

Field Evaluation of Effect of Temperature on Release of Disparlure From a Pheromone-Baited Trapping System Used to Monitor Gypsy Moth (Lepidoptera: Lymantriidae)

PATRICK C. TOBIN,¹ AIJUN ZHANG,² KSENIA ONUFRIEVA,³ AND DONNA S. LEONARD⁴

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ABSTRACT Traps baited with disparlure, the synthetic form of the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), sex pheromone are used to detect newly founded populations and estimate population density across the United States. The lures used in trapping devices are exposed to field conditions with varying climates, which can affect the rate of disparlure release. We evaluated the release rate of disparlure from delta traps baited with disparlure string dispenser from 1 to 3 yr across a broad geographic gradient, from northern Minnesota to southern North Carolina. Traps were deployed over ≈ 12 wk that coincided with the period of male moth flight and the deployment schedule of traps under gypsy moth management programs. We measured a uniform rate of release across all locations when considered over the accumulation of degree-days; however, due to differences in degree-day accumulation across locations, there were significant differences in release rates over time among locations. The initial lure load seemed to be sufficient regardless of climate, although rapid release of the pheromone in warmer climates could affect trap efficacy in late season. Daily rates of release in colder climates, such as Minnesota and northern Wisconsin, may not be optimal in detection efforts. This work highlights the importance of local temperatures when deploying pheromone-baited traps for monitoring a species across a large and climatically diverse landscape.

KEY WORDS biological invasions, IPM, *Lymantria dispar*, pheromone-baited traps, pheromone release rate

The sampling of insect populations is a principle component of IPM programs (Roberts et al. 1993, Fleischer et al. 1999, Pedigo and Buntin 2000). Several management programs use a synthetic version of pheromones specific to the species being monitored as a sampling tool, such as the use of sex pheromone-baited traps (Elkinton and Cardé 1981, Silverstein 1981). Such trapping systems are useful, for example, in determining seasonality and estimating population density. In the United States, traps baited with the synthetic form of the sex pheromone disparlure are used to monitor male gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) (UDSA 2009). *L. dispar* is a non-native univoltine folivore that can exploit >300 species of host trees (Elkinton and Liebhold 1990, Liebhold et al. 1995), causing ecological and economic damage (Leuschner et al. 1996, Sharov and Liebhold 1998, Redman and Scriber 2000).

To monitor *L. dispar*, $\approx 250,000$ traps are deployed across the United States each year, of which $\approx 90,000$ are deployed through the gypsy moth Slow-the-Spread program. This program is an integrated pest management (IPM) strategy that aims to detect and eliminate newly founded colonies along the expanding population front in an effort to reduce the rate of *L. dispar* spread, and is implemented from Minnesota to North Carolina (Tobin and Blackburn 2007, Roberts et al. 2011). The remaining traps are placed in areas outside of the area where gypsy moth is established and the area managed under the Slow-the-Spread program, such as the western United States, to detect new populations that are then targeted in eradication efforts (Hajek and Tobin 2009, UDSA 2009). Consequently, pheromone-baited traps to monitor *L. dispar* are deployed across a geographically large area and are exposed to varying climatic regimes. Moreover, because of the logistical challenges in manually deploying traps before male moth flight, many states deploy traps several weeks before male moth flight begins so that all traps within a state or region are deployed in time. Traps are then left in the field for several weeks to months to capture the full distribution of male moth flight, which generally occurs over a 4–6-wk period (Tobin et al. 2009).

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¹ Corresponding author: USDA Forest Service, Northern Research Station, Morgantown, WV 26505-3101 (e-mail: ptobin@fs.fed.us).

² USDA-ARS, Invasive Insect Biocontrol and Behavior Laboratory, Beltsville Agricultural Research Center-West, Beltsville, MD 20705-2350.

³ Department of Entomology, Virginia Tech, Blacksburg, VA 24061.

⁴ USDA Forest Service, Forest Health Protection, Asheville, NC 28802.

Table 1. Summary information for the locations used in this study

Location	Yr in study	Latitude (°)	Longitude (°)	Date of first trap set
Blacksburg, VA	2008, 2009	37.23	-80.41	5 May
Mason, WI	2008, 2009	46.81	-90.82	23 June
State College, PA	2008, 2009	40.79	-77.86	19 May
Elizabethtown, NC	2009	34.63	-78.61	5 May
Greenup, KY	2009	38.57	-82.83	2 June
Princeton, KY	2009	37.11	-87.88	2 June
Toledo, OH	2009	41.66	-83.56	28 May
Lexington, KY	2009, 2010	38.05	-84.50	19 May
Cold Spring, MN	2008, 2009, 2010	45.46	-94.43	16 June
Madison, WI	2008, 2009, 2010	42.92	-89.22	26 May
Morgantown, WV	2008, 2009, 2010	39.63	-79.95	5 May
Raleigh, NC	2008, 2009, 2010	35.99	-78.90	5 May
Schroeder, MN	2008, 2009, 2010	47.54	-90.89	30 June
Vallonia, IN	2008, 2009, 2010	38.85	-86.09	12 May
Bureau Junction, IL	2010	41.29	-89.36	19 May

Within the area managed under the Slow-the-Spread program (Tobin and Blackburn 2007), *L. dispar* males can be active in flight from late May (e.g., North Carolina) to October (e.g., northern Minnesota) depending upon local climatic conditions. Thus, depending on the state, traps can be set as early as late-April and removed as late as mid-October. Furthermore, traps can remain in the field for up to 3 mo, regardless of the state. Past research has consistently highlighted the positive relationship between the release rate of disparlure from dispensers (e.g., plastic laminate dispensers, dispenser tapes, wicks) and temperature (Bierl-Leonhardt et al. 1979; Doane and McManus 1981; Leonhardt and Moreno 1982; Leonhardt et al. 1990, 1992; Nation et al. 1993). However, this prior work was conducted under laboratory conditions or at specific locations as opposed to the large geographic area over which pheromone-baited traps are now deployed. Moreover, we also were motivated by preliminary observations that the release of disparlure from Disrupt II flakes (Hercon Environmental, Emigsville, PA) used in mating disruption differed significantly depending on the region, or more precisely the local climatic conditions; specifically, that release rates were slower in colder climates (K.O., unpublished data). Thus, we hypothesized that there could also be differences in the release of disparlure from trap lures, which in turn could affect trap efficiency and potentially complicate the interpretation of trap catch data. Because trapping under the Slow-the-Spread program is conducted over a large, climatically diverse area, we sought to analyze the effects of climate on release rates of disparlure when deployed in pheromone-baited delta traps currently used to monitor *L. dispar*.

Materials and Methods

Experimental Design. We conducted this study from 2008 to 2010 at nine (2008), 14 (2009), and eight (2010) locations in total (Table 1; Fig. 1), and we relied on a number of volunteers (see Acknowledgments). In each year, the number of locations differed but always represented a latitudinal gradient between the most northern location (Schroeder, MN) and ap-

proximately the most southern location (Raleigh, NC), both of which were used in all 3 yr (Table 1). At each location, we initiated this study in accordance with each state's guidelines for initially deploying traps, which is based upon a phenology model (Gray et al. 1995) interpolated using BioSIM (Régnière and Sharov 1998) and labor constraints (i.e., each state starts initial trap deployment early enough so that all traps are set before male moth flight; Table 1). At all locations, traps remained under field conditions for ≈ 84 d (range, 82–93 d).

At each location, we initially set 25 delta traps baited with one disparlure string lure, each of which, according to the specifications of the manufacturing contract, are supposed to be initially loaded with 500 ± 50 μg of disparlure (Scentry Biologicals, Inc., Billings, MT). Location-specific trap set dates are presented in Table 1. Before trap set, all string lures were maintained in a freezer ($\approx -12^\circ\text{C}$) until shipped to volunteers, and materials were shipped to volunteers using priority overnight service (<24 h in transit). All lures remained in a freezer at each site until traps were deployed. In 2008, four traps were removed after 1, 4, 7, 14, 28, 42, and 56 d, and the remaining five traps were removed after 84 d. Also, at the time of trap set, three string lures were set aside for immediate processing (see below) and served as a measure of the initial lure load at each site for 2008. Based upon preliminary analysis of the data from 2008, we modified our protocol in 2009 and 2010. In these years, four traps were removed after 14, 28, 42, 56, and 70 d, and the remaining five traps were removed after 84 d. In addition, 25 lures were maintained in their hermetically sealed package and left in a freezer until all lures were sent for chemical analysis; these lures represented the initial lure load at each site for 2009 and 2010. Due to occasional conflicts volunteers had with the trap removal schedule, there were slight deviations in the precise trap removal date, but generally these deviations were only 1–2 d. Traps were set ≈ 1 –2 m above the ground, and all were set within a 10-m radius of each other. At each site, we also deployed one HOBO TidbiT temperature data logger (Onset Computer Corporation, Bourne, MA) to record hourly temperatures. When traps were removed at each interval,

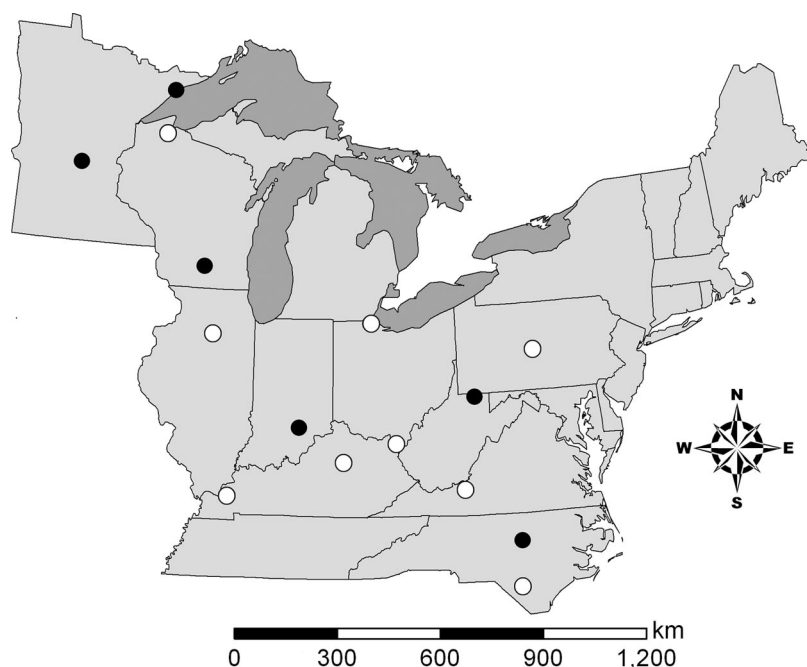


Fig. 1. Map of study locations. Solid circles represent sites used in all 3 yr, and open circles represent sites used in 1 or 2 yr (see Table 1).

each string lure, including each of the three string lures set aside for initial processing in 2008, was individually and tightly wrapped in aluminum foil, placed into a gallon-sized Ziploc freezer bag (one for each date), and maintained in a freezer ($\approx -12^{\circ}\text{C}$). On the last sampling interval, all lures were shipped to the USDA Beltsville Laboratory for chemical analysis by using priority overnight service (<24 h in transit). Although disparlure can be lost from string lures during freezer storage, storage times were maintained consistently at each site.

Temperatures recorded by the HOBO TidbiT were used to estimate the degree-day accumulation (base threshold = 10°C) at each location and at each actual trap removal date (to allow for deviations in the trap removal schedule). Degree-day accumulation was estimated using the trapezoidal method of integration, derived from the first three terms of the Taylor series expansion (Tobin et al. 2001), applied to each hourly interval.

Chemical Analysis of Lures. Chemical residual of disparlure was analyzed by an Agilent Technologies 7890A gas chromatograph (GC) equipped with a 7683B autosampler. A HP-5 capillary column (Agilent Technologies; 30 m by 0.25-mm i.d., 0.25- μm film thickness) in splitless mode with hydrogen carrier gas (2.0 ml/min) was used. Oven temperature was started at 50°C , held for 2 min and then programmed at $15^{\circ}\text{C}/\text{min}$ to 280°C and held for 10 min. The three disparlure string lures set aside in 2008, and four of disparlure string lures from their hermetically sealed package shipped with experimental samples from each location in 2009 and 2010 were used to estimate initial lure load.

Each lure was placed in a 20-ml glass bottle, soaked with 10 ml of solvent (acetone/hexane, 1:1) for 1 d at room temperature and kept in a freezer at -10°C until analysis. The chemical standard of racemic disparlure (Shin-Etsu Chemical Co., Ltd., Chiyoda-ku, Tokyo, Japan) was used as external standard (45 ng/ μl) for quantitative analysis.

Statistical Analyses. We assessed the main effects of accumulated degree-days at the time of lure removal and the latitude of each location, and their interaction, on the residue of disparlure in an analysis of variance (ANOVA). The relationship between accumulated degree-days (ADD) and the residue of disparlure ($Y_{\mu\text{g}}$) was modeled using the exponential decay equation

$$Y_{\mu\text{g}} = N_0 \exp(-r \text{ ADD})$$

where N_0 and r are estimated parameters of the initial lure load and rate of decay, respectively. In a separate analysis, we assessed the main effects of the number of days in the field at the time of lure removal and the latitude of each location, and their interaction, on the residue of disparlure in an ANOVA and used the exponential decay model (same equation as above, but with ADD replaced with the number of days in the field) to model the relationship between lure residue and time. In this case, we also used the estimate of r to estimate the half-life time ($t_{1/2} = (\ln 2)r^{-1}$). The relationship between the mean daily temperature at each site and the mean amount of disparlure release was analyzed using least squares regression. All statistical analyses were conducted in R (R Development Core Team 2011), and nonlinear parameter estimation

Table 2. Mean daily temperature, mean daily degree-days (base threshold = 10°C), and the maximum accumulated degree-days recorded in any year for each study location over the duration of the study period

Location	Mean daily temp (±SD)	Mean daily degree-days (±SD)	Max accumulated degree-days
Schroeder, MN	15.7 (3.1)	5.9 (2.9)	570.8
Blacksburg, VA	18.4 (2.9)	8.5 (2.6)	750.3
Mason, WI	17.8 (3.6)	8.1 (3.2)	769.3
State College, PA	18.6 (2.9)	8.7 (2.7)	787.0
Morgantown, WV	19.5 (3.7)	9.6 (3.4)	846.3
Cold Spring, MN	19.8 (2.9)	9.8 (2.9)	891.6
Toledo, OH	20.9 (2.9)	10.9 (2.8)	929.8
Greenup, KY	21.6 (2.3)	11.6 (2.3)	985.2
Madison, WI	21.4 (2.6)	11.4 (2.6)	1011.7
Elizabethtown, KY	22.9 (2.8)	12.9 (2.8)	1072.5
Vallonia, IN	22.1 (3.8)	12.2 (3.7)	1143.3
Bureau Junction, IL	23.7 (2.4)	13.7 (2.4)	1166.7
Princeton, KY	23.9 (2.8)	14.0 (2.7)	1186.9
Raleigh, NC	24.2 (3.5)	14.2 (3.5)	1308.7
Lexington, KY	25.3 (2.8)	15.3 (2.8)	1404.0

was based upon the Marquardt algorithm (Marquardt 1963).

Results and Discussion

There were considerable differences in temperatures across our study locations, particularly between the most southern and northern locations (Table 2). For example, the accumulated degree-days during the study duration at Schroeder, MN, and Raleigh, NC, both of which were used in all 3 yr, ranged from 445.1 to 570.8, and 1132.8–1308.7, respectively. Despite the range in climatic conditions across locations, the interaction between study location latitude and accumulated degree-days did not significantly affect the rate of disparlure release from lures ($F = 2.10$; $df = 1, 790$; $P = 0.15$), nor did the main effect of latitude ($F = 2.20$; $df = 1, 791$; $P = 0.14$). The main effect of accumulated degree-days, however, did significantly affect the rate of disparlure release ($F = 325.6$; $df = 1, 791$; $P < 0.01$). Across all sites, the exponential decay model fit to lure residue by accumulated degree-days estimated an initial lure load of 525.6 μg ($SE = 7.8$; 95% confidence intervals [CI] = 510.2, 540.9), and a rate of decay of $-0.00048 \mu\text{g}$ ($SE = 0.00003$; 95% CI = $-0.00055, -0.00042$) per degree-day (Fig. 2A). A comparison in the lure residue at one of the warmest (Raleigh, NC) and coldest (Schroeder, MN) locations by accumulated degree-days is shown in Fig. 2B.

The lack of a significant interaction effect between study location latitude and accumulated degree-days, coupled with a significant main effect accumulated degree-days, suggests that lure release rates were affected by temperature in a similar manner regardless of the locations of our study sites (Fig. 2). However, because different sites accumulated different degree-days per day (Table 2), different quantities of disparlure were released in the field. When examining the rate of disparlure release over time across our study locations, we detected significant main effects of latitude ($F = 10.4$; $df = 1, 790$; $P < 0.01$), the number of days lures were in the field ($F = 37.3$; $df = 1, 790$; $P < 0.01$), and a significant interaction effect ($F = 24.0$; $df = 1, 790$; $P < 0.01$). Using

the exponential decay model (equation herein fit to each location, the estimated initial lure load and rate of decay parameters, half-life times, and daily release rates are listed in Table 3. There was considerable variability in half-life times, from 37.3 to 433.2 d, and in the daily release rate, from 0.8 to 5.3 μg (Table 3). Daily release rates from the three most northern sites (Schroeder and Cold Spring, MN, and Mason, WI) were $<1 \mu\text{g}$, whereas in Lexington, KY, the warmest location (Table 2), release rates were 5.3 μg . The daily release rate from our warmer locations is similar to observations from a field study in Florida in which up to 4.1 μg were released from dispenser tape per day (Nation et al. 1993). When comparing the mean difference between the initial and final quantity of disparlure residue at each study location, there was a significant positive relationship between this

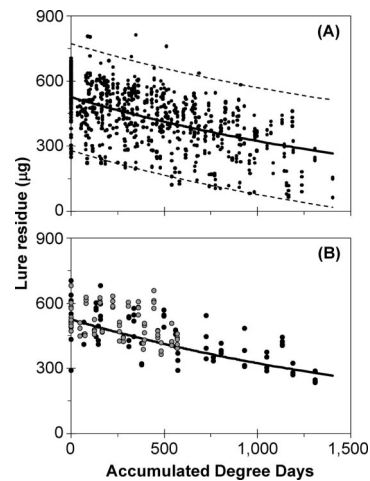


Fig. 2. (A) Release rate of disparlure across all study locations over the location-specific degree-day accumulation (base threshold = 10°C) and the exponential decay fit (predicted, solid line; 95% CI, dashed line). (B) Subset of A showing the data from one of the warmest (Raleigh, NC; black circles) and the coldest location (Schroeder, MN; gray circles). The predicted exponential decay fit from A also is shown.

Table 3. Estimates of location-specific initial lure loads and rate of decay parameters (see equation in Materials and Methods), and extrapolated values for the half-life times and overall daily release rates

Location	Initial lure load, μg ($\pm\text{SE}$)	Rate of decay ($\pm\text{SE}$)	Half-life (d)	Daily release rate (μg)
Schroeder, MN	534.3 (18.5)	-0.0016 (0.0007)	433.2	0.8
Mason, WI	388.7 (34.2)	-0.0026 (0.0019)	266.6	0.9
Cold Spring, MN	426.3 (27.2)	-0.0024 (0.0013)	288.8	0.9
Blacksburg, VA	549.8 (26.6)	-0.0027 (0.0011)	256.7	1.3
State College, PA	440.8 (37.5)	-0.0038 (0.0017)	182.4	1.4
Morgantown, WV	539.3 (19.9)	-0.0043 (0.0008)	161.2	1.9
Elizabethtown, NC	530.5 (35.0)	-0.0046 (0.0015)	150.7	2.0
Madison, NC	556.1 (20.4)	-0.0054 (0.0010)	128.4	2.4
Raleigh, NC	543.0 (17.7)	-0.0058 (0.0008)	119.5	2.5
Vallonia, IN	522.0 (25.2)	-0.0075 (0.0011)	92.4	2.9
Toledo, OH	650.4 (25.5)	-0.0084 (0.0009)	82.5	3.9
Princeton, KY	661.9 (38.9)	-0.0092 (0.0015)	75.3	4.2
Bureau Junction, IL	483.9 (34.6)	-0.0194 (0.0026)	35.7	4.6
Greenup, KY	634.6 (50.4)	-0.0122 (0.0025)	56.8	4.8
Lexington, KY	560.0 (25.1)	-0.0186 (0.0016)	37.3	5.3

difference and the mean daily temperature at each site over the study period ($t = 4.1$; $P < 0.01$; slope estimate = 34.9 ± 8.6 ; Fig. 3). A comparison among three locations (Raleigh, NC; Madison, WI; and Schroeder, MN) that represent the extent of the latitudinal gradient and locations that were used in all 3 yr of this study is presented in Fig. 4, with the corresponding accumulation of degree-days.

The relationship between temperature and disparlure release rates that we observed is consistent with past observations (Bierl-Leonhardt et al. 1979, Doane and McManus 1981, Leonhardt et al. 1990, Leonhardt et al. 1992). However, to our knowledge this is the first attempt to measure pheromone release rates under field locations from a number of climatically diverse locations including from a site as far north as northern Minnesota where mean daily temperatures during *L. dispar* flight were $<16^{\circ}\text{C}$ (Table 2) and were as low as 8.1°C over the course of this study. Prior work has suggested that the attraction of virgin female *L. dispar* is approximately equivalent to 1–6 μg of disparlure (Beroza et al. 1971) and that a trap with at least 10 μg of disparlure would be as attractive to a male *L. dispar* as a trap baited with a live female over a short time (Stevens and Beroza 1972). Although *L. dispar* females only produce a fraction (<25 ng, Giebulowicz

et al. 1992) of the pheromone quantities on lures that are used in gypsy moth traps (500 μg), synthetic sex pheromones also lack other cues, such as visual, that could be important in mate location at short distances (Cardone and Fullard 1988, Rowland et al. 2011). Given prior work on the quantity of disparlure needed to be roughly equivalent in attraction as a live female, and hence useful as a gypsy moth monitoring tool (Beroza et al. 1971, Stevens and Beroza 1972), our data

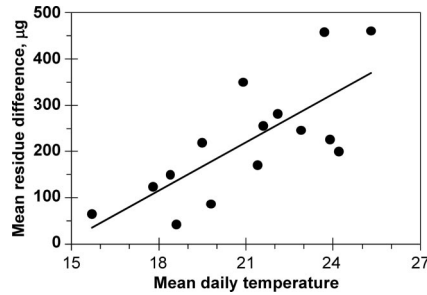


Fig. 3. Difference between the mean initial and final quantities of disparlure at each location based upon the location-specific mean daily temperature ($^{\circ}\text{C}$) over the 12-wk study period ($R^2 = 0.56$).

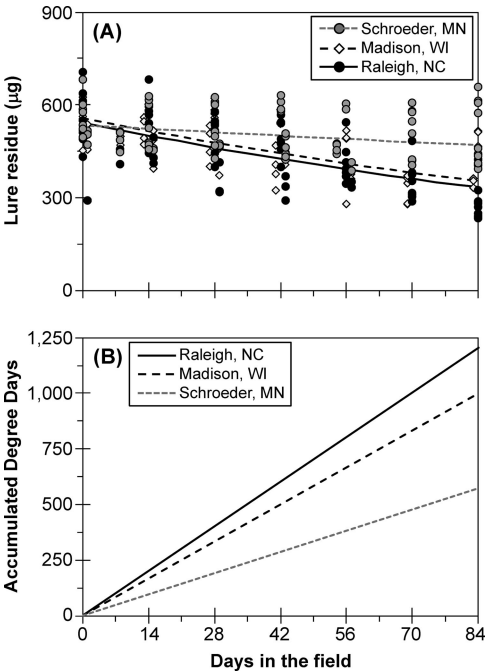


Fig. 4. (A) Release rate of disparlure based upon time under field conditions at three selected sites representing one of the warmest (Raleigh, NC), the coldest (Schroeder, MN), and an intermediate location (Madison, WI). Location-specific exponential decay fits also are shown. (B) Corresponding mean accumulation of degree-days (base threshold = 10°C) at each location across the 3 yr.

suggest that lures in trapping systems deployed in colder climates may not be releasing the desired amount of disparlure (Table 3; Fig. 4). Moreover, in eradication efforts, traps baited with synthetic pheromones should be considerably more attractive to male *L. dispar* than female *L. dispar* to be successful in detecting very low-density populations. To achieve this, pheromone-baited traps, especially those set in cooler climates, could require additional lures regardless of the initial lure load because release rates are temperature-dependent.

It is important to note that in none of our locations, including the warmest ones, did we observe a lack of disparlure residue at the end of the study period despite the fact that traps were deployed over ≈ 12 wk (Fig. 3). However, the estimated half-life time at some of the warmer locations (Table 3) do not always exceed the length of time pheromone-baited traps are deployed in the field (Régnière and Sharov 1998, Tobin and Blackburn 2007, USDA 2009). Also, we did observe instances of a mean difference >450 μg between the mean initial and final quantity of disparlure at two of the warmer sites (Fig. 3). Thus, although the initial lure load seems to be sufficient for most of the locations used in this study, decreases in the initial quantity of disparlure on lures, as well as improper lure storage, could be problematic in these warmer climates where release rates are already high (Table 3). This reinforces concerns raised from a prior study conducted in Florida in which it was suggested that due to rapid release rates in warmer climates, pheromone lures may need to be replaced over the course of the *L. dispar* flight period (Nation et al. 1993).

The mean initial lure load (525.6 μg) of all the lures used in this study is within standard operating guidelines provided to manufacturers for the use of disparlure in monitoring gypsy moth populations, which is 500 ± 50 μg and is based upon prior work suggesting that this is an appropriate amount (Doane and McManus 1981, Leonhardt et al. 1990, Thorpe et al. 1993). However, across all years and study locations, we observed 14 (of 111 lures) with an initial lure load <450 μg , and these 14 ranged from 249.5 to 444.8 μg . Twelve of these lures were from studies conducted in 2008, ranging from 249.5 to 419.8 μg , including five that were <300 μg , whereas two lures were from studies conducted in 2010 (432.5 and 444.8 μg). Moreover, the estimated initial lure load at three locations was less than the minimum standard of 450 μg (Table 3). These observations highlight the importance of quality control guidelines to ensure the integrity of pheromone-baited lures in this and other insect management programs that deploy synthetic pheromone devices.

The use of sex pheromones, which tend to be species-specific, is an important management tool in *L. dispar* as well as in other insect species for which synthetic pheromones are available (Cardé and Minks 1995, Suckling and Karg 2000, El-Sayed et al. 2006, El-Sayed 2011). In the management of non-native species, sensitive survey tools are extraordinarily important in efforts to detect incipient populations that can be more effectively managed or eradicated than pop-

ulations distributed over larger spatial scales. As global trade and travel continue to increase the connectivity among regions, countries, and continents (Work et al. 2005, McCullough et al. 2006, Hulme et al. 2008), there is often a need to deploy survey tools across a diversity of climates. Understanding the relationship between climatic regimes during the period of trapping and the release rate of the synthetic pheromones from lure devices is thus important to ensure that traps are efficient in attracting the target species.

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References Cited

- Beroza, M., B. A. Bierl, E. F. Kniping, and J. C. R. Tardif. 1971. The activity of the gypsy moth sex attractant disparlure vs. that of the live female moth. *J. Econ. Entomol.* 64: 1527–1529.
- Bierl-Leonhardt, B. A., E. D. DeVilbiss, and J. R. Plimmer. 1979. Rate of release of disparlure from laminated plastic dispensers. *J. Econ. Entomol.* 72: 319–321.
- Cardé, R. T., and A. K. Minks. 1995. Control of moth pests by mating disruption: successes and constraints. *Annu. Rev. Entomol.* 40: 559–585.
- Cardone, B., and J. H. Fullard. 1988. Auditory characteristics and sexual dimorphism in the gypsy moth. *Physiol. Entomol.* 13: 9–14.
- Doane, C. C., and M. L. McManus [eds.]. 1981. The gypsy moth: research toward integrated pest management. Technical Bulletin 1584, USDA, Washington, DC.
- El-Sayed, A. M. 2011. The Pherobase: database of insect pheromones and semiochemicals. (<http://www.pherobase.com>).
- El-Sayed, A. M., D. M. Suckling, C. H. Wearing, and J. A. Byers. 2006. Potential of mass trapping for long-term pest management and eradication of invasive species. *J. Econ. Entomol.* 99: 1550–1564.
- Elkinton, J. S., and R. T. Cardé. 1981. The use of pheromone traps to monitor the distribution and population trends of the gypsy moth, pp. 41–55. *In* E. D. Mitchell [ed.], Man-

- agement of insect pests with semiochemicals. Plenum, New York.
- Elkinton, J. S., and A. M. Liebhold. 1990. Population dynamics of gypsy moth in North America. *Annu. Rev. Entomol.* 35: 571–596.
- Fleischer, S. J., P. E. Blom, and R. Weisz. 1999. Sampling in precision IPM: when the objective is a map. *Phytopathology* 89: 1112–1118.
- Giebertowicz, J. M., R. E. Webb, A. K. Raina, and R. L. Ridgway. 1992. Effects of temperature and age on daily changes in pheromone titer in laboratory-reared and wild gypsy moth (Lepidoptera: Lymantriidae). *Environ. Entomol.* 21: 822–826.
- Gray, D. R., F. W. Ravlin, J. Régnière, and J. A. Logan. 1995. 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.
- Hajek, A. E., and P. C. Tobin. 2009. North American eradication of Asian and European gypsy moth, pp. 71–89. *In* A. E. Hajek, T. R. Glare, and M. O'Callaghan [eds.], *Use of microbes for control and eradication of invasive arthropods*. Springer, New York.
- Hulme, P. E., S. Bacher, M. Kenis, S. Klotz, I. Kühn, D. Minchin, W. Nentwig, S. Olenin, V. Panov, J. Pergl, et al. 2008. Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *J. Appl. Ecol.* 45: 403–414.
- Leonhardt, B. A., and D. S. Moreno. 1982. Evaluation of controlled release laminate dispensers for pheromones of several insect species, pp. 159–173. *In* B. A. Leonhardt and M. Beroza [eds.], *Insect pheromone technology: chemistry and applications*. American Chemical Society Symposium Series 190, American Chemical Society, Washington, DC.
- Leonhardt, B. A., V. C. Mastro, and E. D. Devilbiss. 1992. Evaluation of pheromone dispensers for use in gypsy moth detection (Lepidoptera: Lymantriidae). *J. Entomol. Sci.* 27: 280–284.
- Leonhardt, B. A., V. C. Mastro, E. C. Paszek, C. P. Schwalbe, and A. D. Devilbiss. 1990. Dependence of gypsy moth (Lepidoptera: Lymantriidae) capture on pheromone release rate from laminate and other dispensers. *J. Econ. Entomol.* 83: 1977–1981.
- Leuschner, W. A., J. A. Young, S. A. Waldon, and F. W. Ravlin. 1996. Potential benefits of slowing the gypsy moth's spread. *South. J. Appl. For.* 20: 65–73.
- Liebhold, A. M., K. W. Gottschalk, R. M. Muzika, M. E. Montgomery, R. Young, K. O'Day, and B. Kelley. 1995. Suitability of North American tree species to the gypsy moth: a summary of field and laboratory tests. USDA Forest Service General Technical Report NE-211, Radnor, PA.
- Marquardt, D. W. 1963. An algorithm for least squares estimation of nonlinear parameters. *J. Soc. Ind. Appl. Math.* 11: 431–441.
- McCullough, D. G., T. T. Work, J. F. Cavey, A. M. Liebhold, and D. Marshall. 2006. Interceptions of nonindigenous plant pests at US ports of entry and border crossings over a 17-year period. *Biol. Invasions* 8: 611–630.
- Nation, J. L., J. L. Foltz, W. N. Dixon, and H. J. McAuslane. 1993. Evaluation of loss of (+)-disparlure from gypsy moth (Lepidoptera: Lymantriidae) pheromone dispenser tapes under field conditions in Florida. *Fla. Entomol.* 76: 584–589.
- Pedigo, L. P., and G. D. Buntin [eds.]. 2000. *Handbook of sampling methods for arthropods in agriculture*. CRC, Boca Raton, FL.
- R Development Core Team. 2011. The R Project for Statistical Computing. (<http://www.r-project.org>).
- Redman, A. M., and J. M. Scriber. 2000. Competition between the gypsy moth, *Lymantria dispar*, and the northern tiger swallowtail, *Papilio canadensis*: interactions mediated by host plant chemistry, pathogens, and parasitoids. *Oecologia* 125: 218–228.
- Régnière, J., and A. Sharov. 1998. Phenology of *Lymantria dispar* (Lepidoptera: Lymantriidae), male flight and the effect of moth dispersal in heterogeneous landscapes. *Int. J. Biometeorol.* 41: 161–168.
- Roberts, E. A., F. W. Ravlin, and S. J. Fleischer. 1993. Spatial data representation for integrated pest management programs. *Am. Entomol.* 39: 92–107.
- Roberts, E. A., P. C. Tobin, and J. Wu. 2011. Decision-support system for the gypsy moth Slow-the-Spread program. ([www.http://da.ento.vt.edu/](http://da.ento.vt.edu/)).
- Rowland, E., P. W. Schaefer, P. Belton, and G. Gries. 2011. Evidence for short-range sonic communication in lymantriine moths. *J. Insect Physiol.* 57: 292–299.
- Sharov, A. A., and A. M. Liebhold. 1998. Bioeconomics of managing the spread of exotic pest species with barrier zones. *Ecol. Appl.* 8: 833–845.
- Silverstein, R. M. 1981. Pheromones: background and potential for use in insect pest control. *Science* 213: 1326–1332.
- Stevens, L. J., and M. Beroza. 1972. Mating-inhibition field tests using disparlure, the synthetic gypsy moth sex pheromone. *J. Econ. Entomol.* 65: 1090–1095.
- Suckling, D. M., and G. Karg. 2000. Pheromones and other semiochemicals, pp. 63–100. *In* J. E. Rechcigl and N. A. Rechcigl [eds.], *Biological and biotechnological control of insect pests*. CRC, Boca Raton, FL.
- Thorpe, K. W., R. L. Ridgway, and B. A. Leonhardt. 1993. Relationship between gypsy moth (Lepidoptera: Lymantriidae) pheromone trap catch and population density: comparison of traps baited with 1 and 500 μg (+)-disparlure lures. *J. Econ. Entomol.* 86: 86–92.
- Tobin, P. C., and L. M. Blackburn. 2007. *Slow the Spread: a national program to manage the gypsy moth*. USDA Forest Service General Technical Report NRS-6, Newtown Square, PA.
- Tobin, P. C., S. Nagarkatti, and M. C. Saunders. 2001. Modeling development in grape berry moth (Lepidoptera: Tortricidae). *Environ. Entomol.* 30: 692–699.
- Tobin, P. C., K. T. Klein, and D. S. Leonard. 2009. Gypsy moth (Lepidoptera: Lymantriidae) flight behavior and phenology based upon field-deployed automated pheromone-baited traps. *Environ. Entomol.* 38: 1555–1562.
- [USDA] U.S. Department of Agriculture. 2009. *Gypsy Moth Program Manual*. USDA Marketing and Regulatory Programs, Animal and Plant Health Inspection Service, Plant Protection and Quarantine, 09/2009-03, Washington, DC.
- Work, T. T., D. G. McCullough, J. F. Cavey, and R. Komsa. 2005. Arrival rate of nonindigenous insect species into the United States through foreign trade. *Biol. Invasions* 7: 323–332.

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