status of an area have varied but the designation of infested usually resulted from multiple finds of one or more life stages. Trapping of males in pheromone-baited traps is a

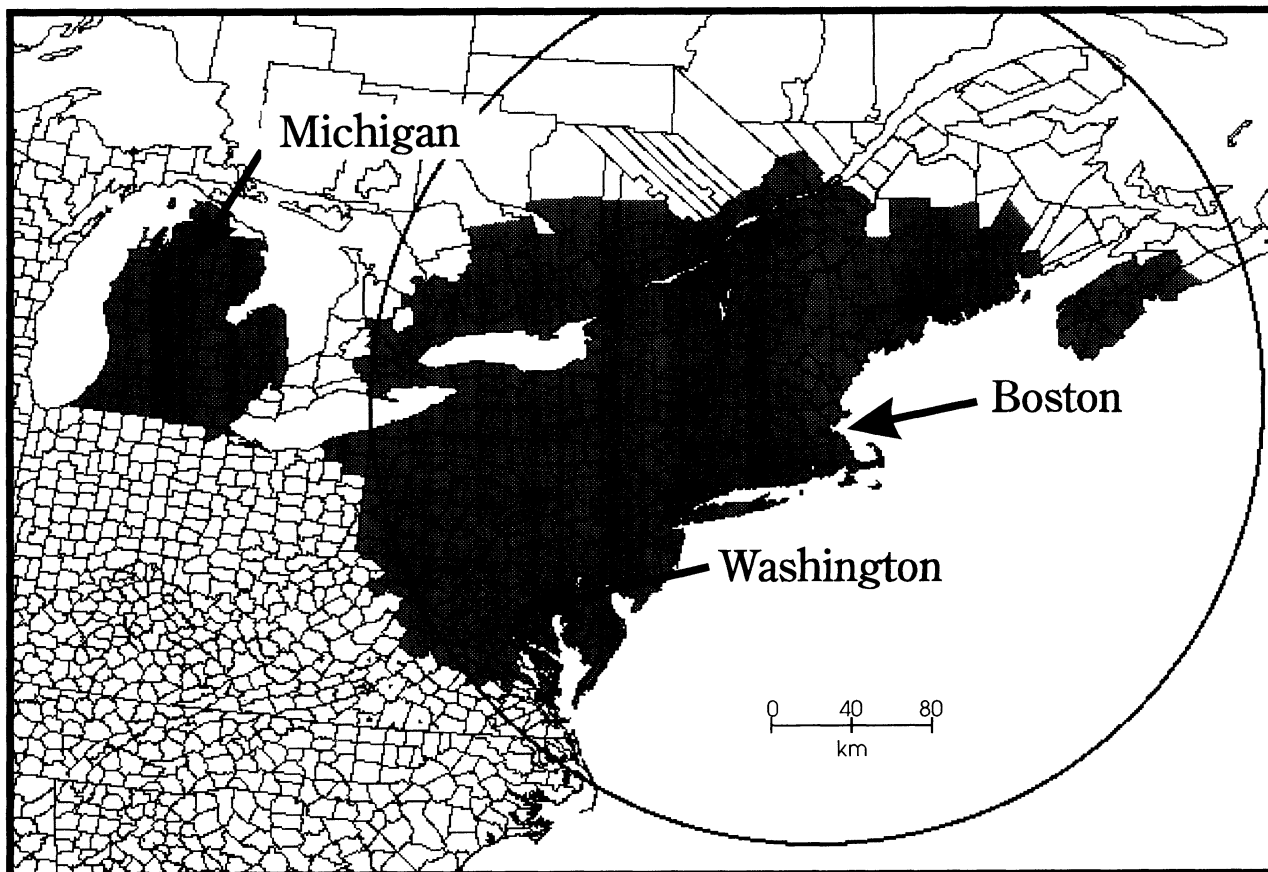


FIG. 1. 1989 generally infested region as defined by US and Canadian quarantine regulations (quarantined isolated counties are not included because historical data indicate these counties usually revert to uninfested because of eradication efforts). The heavy line is 850 km from the 1900 infested region.

powerful tool for detecting incipient gypsy moth populations; these traps have been used to define the infested area since the turn of the century (before the isolation, identification and synthesis of disparlure, agencies often used extracts of live females as trap baits). The official USDA quarantine regulations were used in this study as a method for determining the annual spatial distribution of gypsy moth in the US. Since 1934, the quarantined area has been defined in the annual Code of Federal Regulations under Title 7, chapter 301.45–2a (Administrative instructions designating regulated areas under the gypsy moth and brown-tail moth quarantine and regulation). A county was designated infested if the regulations listed any part of it as part of the generally infested area, suppressive area, high-risk area or low-risk area. In a few cases (mostly isolated infestations), a county was designated as infested one year, but subsequently was not listed as infested; in these cases we designated a county as infested only if it did not later become 'uninfested'. The quarantined area was defined in other publications prior to 1934 (Burgess, 1915, 1930). Various other sources were used to determine gypsy moth distribution between 1900 and 1912 (Anonymous, 1906; 1907a; Burgess, 1913). Canadian officials have similar quarantine regulations and we used their annual or semiannual publications that document the distribution (Agriculture Canada, 1985; 1986) to determine the annual gypsy moth distribution to Canada. No reliable data exists on the distribution of gypsy moth prior to 1900.

The spatial resolution of the historical descriptions of the infested area varied through time and across different regions. Simple lists of infested counties were the most method used in these records to describe the area. Therefore, we used US counties as the smallest unit for describing the annual distribution of the gypsy moth generally infested region. In Canada we used census districts as the basic unit. Several of the Canadian census districts and a few northern US counties were extremely large and we therefore systematically divided them into smaller units comparable to average county area for description of the infested region. The mean size of these polygons was 1647 km² s.d.=936). In 1900, the infested area consisted of three counties; by 1989 482 counties were infested.

DATA MANAGEMENT

The IDRISI geographical information system (GIS) (Eastman, 1987; 1989) was used for managing the infestation and other landscape data. IDRISI is a raster-based system designed for managing and analysing spatial data with particular emphasis in research applications. It runs under the MS/DOS operating system on 80X86 microprocessors. Implementation of IDRISI used an 1150 by 1600 matrix of 2 by 2 km pixels to represent northeastern North America. A base-map of county boundaries (census district boundaries in Canada) was generated from latitude and longitude coordinates obtained from the SAS/GRAPH system (SAS Institute, 1987) and these coordinates were projected using the Azimuthal Equal-Distant Projection (Snyder, 1987). This projection conserves true distance lin-

early from a designated point (Medford, Massachusetts, the site of the original gypsy moth introduction, was used). County boundaries were used to designate the outline of the annual infestation extracted from quarantine records as described above.

CLIMATOLOGIC DATA

Extremely cold winter temperatures are known to cause heavy mortality of overwintering egg masses (Giese & Casagrande, 1981; Madrid & Stewart, 1981). Furthermore, qualitative examination of gypsy moth infestation maps indicated that gypsy moth has not spread to the north at the same rate as to the west and south (Fig. 1). Therefore, winter conditions across northeastern North America were characterized in order to determine how these conditions are related to gypsy moth spread. Thirty-year historical averages of mean January minimum temperatures from 786 weather stations throughout the region were assembled (U.S. National Oceanic and Atmospheric Administration, 1978) and spatially interpolated to develop an estimated mean minimum January temperature for each 2 by 2 km pixel. Interpolation was accomplished using an inverse-distance procedure (Eastman, 1989; Isaaks & Srivistava, 1989). We then assigned to each county the highest temperature of all pixels falling in that county. The highest temperature was used because higher temperatures are more favourable for gypsy moth egg survival.

ANALYSIS OF HISTORICAL SPREAD

We estimated historical rates of gypsy moth range expansion from the quarantine data described above. We used the IDRISI system to measure the distance of each pixel in the scene from the generally infested region in 1900. We then assigned to each county the minimum distance of all pixels contained in the county. The relationship between a county's time of first infestation and its distance from the region infested in 1900 was plotted (Fig. 2). Counties comprising the Michigan infestation were not included in these plots; the Michigan infestation has only been quarantined since 1981. This is an inadequate length of time to adequately study its expansion. Inspection of the data (Fig. 2) indicated that the velocity of range expansion, V , has not been constant throughout the entire 90-year interval. Instead, data suggested that three distinct periods occurred during which the expansion velocities were unique: a high velocity from 1900 to 1915, a low velocity from 1916 to 1965, and a high velocity from 1966 to 1990 (Fig. 2).

Furthermore the data indicated that at counties where the mean minimum January temperature was less than 7°C, the expansion velocity was significantly lower than in the warmer counties (Fig. 2). Least-squares regression was used to fit linear models of distance as a function of time for each of these three intervals (separate equations were developed for counties with mean minimum January temperatures of less than 7°C for the period 1966–90) (Fig. 3). The intercepts of these linear models were *a priori* set at zero and the slope provided an estimate of V . Standard

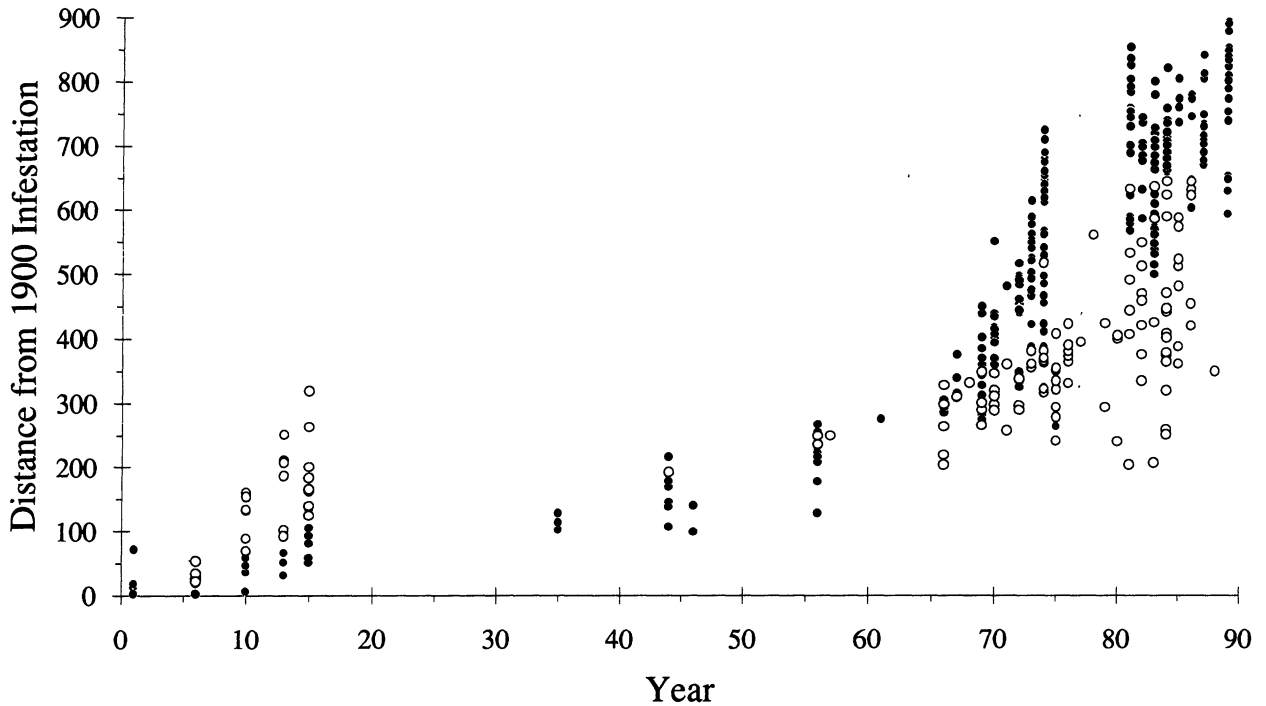


FIG. 2. Relationship between date of first infestation and distance from 1900 generally infested region; each circle represents one county or census district. (●) Counties with a mean minimum temperature >7°C, (○) counties where mean minimum temperature <7°C.

TABLE 1. Empirically derived estimates of *V*, the rate of infestation expansion estimated as the slope from regressing distance from infestation on the time to infestation (forced through intercept) (Fig. 3).

Interval	County subset	No. of counties	Estimate of <i>V</i> *
1900–15	all	52	9.45±0.76
1916–65	all	48	2.82±0.19
1966–89	temperature <7	225	7.61±0.49
1966–89	temperature 7	98	20.78±0.33

Temperature is the mean minimum January temperature.

V* is the velocity of the range expansion and was estimated as the slope of the linear model: distance from infested area=*V years until infestation. *V* is measured as km/year.

errors of the *V* estimates indicated that significant differences in rates of expansion existed (Table 1).

DIFFUSION MODELS:

Skellam (1951) developed the first application of diffusion models to the dynamics of the spread of invading organisms though Fisher (1937) earlier described a similar model of the spread of advantageous genes through populations. Skellam’s (1951) model combined Fick’s law of diffusion with an exponential model of population growth (Okubo, 1980).

Fick’s law states that the concentration, *C*, of particles is normally distributed across any dimension, *x* and thus the concentration at any point in time after release at point *x*=0 is described by:

where *t* is the time since the initial release of *M* particles at

$$C_{x,t} = \frac{Me^{-x^2/4Dt}}{2\sqrt{\pi Dt}} \tag{1}$$

point *x*=0 and *D* is the “diffusivity” or diffusion coefficient” (Okubo, 1980). The diffusion coefficient is constant for any class of particles and environmental conditions (e.g. temperature); *C* is distributed normally at time, *t* with a variance of *Dt*. Fick’s law assumes that particles move randomly.

The exponential population growth model mathematically describes the concept of unlimited population growth:

$$N_t = N_0e^{rt} \tag{2}$$

where *N_t* is the number of individuals at time *t* and *r* is the ‘intrinsic rate of natural increase’ (birth rate—death rate under optimal condition; ie. no crowding) (Varley, Gradwell & Hassell, 1973).

Skellam combined Fick’s law of diffusion with the exponential growth model to obtain a generalized model of the spread of an invading organism:

$$N_{x,t} = \frac{N_{0,0} e^{rt - x^2/4Dt}}{4\pi Dt} \tag{3}$$

where *N_{x,t}* is the density of organisms distance, *x*, from the point of release and time, *t*, from the time of release of *N_{0,0}* organisms at time 0. The assumption of random movement

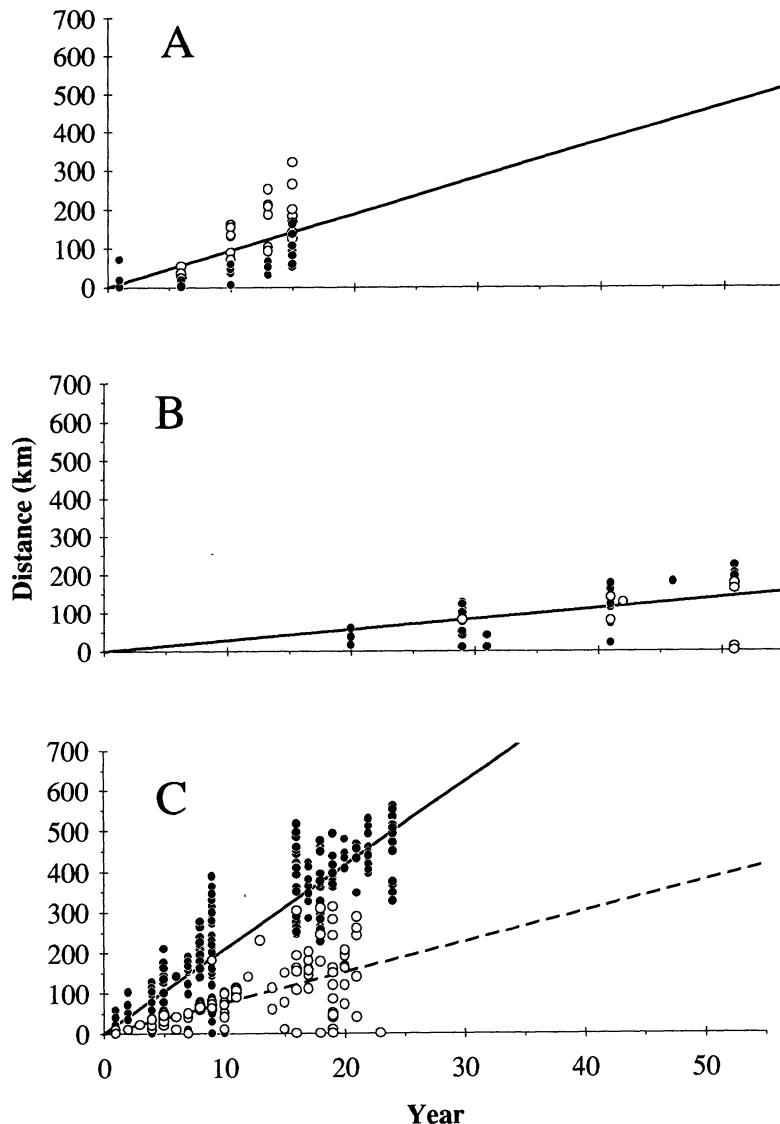


FIG. 3. Relationship between time until first infestation and distance from generally infested region; each circle represents one county or census district. (●) Counties with a mean minimum temperature $>7^{\circ}\text{C}$, (○) counties where mean minimum temperature $<7^{\circ}\text{C}$. Lines are the results of linear regressions forced through the origin. (A) 1900–15, (B) 1916–65, (C) 1966–89.

in this models implies that the population will spread radially, at an equal rate in all directions. 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, V , is constant and can be described:

$$V = 2\sqrt{rD}. \quad (4)$$

The above model assumes that both r and D are constant through both time and space during the period of range expansion of the invading organism, an assumption that does not intuitively seem likely in many cases (i.e. spatial variation in the habitat may profoundly affect birth/death functions as well as dispersal rates). Nevertheless there has generally been a good congruence between predictions of

this model and observed rates of spread of most exotic organisms (Levin, 1989). The expansion of gypsy moth in North America is different from these previous case studies in that expansion has occurred over a long period and over a large, heterogeneous landscape.

We developed an independent estimate of V by using estimates of r and D in equation 4. The intrinsic rate of increase, r , is difficult to characterize for a variety of reasons. Once an area becomes infested by gypsy moth populations, densities typically increase rapidly to outbreak levels but eventually decline; over a period of 20 or more years populations may sporadically rise and fall. Thus, the exponential growth model is not a reasonable model to describe the dynamics of populations that have been established for several years. However, Levin (1989) pointed out that density dependence in the replacement rate model is insignificant near the leading edge of the infested area and con-

sequently, the asymptotic rate of advance of the population front depends only upon r . Populations along the leading edge of the gypsy moth infestation typically increase by 1 or 2 orders of magnitude (Elkinton & Liebhold, 1990). Hence, in these newly established populations, the exponential model is more appropriate and we may assume an r of approximately 4.6 (this corresponds with a 100-fold increase in population density).

Upon hatching, first instar gypsy moth larvae crawl to branch twigs, spin-down on silk threads and are passively dispersed in the wind. Since adult females are flightless this passive movement is considered to be the primary mechanism of gypsy moth dispersal (Mason & McManus, 1981). Unfortunately very little data exists that describes actual dispersal episodes in a quantitative manner. Perhaps the best available data on gypsy moth dispersal magnitude is that collected by Mason & McManus (1981). They attached 1,100,000 gypsy moth eggs to trees within a 10 m radius area and monitored the numbers of first instars trapped in sticky cylinders at distances of 0, 60, 120 and 180 m in all directions. Mason & McManus (1981) estimated that 900,000 larvae hatched and they found 5,245 larvae/cylinder at 0 m, 35.5 larvae/cylinder at 60m, 13.5 larvae/cylinder at 120m, and 5.7 larvae/cylinder at 180 m. From these data, we calculated D as simply the mean squared deviation of larvae (Kareiva, 1983); $D=332$ m/generation.

Using our estimates of r and D we estimated V in equation (4) as 2.5 km/year. This estimate is considerably less than the rates of spread observed during all periods, except the period of 1916-65 (Table 1).

DISCUSSION

Figures 2 and 3 suggest that there have been three distinct periods with unique rates of gypsy moth spread: a high velocity from 1900 to 1915, a low velocity from 1916 to 1965, and a high velocity from 1966 to 1990. This finding is unusual since most invading organisms have generally spread at constant radial velocities (Levin, 1989). There are a variety of possible reasons why the gypsy moth range expansion has occurred with such a variable rate of expansion. One likely explanation of the slow range expansion from 1916 to 1965 was the enactment of the Federal domestic quarantine against movement of gypsy moth life stages in 1912 and the establishment of a barrier-zone extending from Canada to Long Island, largely along the Hudson River and Champlain Valleys (Perry, 1955; McManus & McIntyre, 1981). In this zone, federal and state authorities intensively monitored and chemically treated new populations in order to stop the spread of the infested area. This activity was discontinued during World War II but was re-established in 1952 using DDT but then again largely abandoned by 1965. One reason for the very rapid rate of range expansion from 1965 to 1989 is that forests were older and more continuous in northeastern North America during this period than they were 50 years ago and this may have caused an increase in the rate of spread. It is also possible that the forests of Pennsylvania, Maryland and Virginia were better gypsy moth habitats

than New England because of greater proportions of host species and thus populations have spread through these areas faster. Alternatively, the increased rate of spread could be due to increased rates of inadvertent movement of gypsy moth life stages by humans. Yet another possible reason for the variation in spread rate would be a dispersal distribution with long tails which Mollison (1986) demonstrated can result in an unsteady rate of expansion. Other explanations of the observed rate of spread include decreases in the effectiveness of control and eradication efforts, possible changes in the detection and quarantine procedures, and possible changes in climate. Which, if any, of these reasons ultimately are responsible for the apparent change in spread remains unclear and should be the focus of continued study.

Data indicated that the expansion velocity at counties where the mean minimum January temperature was less than 7°C was significantly lower than in the warmer counties (Fig. 3). Extremely cold winter temperatures are known to cause heavy mortality of overwintering egg masses (Giese & Casagrande, 1981, Madrid & Stewart, 1981). Presumably, this mortality has a negative impact on r and thus on the rate of spread of the species into cold climates. It is not clear why this pattern is pronounced in the 1966-89 period but not evident during previous years (Figs 2 and 3).

Estimates of r and D derived from other studies, were used to estimate V , the rate of range expansion, as 2.5km/year using equation (4). This estimate of spread is substantially lower than the empirically derived estimates in Table 1. It seems unlikely that our estimate of r , is too low, since populations rarely increase more than 100-fold. It is more likely that the estimate of D , 322 m/generation, is too low. There are two possible explanations for this error. The first possibility is that we have under-estimated the magnitude of 1st instar dispersal; movement may be greater in terrain that is more mountainous than in the area where Mason & McManus (1981) conducted the experiment that was used to parameterize D . The current gypsy moth range (Fig. 1) indicates that there has not been substantially greater spread along the ridges of the Allegheny mountains, which run from the northeast to the southwest, indicating that the effect of mountainous terrain on expansion rates has been minimal. A more likely explanation of the under-estimation of D is that 1st instar dispersal is not the only process that causes the spread of the generally infested region. Instead, accidental transportation of gypsy moth life stages by humans may be the principle movement mechanism responsible for the spread. Ultimately, this type of movement is difficult to quantify directly and can only be practically estimated using empirical methods as done here.

Ultimately, Skellam's (1951) model may be inadequate to explain the complex dynamics of the spread of exotic organisms. Models have been developed for disease spread in human populations that incorporate heterogeneity of the landscape over which the organism spreads (e.g. Cliff *et al.*, 1981). Habitat heterogeneity could affect spread via either habitat-dependent rates of movement, as measured by D , or habitat-dependent rates of population increase, as measured by r . Other important modifications to Skellam's

(1951) model would be incorporation of more complex population growth models that incorporate density dependence, more complex movement models that incorporate anisotropic and/or non-gaussian movement, discrete time steps and stochasticity (Mollison, 1977; Kot & Schaffer, 1986; Levin 1986). Unfortunately, quantitative data on these relationships are largely lacking; parameterization and testing of these models will only be possible when the population biology of the invading species is better understood.

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