ORIGINAL ARTICLE

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Phenology of *Lymantria dispar* (Lepidoptera: Lymantriidae), male flight and the effect of moth dispersal in heterogeneous landscapes

Abstract A model of *Lymantria dispar* development was assembled from the published literature and used to predict the period of male moth flight in the United States. Model predictions were compared with observations made with pheromone traps in several locations throughout the United States but especially in Virginia, West Virginia and North Carolina between 1995 and 1996. The model was found to provide accurate and unbiased forecasts of the dates of 5%, 50% and 95% cumulative trap catch, particularly at lower elevations. In areas of high topographic diversity (such as West Virginia), deviations between model output and observations were minimized by basing predictions of 5% and 50% cumulative catch on minimum elevation within neighborhoods of 25–81 km^2. This model of *L. dispar* male flight phenology can be used to time the deployment and retrieval of pheromone traps in intensive or extensive monitoring programs. However, a better understanding of moth movement is needed to fully explain the patterns of local trap catch.

Key words Flight · Gypsy moth · Modeling · Pheromone traps · Seasonality

Introduction

Lymantria dispar L. (the gypsy moth) was introduced from Europe into North America around 1869 near Boston, Massachusetts, and its present range encompasses the northeastern United States, including portions of Michigan, Ohio, West Virginia, Virginia and North Carolina, as well as portions of southeastern Canada (Liebhold et al. 1992). Isolated populations have been detected in several western states and western Canada but they have either failed to establish or have been eradicated (Hunter and Lindgren 1995).

Monitoring and management of *L. dispar* populations requires accurate information about its seasonal biology. Because pesticide treatments are applied against small larvae, most previous studies of *L. dispar* phenology focused on eggs and early larval stages. Johnson et al. (1983) developed a degree-day model for development of *L. dispar* eggs. This model was later improved (Sheehan 1992) by modifying predicted hatch synchrony as a function of cumulative exposure to temperatures below 5°C (Masaki 1965). Waggoner (1984) published a model of egg development that incorporated individual variation in development rate. Other empirical non-linear egg hatch models were proposed by Lyons and Lysyk (1989) and Hunter (1993). More sophisticated models of egg diapause were developed by Tauber et al. (1990) and Gray et al. (1994). The development of *L. dispar* larvae and pupae was studied by Casagrande et al. (1987), and these data were used in a series of phenological models (Logan et al. 1991, Sheehan 1992). Russo et al. (1993) developed a method to generate landscape-wide predictions of egg hatch based on the model of Johnson et al. (1983). Schaub et al. (1995) integrated a model of *L. dispar* phenology with a geographic information system to predict spatial patterns of population development which can be readily used for management purposes.

The use of pheromone traps for monitoring *L. dispar* populations has increased in the last decade. Moth catches are generally poor predictors of expected defoliation (Liebhold et al. 1995), but they are useful for detecting low-density populations beyond the expanding front of the species' range (Schwalbe 1981; Leonard and Sharov 1995). Also, they can be used for delineating areas for egg mass sampling (Kolodny-Hirsch and Schwalbe 1990; Ravlin et al. 1990) and for measuring the rate of population spread (Sharov et al. 1996).

The proper use of pheromone traps requires knowledge of the phenology of *L. dispar* male flight. Usually, traps are set for the entire flight season and thus it is nec-

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Fig. 1 Location of the 1995 and 1996 pheromone traps used in the validation of the *Lymantria dispar* flight phenology model

Materials and methods

Pheromone traps in southern states

USDA milk-carton pheromone traps baited with (+)-disparlure impregnated dispensers (Schwalbe 1981) were used to monitor the dynamics of male moth flight in Virginia, West Virginia and North Carolina in 1995 and 1996 (Fig. 1). The location of traps was read from standard 1:24,000 topographic maps. The efficiency of *L. dispar* pheromone traps dramatically declines as they become saturated at about 500 male moths per trap (Elkinton 1987). Therefore, we restricted our analysis to areas where population densities were sufficiently low to prevent trap saturation. Traps were set before the start of moth flight (23 May–5 July, depending on location). Moths were counted and removed from traps twice a week. There were several instances when a trap was not checked as scheduled, but intervals between trap inspections never exceeded 1 week. Traps were generally removed after three consecutive zero captures. However, five traps at high elevation in West Virginia in 1996 were removed earlier (on 29 August), before the termination of moth flight. Probably <2% of moths were missed because of early removal of these traps (estimated assuming a symmetrical moth flight curve). Because the loss of moths was low, it had a negligible effect on the results. We therefore included the data from these traps in our analysis.

Traps were placed in an area with large variation in elevation to cover as much as possible of the regional variation in the phenology of male moth flight. In 1995, 20 traps were set in Virginia (five in each of Buena Vista, Millboro, Bath Alum, and Sunrise) and 19 traps were set in West Virginia (Fig. 1). In 1996, 20 traps were set in Virginia at the same locations as in 1995, and 25 traps were set in new locations in West Virginia. Additional clusters of traps were set in 1996 in central and eastern Virginia (Kelly, four; Farmsville, two; Chesterfield, four) as well as in isolated infestations in North Carolina (11 traps). Five of the 11 North Carolina traps caught fewer than ten moths and were not used in the analysis. Within clusters, traps were set >2 km apart from each other.

Pheromone traps in northern states

Historical pheromone trapping data collected in various northern states were used to extend the geographical range covered by this study. Elkinton and Cardé (1984) studied the patterns of male moth flight in a defoliated hardwood site near Amherst, Mass. (Prescott Peninsula, Quabbin Reservoir) in 1981. Pheromone traps were inspected daily.

essary to place all traps before moth flight starts and to collect them only once it has ended. Large sampling programs operate with >10,000 traps and the processes of trap setup and removal must be optimized for cost and efficacy. Thus, timing is an important aspect of the management of pheromone traps as sampling tools, and accurate adjustment of trap operations to local conditions requires modeling of the phenology of *L. dispar* male flight.

Another area of application of pheromone traps is the detection of long-range moth dispersal. Bimodal moth capture patterns were observed for several years in the Michigan Upper Peninsula (B.C. Pijanowski, personal communication, Michigan State University). It was suggested that the first peak corresponded to migrants traveling over Lake Michigan from the Lower Peninsula of Michigan and that the second peak corresponded to local populations. There is a considerable delay in moth flight between the Upper and Lower Peninsula that makes it possible to distinguish resident moths from migrants. Information on the phenology of male moth flight may reveal other areas where long-distance dispersal of moths can be detected from the patterns of moth capture in pheromone traps.

Despite intensive research efforts in modeling *L. dispar* phenology, the only published attempt to apply existing models to the forecasting of male moth flight was that of Hunter and Lindgren (1995).

In this paper we report on the performance of a model, assembled from published literature, that predicts male *L. dispar* flight. We compare its output with extensive pheromone trapping data from various locations in the United States. Differences between expected and observed timing of moth capture are interpreted in the context of short-range movement of moths.

More data were obtained from reports on sterile insect release programs conducted by the USDA Animal and Plant Health Inspection Service (V. Mastro, Otis Methods Development Center, USDA APHIS, personal communication). We used pheromone trap catch data (wild *L. dispar*) from Bellingham Co. (Wash.), 1985–1986; Allen Co. (Ohio), 1986–1987; Benton Harbor (Mich.), 1980–1981 and Kent Co. (Md.), 1983 and 1985. All sites had low *L. dispar* density.

Pheromone traps were checked at intervals of 1–3 days except in Kent Co., where traps were checked weekly. Several traps were operated in each location and the catch data were pooled by location. Exact trap locations were not known, so the coordinates of the nearest weather station were used.

Phenology model

A temperature-driven model of *L. dispar* development from overwintering eggs to the end of the adult male lifespan was assembled from published literature. Egg hatch was simulated with the degree-day model of Johnson et al. (1983), as modified by Sheehan (1992). This submodel outputs a daily time series of expected numbers of eggs hatching from an initial population of N_0 individuals. Each day's newly hatched eggs constitute input into the first larval stage. Development of instars 1–4 was simulated with the submodel of Logan et al. (1991), which describes the stage-specific, nonlinear relationships between temperature and development, as well as the associated variability. This submodel outputs time series of the frequency of larval stages 1–4. The development of subsequent immature stages (fifth instar, female sixth instar, and pupae) was simulated using the degree-day models of Sheehan (1992). Differences in development rates in this model occur in the fifth and sixth instars, as well as during the pupal stage. Longevity of adult male *L. dispar* was never determined. From experience with laboratory rearing of this species, we assumed that they lived for 10 days at 25°C and that longevity increased, up to a point, at lower temperatures as is the case in other moth species (e.g. Régnière 1983). Thus, we used an aging rate of 0.004 days per °C above 0°C, with a maximum longevity of 25 days (at 10°C). The model incorporates continuous stage-specific mortality of *L. dispar*. However, the phenology of male moth flight is affected only by adult mortality, which was set to 0.50 per moth life span (this value was adjusted by graphical comparison of model output with 1995 trapping data).

Input for this phenology model was a time series of daily minimum and maximum air temperatures, starting on 1 January. Air temperatures were interpolated within the model at a time increment of 4 h between the minima and maxima of successive days by the method of Allen (1976). Model output consists of a daily time series of the numbers of male moths in the population.

Weather databases

Weather data used in this study consisted of daily minima and maxima. The BioSIM simulation control system (Régnière 1996) was used to provide the simulation model with temperature data adjusted for differences in elevation and latitude between the source station and the trap locations. For the 1995 and 1996 simulations, BioSIM was provided with vertical lapse rates estimated using 30-year monthly average minimum and maximum temperatures from 58 weather stations located in the trapping region. For the simulations of northern locations, the vertical lapse rates estimated by Régnière and Bolstad (1994) were used. Daily air temperature data for 1995 and 1996 for North Carolina, Virginia and West Virginia were obtained from the Southeast Regional Climate Center, National Weather Service. For earlier years, data were extracted from the U.S. National Climatic Data Center's TC-3200 Summary of the Day Cooperative Observer Network database (EarthInfo, Boulder, Colo.).

Missing temperature data were estimated using data from the nearest weather station with a complete record for the same day. These estimates were obtained from:

$$t_1 = t_2 + (T_1 - T_2) \tag{1}$$

where t_i is the temperature (minimum or maximum) for a specific day at weather station i, and T_i is the 30-year monthly average temperature (minimum or maximum, respectively).

Elevation

Elevation data were obtained from U.S. Geological Survey 1:250,000 Digital Elevation Models (DEM) (Elassal and Caruso 1983). A 1 km² resolution map was created by averaging elevations at four points separated by 500 m. Because of local moth movement, there was no need for a higher resolution.

Preliminary results suggested that moth movement may affect trap catch patterns. Elevation at the trap location may not be the only information from which to predict the flight season, because male moths captured in pheromone traps may have originated in neighboring areas. We simulated *L. dispar* development not only for the elevation at which a trap was located but also for the minimum, maximum and average elevation in neighborhoods of 1, 9, 25, 81 and 225 km² consisting of square areas with the trap in the center cell. For all possible combinations, we estimated the bias (average difference) between simulated and observed dates of 5%, 50% and 95% cumulative catch, the correlation and the slope of the regressions of observed versus simulated dates.

Statistical analysis

Dates of 5%, 50% and 95% cumulative moth catch were estimated at each location by linear interpolation between cumulative catches on successive dates when traps were checked. Simulated dates of 5%, 50% and 95% cumulative moth numbers were estimated, to the nearest day, from cumulative output male moth frequency, under the assumption that moth capture in pheromone traps is in direct relation to moth density.

For the trapping data sets from the southern states, relationships between dates of 5%, 50% and 95% cumulative trap catch and elevation were tested using a linear regression analysis. Differences between observed and simulated dates, or between years, were tested using a General Linear Models (GLM) procedure, using elevation as a covariate. In the neighborhood-elevation analysis, model bias (the average difference between simulated and observed flight dates) was tested for significance using *t*-tests. To test improvements in model accuracy resulting from the use of neighborhood rather than local elevations, observed dates of 5%, 50% and 95% trap catch were regressed on simulated dates and the slopes (m) were tested for significance as well as for deviation from unity. The first null hypothesis (H_0: $m = 0$) was used to test if the model helped to predict dates of *L. dispar* flight. If this hypothesis was not rejected then the model had no predictive value. The second null hypothesis (H_0: $m = 1$) was used to compare actual and predicted dates. If this hypothesis was not rejected, the model fit observed dates without bias over the observed range. Rejection of this hypothesis meant that the fit between model and observations was biased over part of the range of observed dates, but that the model may still have predictive value given that the first null hypothesis was rejected.

Observed dates of 5%, 50% and 95% trap catch from the nine northern data sets were regressed on simulated dates and the slopes (m) were tested for significance (H_0: $m = 0$) as well as for deviation from unity (H_0: $m = 1$). Model bias was tested with Mann-Whitney's rank test because of small sample size and pronounced non-normality.

Results

Data from southern states

The simulation model generated realistic patterns of male moth abundance, based on a graphical comparison with average cumulative catch of male *L. dispar* in pher-
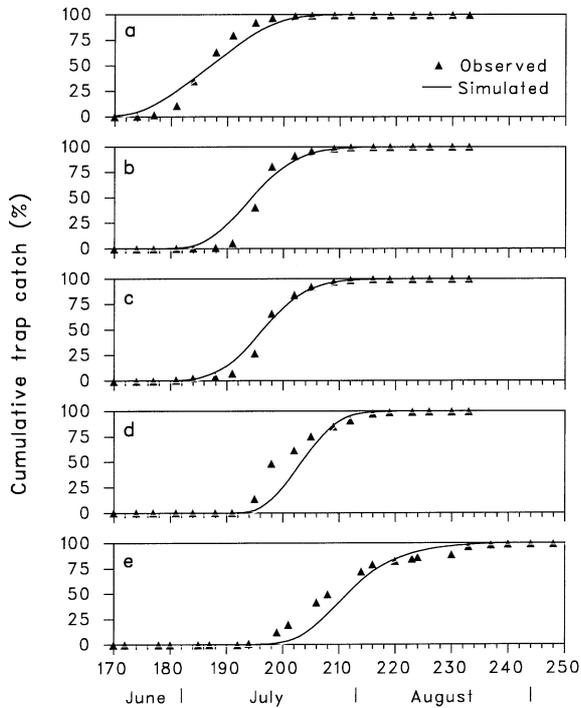
Fig. 2 Comparison of observed and simulated cumulative catch in 1995 (data and simulation output pooled by trap cluster): **a** Buena Vista, Va.; **b** Bath Alum, Va.; **c** Millboro, Va.; **d** Sunrise, Va.; **e** West Virginia

omone traps in the five 1995 trap clusters (Fig. 2). A summary of the cumulative pheromone trap data from the 1995 and 1996 trap clusters and of the corresponding simulation model output is given in Table 1. The average absolute difference in predicted and observed dates was 5.2 and 3.2 days in 1995 and 1996 respectively.

Simulated average dates of 5% and 50% moth catch in 1995 were considerably later than observed (5%: 9 days, $t = 7.5$, $P < 0.001$; 50%: 7 days, $t = 6.03$, $P < 0.001$), but the model predicted the dates of 95% catch without significant bias ($t = 0.5$, $P > 0.05$). In 1996, average dates of simulated 5%, 50% and 95% catch were significantly but only slightly different from observed dates (5%: 2 days, $t = 2.9$, $P < 0.006$; 50%: 1 day, $t = 2.5$, $P < 0.017$; 95%: 3 days, $t = 4.5$, $P < 0.001$).

There were strong and significant ($P < 0.05$) relationships between elevation and the dates of 5%, 50% and 95% trap catch, whether simulated or observed, in 1995 and 1996 (Fig. 3, Table 2). In both 1995 and 1996, the slopes of these regressions were significantly different between observed and simulated dates of 5% catch (1995: $F = 69.3$, df = 1,74, $P < 0.001$; 1996: $F = 32.9$, df = 1,118, $P < 0.001$) and 50% catch (1995: $F = 20.7$, $P < 0.001$; 1996: $F = 10.4$, $P < 0.002$). There were no significant slope differences between observed and simulated dates of 95% catch in either year (1995: $F = 0.02$, $P > 0.876$; 1996: $F = 2.09$, $P > 0.151$).

The fact that observed dates of 5% and 50% trap catch were less dependent on elevation than simulated dates indicates that moths originating at varying elevations may mix with each other. In 1995, moth flight at high elevations started much earlier than predicted from local weather conditions, but in 1996 model predictions were far closer to observations (Table 1).

The discrepancies between simulated and observed dates of 5% trap catch in 1995 decreased considerably when weather conditions were predicted from the minimum elevation in 81-km^2 blocks (Fig. 4a). The same was true for dates of 50% catch (Fig. 4b). Average elevation provided unbiased estimates of the dates of 95% catch, regardless of neighborhood size (Fig. 4c).

Table 1 Lowest and highest elevation, total trap catch and dates of observed and simulated 5%, 50% and 95% cumulative trap catch among the trap clusters in the southern states in 1995 and 1996

Trap group	n	Elevation		Total catch		Observed dates			Simulated dates		
		Low	High	Mean	CV	5%	50%	95%	5%	50%	95%
1995											
Bath Alum, Va.	5	291	665	236	56	190	195	204	191	199	209
Buena Vista, Va.	5	423	565	265	65	178	187	197	183	191	201
Millboro, Va.	5	433	617	189	69	187	197	207	191	199	210
Sunrise, Va.	5	594	689	266	29	193	199	214	201	208	216
West Virginia	19	707	1129	247	78	197	209	229	212	219	227
1996											
North Carolina	6	0	1	425	126	169	178	192	165	173	185
Chesterfield, Va.	4	61	66	41	32	176	183	195	177	186	197
Farmsville, Va.	2	98	105	27	26	178	188	198	176	186	196
Kelly, Va.	4	156	220	23	148	182	189	195	176	184	195
West Virginia 1	10	366	488	199	25	189	205	216	193	201	211
Buena Vista, Va.	5	282	653	75	75	187	197	209	187	195	206
Bath Alum, Va.	5	424	575	18	111	186	202	212	190	198	210
Millboro, Va.	5	431	66	28	79	192	204	213	191	198	208
Sunrise, Va.	5	613	696	172	51	201	210	222	200	208	217
West Virginia 2	15	575	1029	1052	39	203	216	229	211	220	222

Fig. 3 Relationships between local elevation and observed or simulated dates of cumulative trap catch of 5% (**a, d**), 50% (**b, e**) and 95% (**c, f**) in 1995 (**a–c**) and 1996 (**d– f**)
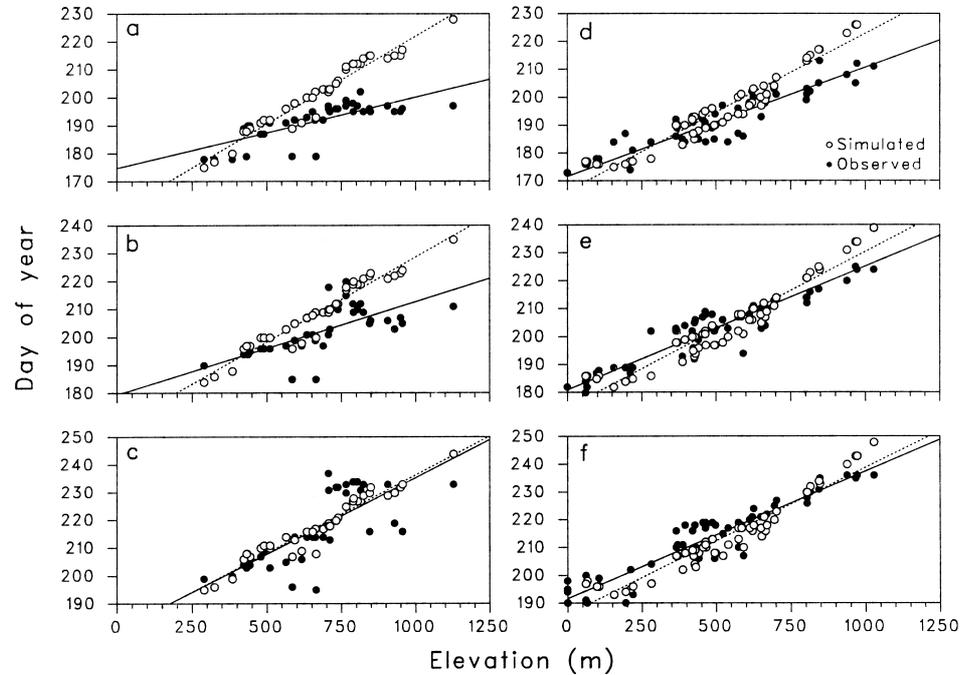
Table 2 Comparison of observed and simulated dates of 5%, 50% and 95% cumulative trap catch in relation to local elevation among the pheromone traps set in the southern states in 1995 and 1996

Cumulative catch	Observed dates				Simulated dates			
	Mean	Intercept	Slope	R^2	Mean	Intercept	Slope	R^2
1995								
5%	192	174.7	2.54	0.56	201*	159.1	6.28*	0.94
50%	202	179.4	3.33	0.51	209*	168.1	6.05*	0.94
95%	217	180.4	5.49	0.59	218	180.1	5.61	0.93
1996								
5%	190	171.6	3.90	0.88	192	167.4	5.30*	0.95
50%	201	180.9	4.41	0.90	200	175.5	5.25*	0.94
95%	213	191.6	4.57	0.89	210	187.2	4.95	0.94

* Significant difference, $\alpha = 0.05$

Table 3 Locations and dates of observed and simulated 5%, 50% and 95% cumulative trap catch among the nine datasets from northern states

Trap	Location			Observed dates			Simulated dates		
	Latitude	Longitude	Elevation	5%	50%	95%	5%	50%	95%
Amherst, Mass. 1981	43° 23′	72° 32′	180	185	190	198	194	201	210
Bellingham, Wash. 1985	48° 48′	122° 32′	150	210	224	236	221	230	247
Bellingham, Wash. 1986	48° 48′	122° 32′	150	225	237	246	221	232	247
Lima, Ohio 1986	40° 43′	84° 8′	850	194	199	209	178	185	194
Lima, Ohio 1987	40° 43′	84° 8′	850	186	193	203	176	183	192
Benton Harbor, Mich. 1980	42° 8′	86° 26′	63	212	218	225	202	209	217
Benton Harbor, Mich. 1981	42° 8′	86° 26′	63	206	214	224	196	203	212
Chestertown, Md. 1983	39° 13′	76° 4′	40	186	200	207	182	190	199
Chestertown, Md. 1985	39° 13′	76° 4′	40	176	189	203	173	182	192

In 1996, simulated dates of 5% catch were best predicted (non-significant bias) from minimum elevation in neighborhoods of 9 km², although using local elevation would have led to a slight if significant bias (Fig. 4d). The dates of 50% catch were best predicted from local elevation (Fig. 4e). The end of the flight season was best predicted from average elevation in neighborhoods of 9 km², although the use of local elevation would have been nearly as good a predictor (Fig. 4f).

Using minimum elevation in neighborhoods of 81 km² to predict 5% and 50% moth catch in 1995 improved model accuracy considerably. Regression slopes

Fig. 4 Mean bias (simulated - observed) in predictions of trap catch of 5% (**a, d**), 50% (**b, e**) and 95% (**c, f**) in 1995 (**a–c**) and 1996 (**d–f**), based on minimum (○), average (□) and maximum (△) elevation in neighborhoods of increasing dimensions. *Open symbols* Bias ≠ 0, $P < 0.05$; *closed symbols* bias = 0
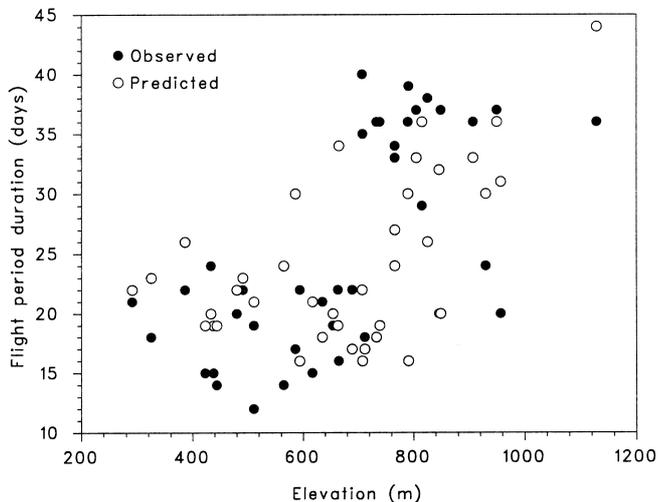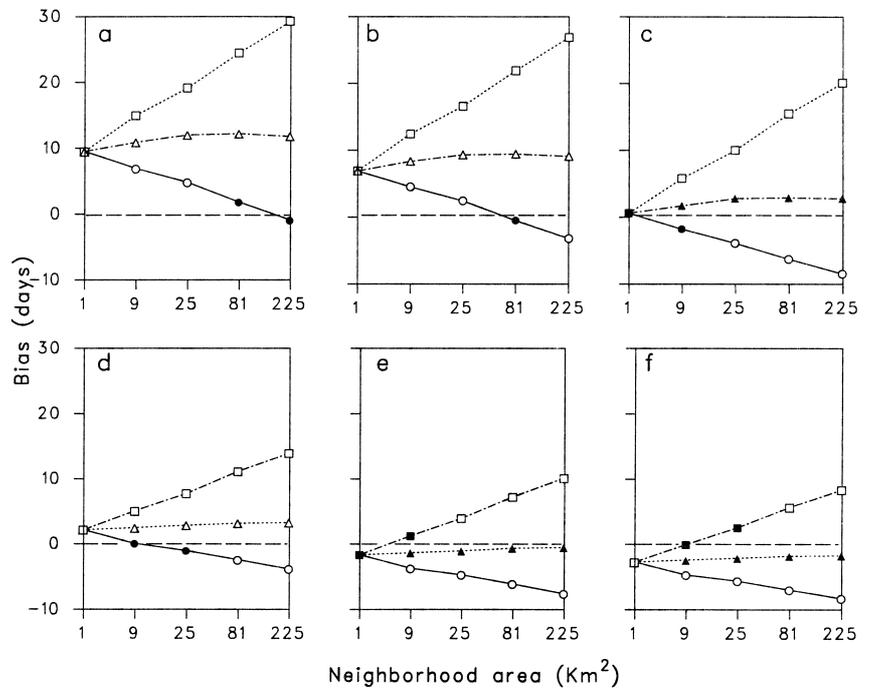
Fig. 5 Relationship between local elevation and the observed (●) and simulated (○) duration of the flight period among the 1995 traps

between observed and predicted dates were all significantly different from zero (5%: $m = 0.552$, $F = 80$, $P < 0.001$; 50%: $m = 0.80$, $F = 60$, $P < 0.001$; 95%: $m = 1.01$, $F = 78$, $P < 0.001$). Only for the 5% dates was the slope significantly different from unity (5%: $F = 53$, $P < 0.001$; 50%: $F = 3.8$, $P > 0.057$; 95%: $F = 0.01$, $P > 0.91$). Using these predictions based on neighborhood elevations also improved considerably the correspondence between the observed and predicted duration of the flight season (Fig. 5; observed: 25.4 ± 9.0 days; predicted: 24.2 ± 9.0 days; $t = 0.67$, $P > 0.51$). When predictions are based on local elevation only, the simulated flight season tends to decrease slightly in duration at

higher elevations. This improvement in model accuracy suggests considerable net movement upward from low-lying areas in the vicinity of trap sites in 1995. Such improvements were only marginal in 1996, suggesting that such movement was not as important in that year.

Data from northern states

Observed and simulated dates of 5%, 50% and 95% trap catch from the nine northern data sets are presented in Table 3. Slopes of regressions between observed and simulated dates were all significantly different from zero (Fig. 4; 5%: $m = 0.77$, $F = 22$, $P < 0.001$; 50%: $m = 0.78$, $F = 29$, $P < 0.001$; 95%: $m = 0.63$, $F = 27$, $P < 0.001$) but did not differ from unity (5%: $F = 2.02$, $P > 0.199$; 50%: $F = 2.07$, $P > 0.193$; 95%: $F = 5.69$, $P > 0.048$). There was no significant overall bias in either simulated dates (5%: Mann-Whitney's $W = 93$, $P > 0.535$; 50%: $W = 93.5$, $P > 0.503$; 95%: $W = 92$, $P > 0.596$) or duration of the simulated flight season (observed: 19.0 days, simulated: 18.5 days, $W = 88$, $P > 0.859$), although the average absolute difference between predicted and observed dates was 9.2 days, considerably larger than in the southern states.

Discussion

The model of *L. dispar* phenology used here performed well in predicting the dates of male moth flight recorded by pheromone traps over a large geographic area. The best predictions were generated for Virginia, West Virginia and North Carolina, where the average absolute difference between predicted and observed dates of flight
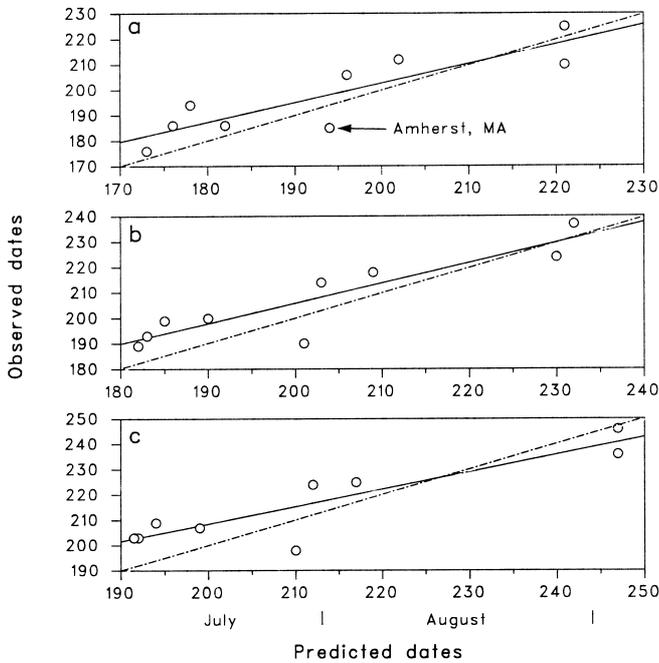
Fig. 6 Relationship between local elevation and observed or simulated dates of cumulative trap catch of 5% (**a**), 50% (**b**) and 95% (**c**) among the nine datasets from northern states. *Solid line* Regression; *dotted line* line of equality

was 3.2–5.2 days. In northern states, predictions were less accurate. This may have been caused by a combination of factors. Moth catch was pooled from many traps and exact trap location was unknown. In addition, populations were much higher in many instances than in the Virginias, and *L. dispar* phenology is more variable in outbreak populations (Lance et al. 1987). Model parameters were not adjusted or calibrated, except for moth longevity and survival rate. Thus, our analysis can be considered a successful model validation.

The model predicts *L. dispar* flight from temperature data. However, several other factors may also have a significant influence. Host plant quality has a considerable effect on *L. dispar* development rate (Barbosa and Capinera 1977; Barbosa et al. 1983; Casagrande et al. 1987). The rate of development on poor host species like red maple (*Acer rubrum*) is about 33% lower than on preferred host species, e.g. white oak (*Quercus alba*). In areas of extensive defoliation, larval development is accelerated so that pupation and moth flight occurs up to 3 weeks earlier than in the absence of defoliation (Campbell 1978). Lance et al. (1987) suggested increased exposure to sunlight as a cause of this accelerated development. The data presented here comes mostly from low-density *L. dispar* populations. However, data from Amherst (Mass.) were from a high-density area, and moth flight dates were considerably earlier than the model output (Fig. 6; Table 3). The effect of ambient temperature on flight activity can cause additional variability in moth catch patterns. Lavallée et al. (1988) showed that daily fluctuations in air temperature had a considerable effect

on the pattern of pheromone trap catch in *Zeiraphera canadensis* (Mut. and Free.). Sanders et al. (1978) showed that flight activity of the spruce budworm, *Choristoneura fumiferana* (Clem.), increased with temperature. It is likely that a similar effect exists in *L. dispar*.

Moth movement is another factor that can have considerable influence on the pattern and duration of the moth flight period. This study indicates that short-range movement (in the order of 5–9 km) can have considerable importance. Male *L. dispar* dispersal was studied quantitatively only at small spatial scales. Mark-recapture studies of Schwalbe (1981) and Elkinton and Cardé (1981) indicated that >95% of *L. dispar* males were recaptured at distance <800 m from the release point. However, recaptured males do not represent a random sample of all males. It may be that the males that were not recaptured dispersed much further than recaptured males.

There is also evidence of long-distance dispersal of male moths. Bimodal patterns of trap catch have been reported from the Upper Peninsula of Michigan, which indicated dispersal of male moths over Lake Michigan, a distance of >100 km (B.C. Pijanowski, personal communication). The size distribution of moths caught in pheromone traps also indicates moth migration. The majority of moths that emerge in defoliated areas are smaller than moths from non-defoliated areas (Carter et al. 1991), whereas moths that emerge in non-defoliated areas tend to be large. However, pheromone traps in non-defoliated areas often capture large proportions of small moths (Carter et al. 1994). These moths apparently migrated from defoliated areas.

A better understanding of male moth movement could considerably improve model predictions. Additional information is needed on the distance and orientation of moth dispersal. Here, we suggested the hypothesis of considerable population mixing in neighborhoods of 5–9 km (25–81 km^2), particularly from lower to higher elevations. In this respect, trap catch data from 1995 and 1996 differed, and this difference needs to be investigated.

Despite all these factors reducing the predictability of *L. dispar*'s male flight period, the model should be a useful tool in planning the deployment of pheromone traps over the entire present range of *L. dispar* in North America.

References

Allen JC (1976) A modified sine wave method for calculating degree days. Environ Entomol 5:388–396

Barbosa P, Capinera JL (1977) The influence of food on developmental characteristics of the gypsy moth, *Lymantria dispar* (L.). Can J Zool 55:1424–1429

Barbosa P, Waldvogel M, Martinat P, Douglass LW (1983) Developmental and reproductive performance of the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), on selected hosts common to mid-Atlantic and southern forests. Environ Entomol 12:1858–1862

Campbell RW (1978) Some effects of gypsy moth density on rate of development, pupation time, and fecundity. Ann Entomol Soc Am 71:442–448

Carter MR, Ravlin FW, McManus ML (1991) Changes in gypsy moth (Lepidoptera: Lymantriidae) fecundity and male wing length resulting from defoliation. Environ Entomol 20:1042–1047

Carter MR, Ravlin FW, McManus ML (1994) Estimating gypsy moth (Lepidoptera: Lymantriidae) egg mass density using male moths captured in pheromone-baited, milk-carton traps. Environ Entomol 23:556–561

Casagrande RA, Logan PA, Wallner WE (1987) Phenological model for gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), larvae and pupae. Environ Entomol 16:556–562

Elkinton JS (1987) Changes in efficiency of the pheromone-baited milk-carton trap as it fills with male gypsy moths (Lepidoptera: Lymantriidae). J Econ Entomol 80:754–757

Elkinton JS, Cardé RT (1981) The use of pheromone traps to monitor the distribution and population trends of the gypsy moth. In: Mitchell ED (ed) Management of insect pests with semiochemicals. Plenum, New York, pp 41–55

Elkinton JS, Cardé RT (1984) Effect of wild and laboratory-reared female gypsy moths, *Lymantria dispar* L. (Lepidoptera: Lymantriidae), on the capture of males in pheromone-baited traps. Environ Entomol 13:1377–1385

Elassal AA, Caruso VM (1983) Digital elevation models. U.S. Geological Survey Circular 895-B

Gray DR, Ravlin FW, Régnière J, Logan JA (1994) Further advances toward a model of gypsy moth (*Lymantria dispar* (L.)) egg phenology: respiration rates and thermal responsiveness during diapause, and age-dependent developmental rates in postdiapause. J Insect Physiol 41:247–256

Hunter AF (1993) Gypsy moth population sizes and the window of opportunity in spring. Oikos 68:531–538

Hunter AF, Lindgren BS (1995) Range of gypsy moth in British Columbia: a study of climatic suitability. J Entomol Soc Br C 92:45–55

Johnson PC, Mason DP, Radke SL, Tracewski KT (1983) Gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), egg eclosion: degree-day accumulation. Environ Entomol 12:929–932

Kolodny-Hirsch DM, Schwalbe CP (1990) Use of disparlure in the management of the gypsy moth. In: Ridgeway RL, Silverstein RM, Inscoe MN (eds) Behavior-modifying chemicals for insect management: application of pheromones and other attractants. Dekker, New York, pp 363–385

Lance DR, Elkinton JS, Schwalbe CP (1987) Microhabitat and temperature effects explain accelerated development during outbreaks of the gypsy moth (Lepidoptera: Lymantriidae). Environ Entomol 16:202–205

Lavallée R, Régnière J, Morissette J (1988) Influence de la température et des précipitations sur le vol des mâles de *Zeiraphera canadensis* en plantations d'épinettes blanches. Phytoprotection 69:99-103

Leonard DS, Sharov AA (1995) Slow the spread project update: developing a process for evaluation. In: Wallner WE, McManus KA (eds) Lymantriidae: a comparison of features of new and old world tussock moths. US For Serv Gen Tech Rep NE 213

Liebhold AM, Halverson JA, Helmes GA (1992) Gypsy moth invasion in North America: a quantitative analysis. J Biogeogr 19:513–520

Liebhold AM, Elkinton JS, Zhou G, Hohn ME, Rossi RE, Boettner GH, Boettner CW, Burnham C, McManus ML (1995) Regional correlation of gypsy moth (Lepidoptera: Lymantriidae) defoliation with counts of egg masses, pupae, and male moths. Environ Entomol 24:193–203

Logan JA, Casagrande RA, Liebhold AM (1991) Modeling environment for simulation of gypsy moth (Lepidoptera: Lymantriidae) larval phenology. Environ Entomol 20:1516–1525

Lyons DB, Lysyk TJ (1989) Development and phenology of eggs of gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), in Ontario. In: Wallner WE, McManus KA (eds) Lymantriidae: a comparison of features of new and old world tussock moths. US For Serv Gen Tech Rep NE 123, pp 351–366

Masaki S (1965) The effect of temperature on the termination of diapause in the egg of *Lymantria dispar* L. (Lepidoptera: Lymantriidae). Jpn J Appl Zool 21:148–157

Ravlin FW, Fleischer SJ, Rutherford SL (1990) Shenandoah National Park long-term ecological monitoring system, section IV. Gypsy moth component user manual. National Park Service, Denver

Régnière J (1983) An oviposition model for the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can Entomol 115:1371–1382

Régnière J (1996) Generalized approach to landscape-wide seasonal forecasting with temperature-driven simulation models. Environ Entomol 25:869–881

Régniere J, Bolstad P (1994) Statistical simulation of daily air temperature patterns in eastern North America to forecast seasonal events in insect pest management. Environ Entomol 23:1368–1380

Russo JM, Liebhold AM, Kelley JGW (1993) Mesoscale weather data as input to a gypsy moth (Lepidoptera: Lymantriidae) phenology model. J Econ Entomol 86:838–844

Sanders CJ, Wallace DR, Lucuik GS (1978) Flight activity of female eastern spruce budworm (Lepidoptera: Tortricidae) at constant temperatures in the laboratory. Can Entomol 110: 627–632

Schaub LP, Ravlin FW, Gray DR, Logan JA (1995) Landscape framework to predict phenological events for gypsy moth (Lepidoptera: Lymantriidae) management programs. Environ Entomol 24:10–18

Schwalbe CP (1981) Disparlure baited traps for survey and detection. In: Doane CC, McManus ML (eds) The gypsy moth: research toward integrated pest management. USDA Tech Bull 1584, pp 542–548

Sharov AA, Liebhold AM, Roberts EA (1996) Spread of gypsy moth (Lepidoptera: Lymantriidae) in the central Appalachians: comparison of population boundaries obtained from male moth capture, egg mass counts, and defoliation records. Environ Entomol 25:783–792

Sheehan KA (1992) User's guide for GMPHEN: Gypsy Moth Phenology Model. US For Serv Gen Tech Rep NE 158.

Tauber MJ, Tauber CA, Ruberson JR, Tauber AJ, Abrahamson LP (1990) Dormancy in *Lymantria dispar* (Lepidoptera: Lymantriidae): analysis of photoperiodic and thermal responses. Ann Entomol Soc Am 83:494–503

Waggoner PE (1984) The hatching of gypsy moth eggs, a phenological model. Agric For Meteorol 33:53–65