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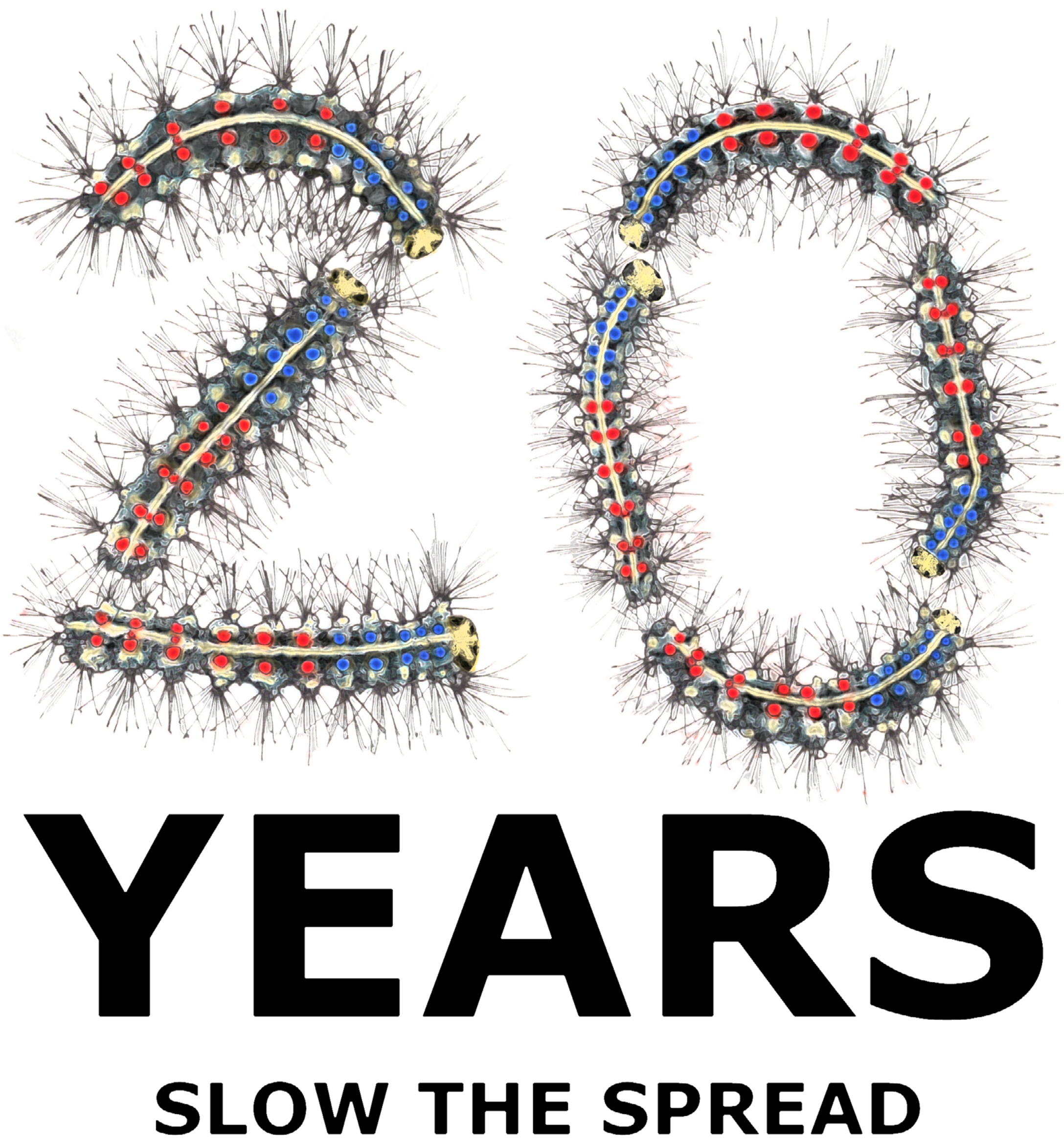
Slow the Spread: A 20-Year Reflection on the National *Lymantria dispar* Integrated Pest Management Program

Edited by Tom W. Coleman and Andrew M. Liebhold



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Abstract

The spongy moth, *Lymantria dispar* L. (Lepidoptera: Erebidae), formerly known as the "gypsy moth," continues to spread throughout North America, threatening deciduous trees, impacting humans, and directing state, federal, and private funds to population suppression and regulatory compliance. This non-native, foliage-feeding insect species currently occupies only about one-third of its possible host distribution in the United States. Efforts to reduce its impact and invasion spread represent one of the largest and most successful federal and state agency integrated pest management programs against a forest pest. The U.S. Department of Agriculture (USDA) National Spongy Moth Management Strategy is a four-pronged, multidisciplinary, and geographically coordinated approach to suppress outbreaks in generally infested areas, slow the spread of the advancing invasion front along a transition area, eradicate newly founded populations in uninfested areas, and regulate the anthropogenic movement of life stages from quarantined areas. The National Slow the Spread (STS) Program, which has been actively managing low density *L. dispar* populations along the expanding invasion front (i.e., transition zone) since 2000, represents a primary component of the multidisciplinary USDA strategy and has significantly contributed to lessening the impacts and spread of *L. dispar* in the United States. The objective of this report is to synthesize new information about the STS Program's standard operating procedures, accomplishments, and advancements for managing the spread of *L. dispar* since 2000 and to provide a guide and framework for future landscape-level integrated pest management programs. Building on Tobin and Blackburn (2007), this report includes five papers that (1) provide an overview of *L. dispar* in the United States, including the impacts and changes in *L. dispar* management since the late 1800s and advancements of *L. dispar* integrated pest management programs; (2) explain the STS Program, including advancements in monitoring data collection and management, workflow and processes of the centralized database, updates to the information delivery of the program, and funding trends; (3) report annual trends and assessments for trapping, the STS decision algorithm, treatments, and spread; (4) present current understanding and research about *L. dispar* spread and considerations about future directions; and (5) describe recent methods development work focusing on mating disruption applications and use of pheromone-baited traps supported by the STS Technical Committee.

Keywords: area-wide management, *Bacillus thuringiensis* var. *kurstaki,* barrier zone, biological invasion, gypsy moth, integrated pest management, mating disruption, spongy moth

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Contents

Chapter 1

Lymantria dispar and Progression of Management Strategies in the United States

Tom W. Coleman

Abstract

For more than 150 years, the exotic defoliator spongy moth, *Lymantria dispar* L. (Lepidoptera: Erebidae, formerly known as the "gypsy moth"), has impacted forests and been a nuisance to residents in the eastern United States. Management of this non-native, invasive species dates back to the late 1800s, and more recent eradication and suppression techniques have evolved from intensive, tedious management actions to integrated pest management programs that are coordinated by state and federal agencies. Five previous management programs dating from 1923 to 1999 have laid the framework for the current *L. dispar* management program. Specifically, three integrated pest management programs located in Maryland and the southern Appalachian Mountains developed the program structure and management actions used in the National Slow the Spread Program, which represents the main strategy of U.S. Department of Agriculture's National Spongy Moth Management Program.

Keywords: *Bacillus thuringiensis* var. *kurstaki,* defoliator, gypsy moth, integrated pest management, invasive insect, mating disruption, spongy moth

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Citation

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BACKGROUND

Lymantria dispar L. (Lepidoptera: Erebidae), has been referred to by numerous common and scientific names since its initial species description in 1758 by C. Linneaus (Fig. 1). The literal translations of its common names in various languages include apricot-spinner, big head moth, brown arches, common caterpillar, dancing moth, dancing poison moth, deciduous nun moth, disparate silkmoth, dissimilar bombyx, dissimilar nocturnal-moth, dissimilar spinner, forest wool butterfly, fungus-caterpillar, fungus moth, fungus-spinner, garden nun moth, great fungus-caterpillar, great-head, great-head bear, great-head spinner, gubar moth, gypsy butterfly, gypsy moth, hairy caterpillar of cork, hairy lizard of the holm oaks, hairy oak caterpillar, hairy oak moth, leaf nun, large-headed nun, prairie moth, rose-spinner, silkspinner, silkworm unpaired, sponge knitter moth, spongy moth, spongy silk moth, stem caterpillar, stem-moth, thick-head, thick-headed bear, tree-caterpillar, two-fold, uneven moth, and zig-zag moth, and all make reference to its larval and adult appearance, behavior, and host preference (Forbush and Fernald 1896, Pogue and Schaeffer 2007). These names originate from the many countries across its native and introduced regions.

Figure 1.—Life stages of *Lymantria dispar:* (A) late instar caterpillars, (B) male and female pupae (note the smaller male pupa), (C) adult male and female mating, (D) females laying egg masses) of *Lymantria dispar* collected in the United States. (Photographs by T.W. Coleman, USDA Forest Service)

The species name has also undergone numerous revisions [*Palaena (Bombyx) dispar* 1758 Linn., *Laria dispar* 1801 Schrank, *Liparis dispar* 1810 Ochsenheimer, *Porthetria dispar* 1822 Hubner, *Ocneria dispar* Studinger 1822, *Hypogymna dispar* 1829 Stephens] (Forbush and Fernald 1896) prior to *Lymantria dispar* and subsequently *Lymantria dispar dispar* Linnaeus, distinguishing it from the Asian subspecies, *Lymantria dispar asiatica* Vnukovskij, and other Asian variants. *Lymantria dispar* remained in the genus *Porthetria* until it was returned to the genus *Lymantria* in the 1970s. Linneaus aptly named the species because the roots of the binomial name further align with its behavior [*lyma* (Greek) = "destruction, filth"] and sexually dimorphic adult stage [*dispar* (Greek) = "unequal, unlike"] (Borror 1960, Morwood 1990). The numerous common and species names also make reference to the ubiquitous nature and impact *L. dispar* has had on people throughout its native region, which encompasses regions throughout Europe, North Africa, central Asia, and east Asia including the Russian Far East (Giese and Schneider 1979, Pogue and Schaefer 2007). The impact and nuisance from *L. dispar* continue in its introduced region of North America. However, the common name of gypsy moth can be offensive to some groups, so is no longer recognized as the common name in the United States. In 2022, the Entomological Society of America adopted spongy moth as the new common name for *L. dispar*.

An accidental release of *L. dispar* in 1868 or 1869 by Étienne Léopold Trouvelot, a French artist, amateur entomologist, and astronomer with an interest in rearing silk moths, introduced the non-native species into the yard behind Trouvelot's home in Medford, Massachusetts (Forbush and Fernald 1896, Liebhold et al. 1989). Approximately 12 years later, the first report of defoliation and nuisance of caterpillars came from people living in Trouvelot's neighborhood and thus began the first large-scale eradication attempt against *L. dispar* and the start of a long history of *L. dispar* management in the United States. The U.S. Department of Agriculture (USDA) and state partners have successfully coordinated eradication efforts in 26 states since 1967, with the largest acreages treated in Wisconsin, North Carolina, Oregon, Utah, Tennessee, and Arkansas (Epanchin-Niell et al. 2021, Hajek and Tobin 2009, USDA FS 2021b), ultimately restricting the distribution of the population to 20 states in the eastern United States (Fig. 2). Since the early 1990s, an international program has been implemented to monitor east Asian *L. dispar asiatica* populations in an attempt to track introductions to North America (Mastro et al. 2021).

LIFE HISTORY

Lymantria dispar is univoltine, progressing from egg to larva to pupa and finally to adult (Fig. 1). Details on its biology and life history can be found in Doane and McManus (1981). Egg embryonation occurs shortly after oviposition, but larvae remain inside the egg chorion through the winter until spring, when hatch occurs. A chilling period and subsequent incubation period are needed for egg hatch (Giese and Casagrande 1981, Gray et al. 1991), which is synchronized with preferred host leaf expansion and can occur from April to May in eastern North America (Leonard 1981, Nealis and Erb 1993). First instar larvae can disperse short distances by "ballooning" on silk threads to surrounding areas (McManus and Mason 1983). Larvae progress through five to six instars in approximately 6 to 8 weeks and can be differentiated by head capsule width and coloration (Jobin et al. 1992). An instar feeds for 7 to 10 days before molting. Late instar caterpillars seek protected areas to pupate, usually under tree branches, logs, rocks, bark cracks, leaf

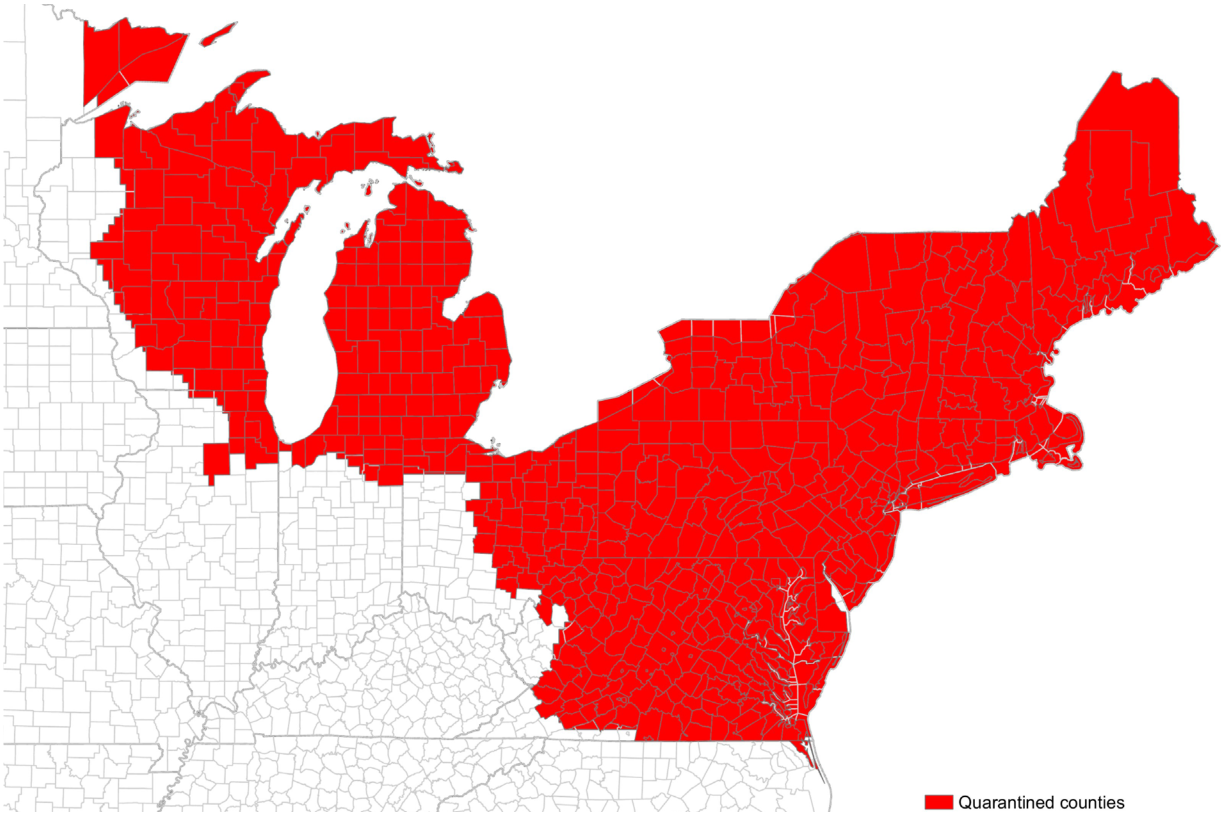

Figure 2.—*Lymantria dispar* is quarantined in 20 U.S. states. Counties are quarantined by local state agencies and USDA Animal and Plant Health Inspection Service.

litter, and human-made structures. Pupal development can last for 14 to 17 days before adult moth eclosion. Male moths commonly emerge 1 to 2 days prior to females and fly primarily from late morning into late afternoon, with a second, smaller crepuscular flight (Odell and Mastro 1980, Tobin et al. 2009). Adult moths do not feed and commonly live for about a week. Male moths can be trapped from late May to September throughout the moth's distribution in North America (Leonard 1981, Nealis and Erb 1993). The flightless females mate and subsequently lay eggs in a single mass near their pupal resting site, which is covered with buff-colored hairs from their abdomen. As a result, egg masses can be found on various items (e.g., tree branches and stems, rocks, walls, household articles, vehicles) and can contain a few hundred to a thousand eggs, facilitating the moth's capacity to travel and establish in other areas[1] (Fig. 3). Counts of egg mass densities in fixed-radius plots [e.g., 0.16 ha (1/40th acre)] may be the best tool to predict population densities, level of defoliation the following year, and, if necessary, additional management actions (Gottschalk 1993, Liebhold et al. 1994, Wilson and Fontaine 1978).

HOST SPECIES AND IMPACT

Lymantria dispar is extremely polyphagous and can feed on more than 300 tree and shrub species, which has likely contributed to its ability to establish and spread across various landscapes (Liebhold et al. 1995b). In North America, *L. dispar* larvae prefer feeding

[1] See Walter and Liebhold (2023) in this report for additional discussion about natural and human-assisted spread of *L. dispar* in the United States.

Figure 3.—A collection of *Lymantria dispar* adults and their egg masses during an outbreak in northern Michigan. (Photograph by T.W. Coleman, USDA Forest Service)

on oaks (*Quercus* spp. L.), poplars (*Populus* spp. L.), some birches (*Betula* spp. L.), apples (*Malus* spp. Mill.), sweetgum (*Liquidambar styraciflua* L.), basswoods (*Tilia* spp. L.), hawthorns (*Crataegus* spp. Tourn. *ex* L.), and willows (*Salix* spp. L.) in North America. Liebhold et al. (1995a) and USDA FS and APHIS (2012a) provide an extensive host list of susceptible, resistant, and immune species. First instar larvae require susceptible host species to survive, whereas later instar larvae can feed on susceptible and immune host species. Immune host species will escape high levels of herbivory even during high population pressure.

Since the 1920s, cumulative defoliation attributed to *L. dispar* has surpassed 39 million hectares with over 5.2 million hectares defoliated in a single year (1981), impacting all land ownerships (Figs. 4 and 5) (USDA FS 2021a, USDA FS 2021b, Williams 1982). *Lymantria dispar* populations progress through four phases (innocuous or endemic, release, outbreak, and decline) and can remain at endemic levels for several years. Mortality caused by small mammals and introduced parasitoids and predators contribute to sustaining populations in the endemic phase but have little effect on controlling larger population densities (Elkinton and Liebhold 1990). During the release phase, populations can build to high levels for 1 or more years then reach outbreak levels that can persist for 1 to 3 years before declining and returning to endemic levels. At a regional scale, outbreaks exhibit a statistical periodicity with 5 to 10 years between outbreaks (Johnson et al. 2005). Two pathogens, *Entomphaga maimaiga* Humber, Shimazu, and R.S. Soper (Entomophthorales: Entomophthoraceae) and *L. dispar* nucleopolyhedrosis virus (NPV), regularly contribute to the collapse of outbreaks. In the past 10 years, outbreaks and high levels of defoliation have occurred in 2021 in Maine, Maryland, Massachusetts, Michigan, New Jersey, New York, Pennsylvania, Vermont, and Ontario, Canada; in 2010 and from 2019 to 2021 in Michigan and Pennsylvania; from 2013 to 2015 in Pennsylvania and New York; from 2015 to 2017 in Connecticut, Massachusetts, and Rhode Island; from 2015 to 2016 in West Virginia; and from 2015 to 2018 in Virginia. During these outbreaks, defoliation ranged from tens of thousands to hundreds of thousands of hectares annually (USDA FS 2021). Low and moderate levels of defoliation can injure trees, reducing radial growth, reducing the amount and size of leaves the following year, causing crown dieback, killing fine roots, and inducing epicormic shoots on injured trees (Gottschalk 1993). Tree mortality often results after several consecutive years of severe defoliation (>75 percent) and tends to increase rapidly during the second year after defoliation (Fig. 6) (Davidson et al. 2001). Defoliation from *L. dispar* occurs early in the growing season, and although heavily defoliated trees can often refoliate in the same season, doing so is energetically costly and can quickly deplete a tree's resources. Forest stands with a higher proportion (>50 percent) of oak species (e.g., chestnut oak, *Q. prinus* Willd. and white oak, *Q. alba* L.), abundant refuges for larvae, unfavorable habitat for small mammals, and those that are located on poorer sites often experience the highest levels of tree mortality (Gottschalk 1993, Herrick and Gansner 1986, Houston and Valentine 1977). In the northeastern United States, susceptible, or favored, host and oak species experienced higher defoliation and tree mortality following a *L. dispar* outbreak (Davidson et al. 1999). Trees with intermediate and suppressed crowns and poor crown conditions have higher mortality rates compared to dominant canopy trees (Campbell and Sloan 1977, Campbell and Valentine 1972). As defoliation intensity, duration, and frequency increase, tree mortality likewise increases (Davidson et al. 1999), but stands with greater tree species diversity reduced the impact of *L. dispar* defoliation. Pines, *Pinus* spp. L., that experienced high levels of defoliation (81 to 100 percent) succumbed following a single bout of injury (Baker 1941). Coniferous species, including pitch pine, *Pinus rigida* Mill., white pine, *P. strobus* L., red pine, *P. resinosa* Sol. Ex. Aiton, and spruce, *Picea* spp. Mill., are often consumed by late instar caterpillars, which will feed on old and new foliage. A single year of severe defoliation can cause mortality of these conifer species. Trees weakened by drought, late spring frosts, secondary insects and diseases, and other stressors will succumb to high levels of defoliation often several years after an outbreak has subsided (Campbell and Sloan 1977, Campbell and Valentine 1972, Davidson et al. 2001, Gansner and Herrick 1984, Gottschalk and MacFarlane 1992).

Figure 4.—Defoliation caused by the *Lymantria dispar* during an outbreak in Wisconsin. Note the varying levels of defoliation with several areas of severe injury (brown coloration). (Photograph by M. Roberts, USDA Forest Service)

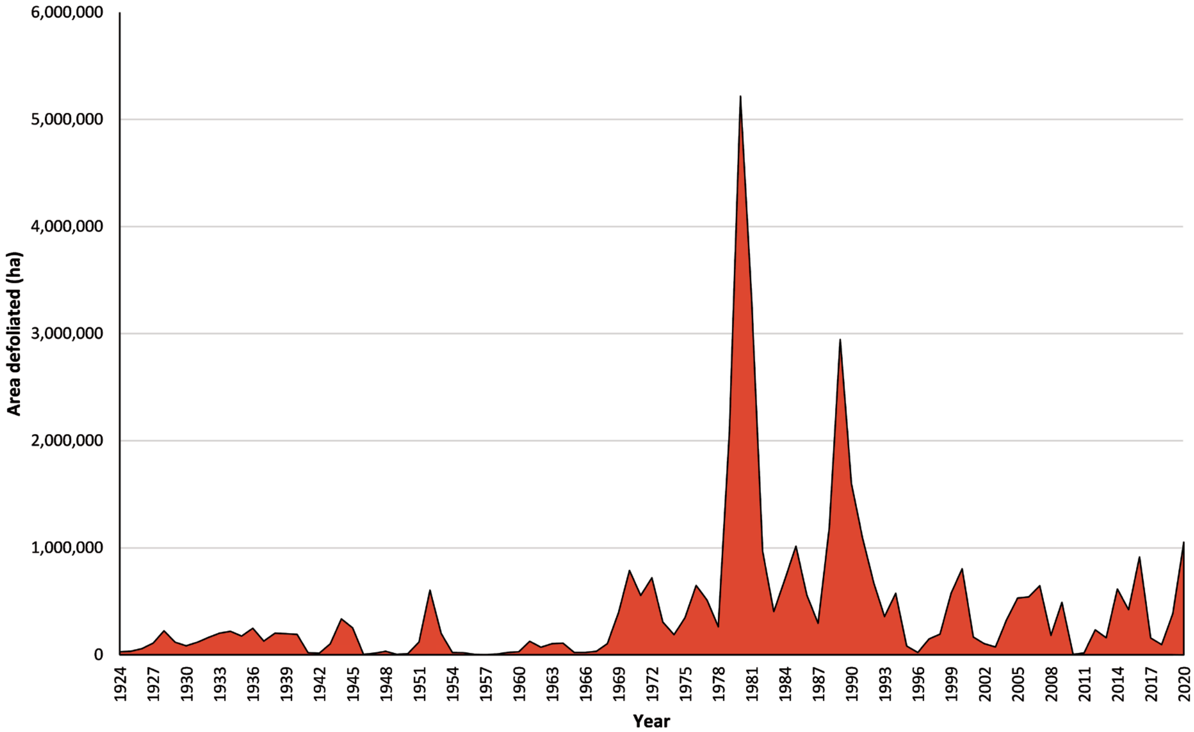

Figure 5.—*Lymantria dispar* defoliation mapped by detection surveys from 1924–2021 in the United States. Regional outbreaks occur every 5 to 10 years and commonly persist for 1 to 3 years.

Oak-hickory and oak-pine forest types represent optimal habitat for *L. dispar* outbreaks (Morin and Liebhold 2015) and those stands with 60 percent, 40 percent, or 15 percent of preferred host species represent high, medium, or low susceptibility to injury, respectively (Fig. 7) (Campbell 1974, Gottschalk 1993, Herrick and Gansner 1986). Many susceptible forest types located throughout the southern United States are still uninvaded (Liebhold et al. 1997). Leuschner et al. (1996) details the ecological and economic impacts on timber (e.g., reduced yield, increased rotation timing, decreased wood quality or negative changes in species composition, regeneration, or a combination of these factors); recreation (e.g., visits lost, postponed, substituted, or less enjoyable, as well as suppression costs and cleanup, removal, and replacement expenditures); and residential areas (e.g., suppression costs and cleanup, removal, and replacement expenditures) when the spread of *L. dispar* outbreaks are unmanaged.

Short-term changes in microclimate can result from moderate and severe defoliation, increasing temperature, light, nutrients, and moisture reaching the forest floor (USDA FS and APHIS 2012a). These changes can lead to subsequent increases in shrub and herbaceous cover (Gansner 1985, Hix et al. 1991, McEwan et al. 2009). Water quality can be affected by increased runoff and direct contamination from the deposition of frass, but these changes are typically short-lived (Smith-Tripp et al. 2020, USDA FS and APHIS 2012a). Tree injury and mortality to oaks can affect mast production for animals that rely on acorns for food but increase the availability of nesting and foraging resources for several bird species that utilize snags and dense shrub cover (Showalter and Whitmore 2002).

Figure 6.—Tree mortality as a result of consecutive years of severe *Lymantria dispar* defoliation and consecutive years of drought that impacted several states from 2015 to 2017 in the northeastern United States. In the image, oaks (*Quercus* spp.) experienced the highest levels of injury and mortality. (Photograph by K. Dodds, USDA Forest Service)

Presence of outbreak populations can lead to aesthetic and nuisance concerns and health issues due to the densities of caterpillars often aggregating on structures, the presence of frass raining down from defoliated trees, caterpillars falling from the canopy, and injury and mortality of trees. Aesthetic and nuisance concerns commonly arise in public parks and recreational areas in forested communities where tree cover is abundant. Nuisance and defoliation were the primary concerns noted by private landowners and land managers in the northeastern United States during *L. dispar* outbreaks (Moeller et al. 1977). Dense, late-instar caterpillar populations are very noticeable and apparent and can cause stress and anxiety to the public. Furthermore, skin contact with hairs from the caterpillar can cause wheals and rashes, leading to severe itching and allergic reactions that may require medical treatment (Gooderham et al. 2021, Marshall 1981, Montgomery and Wallner 1988).

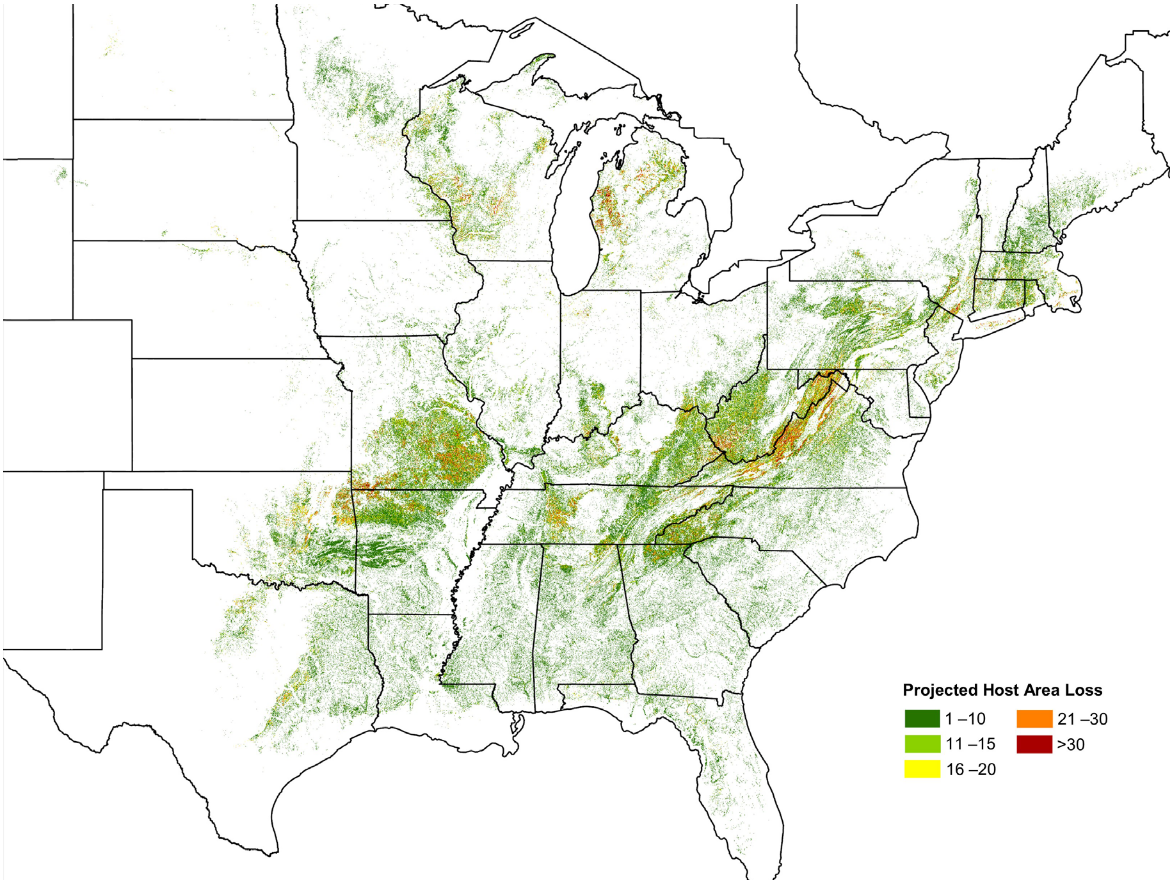

Figure 7.—Forest stands at risk (percent host basal area loss) to *Lymantria dispar* injury in the eastern United States. Risk data was developed by Krist et al. (2014) for the 2013–2027 National Insect and Disease Risk Map. Uninfested areas in the southern United States represent widespread risk to *L. dispar,* but regions of the Cumberland Plateau, Southern Appalachian Mountains, and Ozarks possess the highest risk (>30% basal area loss).

MANAGEMENT STRATEGIES

Numerous management strategies, including intensive monitoring, biological control, physical control, cultural control, and chemical control were used in the early 1900s to reduce the rate of spread and impact of *L. dispar* in the United States (Forbush and Fernald 1896, McManus and McIntyre 1981, USDA FS and APHIS 2012a). McManus (2007) provides a detailed timeline of *L. dispar* events from 1869 to 2005 in the United States. The initial eradication and New York barrier programs in the late 19th and early 20th century relied heavily on ground and aerial chemical applications, including copper acetoarsenite, lead arsenate, dichorodiphenyltrichoroethane (DDT), and carbaryl to suppress outbreaks (Fig. 8) (Liebhold and McManus 1999, White et al. 1981). Early efforts of cultural and physical control focused on the destruction of egg masses by removing and burning them, pouring boiling water on them, or treating them with creosote (Fig. 8). Infested trees and shrubs were also burned (Forbush and Fernald 1896). Trees were banded with burlap skirts to trap larvae moving up and down trees, and caterpillars found under the bands were killed daily. Egg mass counts, burlap bands, and primitive pheromone traps (baited with live, caged females) were used to monitor the presence and density of populations (Forbush and Fernald 1896, Kolodny-Hirsch 1986). The U.S. Civilian Conservation Corps

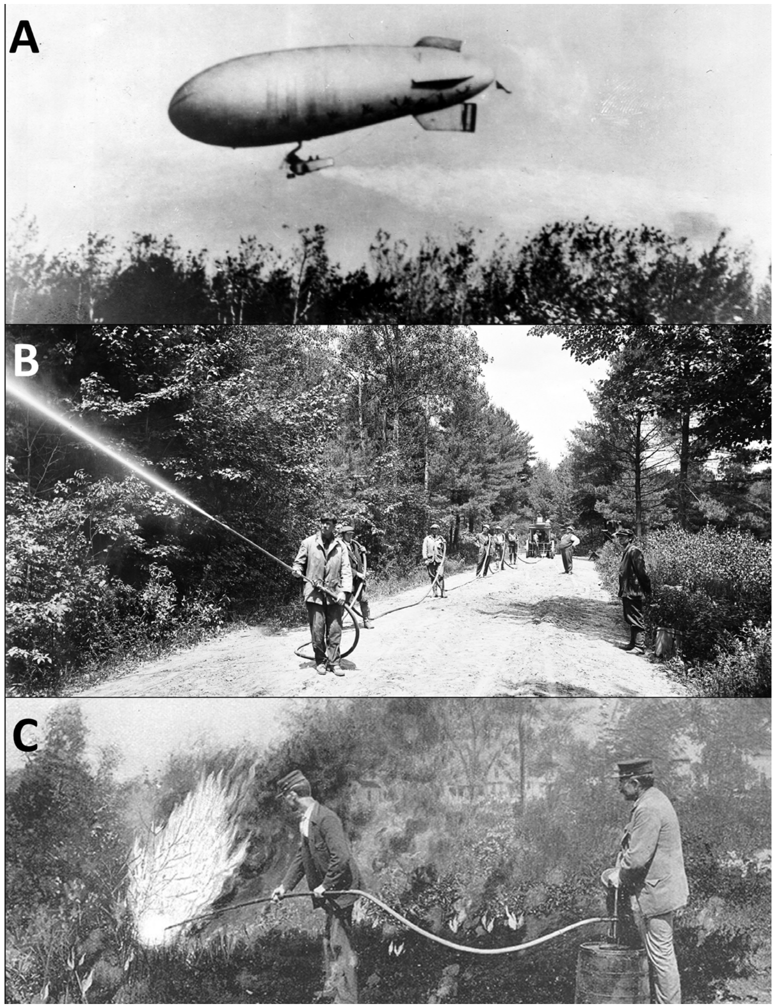

Figure 8.—Aerial applications were used to suppress *Lymantria dispar* populations with an U.S. Army blimp following World War I in New Hampshire (A). Arsenate of lead was used to treat the populations. Ground applications were also utilized to treat (B) and destroy (C) populations. (USDA archive photographs)

provided labor for much of these management activities in the 1930s and 1940s, which made such tedious tasks feasible (Fig. 8).

The identification of the *L. dispar* sex pheromone [cis-7, 8-epoxy-2-methyloctadecane (disparlure)] significantly enhanced monitoring techniques, which initially used caged female moths or crude extracts from the tip of female abdomens (Bierl et al. 1970, Forbush and Fernald 1896). Subsequently, the plus enantiomer or (7R,8S)-cis-7,8-epoxy-2-methyloctadecane [(+)-disparlure] was shown to possess exclusive and elevated attractiveness to male *L. dispar* in North America (Cardé et al. 1977, Plimmer et al. 1977). The synthetic sex pheromone and use of delta and milk carton traps are invaluable for detecting newly established, low-density populations and directing treatment decisions for eradication efforts.

During the early 1990s, 34 species of parasitoids and predators were released in classical biological control programs (Blackburn and Hajek 2018, Elkinton and Liebhold 1990, Fuester et al. 2014, Reardon 1991). However, only 12 species have established, and their impacts on *L. dispar* population dynamics are not clear (Fuester et al. 2014, Kenis and Lopez Vaamonde 1998). As a result, and because virtually all of the good candidate agents have already been introduced, classical biological control options have been abandoned. At least one of the parasitoid species introduced during these early programs, *Compsilura concinnata* Meigen (Diptera: Tachnidae) is polyphagous and utilizes other Lepidopteran species as hosts, which may have adverse impacts on populations of some of these species (Blackburn and Hajek 2018, Elkinton and Boettner 2012).

Environmental concerns in the 1950 and 1960s led to changes in forest pest management tactics and the development of integrated pest management (IPM) strategies and utilization in *L. dispar* management programs over the next two decades. In the early 1970s, the need for *L. dispar* management intensified because the moth's range increased dramatically and caused defoliation over approximately 809,000 hectares (McManus 1978). Collectively, two research programs, the Accelerated Program (1971–1974) and USDA Expanded Gypsy Moth Management Program (1975–1978), focused on the following goals (Doane and McManus 1981):

- developing and evaluating the synthetic sex pheromone and microbial controls for suppression and eradication
- increasing foreign exploration for classical biological control and evaluating effectiveness
- refining population prediction models, sampling methodology, and impact assessments
- evaluating *L. dispar* NPV testing and registration and evaluating new chemical insecticide candidates
- assessing sterile male release techniques
- developing mass rearing protocols

These programs benefited from cooperative studies that involved the USDA Forest Service (USDA FS), the USDA Agricultural Research Service, the USDA Animal and Plant Health Inspection Service (USDA APHIS), the Cooperative State Research Service, universities, and state agencies.

The Expanded Gypsy Moth Management Program was part of the Combined Forest Pest Research and Development Program, which also addressed research gaps for the Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough) (Lepidoptera: Erebidae), in the Pacific Northwest and southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae), in the southeastern United States.

From the early 1970s through the late 1980s, chemical applications for suppression of outbreak populations relied on organophosphate (trichlorfon) and carbamate (carbaryl) insecticides for suppression of *L. dispar* outbreaks (Liebhold and McManus 1999, USDA FS 2021b, White et al. 1981). Insect growth regulators became a viable option for *L. dispar* management in the late 1970s. Diflubenzuron, a chitinase inhibitor, was used heavily from the early 1980s to the early 2000s in state and federal *L. dispar* suppression projects, whereas tebufenozide, which disrupts molting, has been used more predominately since 2013. Tebufenozide is typically favored more than Diflubenzuron in applications because it has fewer non-target impacts and is less toxic to aquatic invertebrates (USDA FS and APHIS 2012a).

Biopesticide options for *L. dispar* began to flourish in the 1980s. In 1980, *Bacillus thuringiensis* var. *kurstaki (Btk),* a naturally occurring soil bacterium, was first used as a microbial biopesticide and has been used continuously since 1980 for state and federal suppression and eradication projects (Fig. 9) (USDA FS 2021). Its effectiveness at suppressing high population densities of *L. dispar* along with its limited non-target effects (i.e., only impacting caterpillars that ingest the bacteria), and short environmental persistence (less than 1 week), make *Btk* an excellent management tactic (USDA FS and APHIS 2012a). Since the 1980s, it has been the most widely used *L. dispar* larvicide in government-administered operations (Hajek and Tobin 2010, USDA FS 2021b).

Lymantria dispar NPV is hypothesized to have been unintentionally introduced to North America in the early 1900s with parasitoids introduced for classical biological control (Howard and Fiske 1911). The virus spreads when larvae ingest viral bodies on leaves or the egg surface after eclosion. Like other NPVs, the effect on caterpillars depends on density: the virus spreads easily through high-density populations and impacts early instar larvae and late instar larvae within a year (Blackburn and Hajek 2018). Caterpillars infected by NPV can be found hanging dead by their abdominal prolegs, creating an inverted V shape with their limp body (Blackburn and Hajek 2018). The infected caterpillar eventually ruptures, raining viral particles on plant material below. Nucleopolyhedrosis virus is specific to *L. dispar* and has been formulated into a microbial biopesticide, Gypchek (Podgwaite 1999). Gypchek has been used in government management programs since the late 1980s (USDA FS 2021b) and is predominantly used in treatment applications where sensitive, threatened, or endangered Lepidoptera species are present because its impacts are limited only to *L. dispar.* Gypchek is not commercially available and is only used in treatment operations sponsored by the Forest Service. The product is costly and time-intensive to produce because it requires the mass rearing of NPV-infected caterpillars. *Lymantria dispar* NPV and *Btk* applications are most effective

Figure 9.—*Bacillus thuringiensis* var. *kurstaki (Btk)* applications for *Lymantria dispar* in western Virginia. Double applications of *Btk* are commonly used for slow the spread and eradication treatments. (Photograph by T.W. Coleman, USDA Forest Service)

when targeting first and second larval instars, whereas some insect growth regulators are more effective when treating older instar larvae (Coleman et al. 2020).

The fungal pathogen *E. maimaiga* is widespread in Japan, where it is an important mortality agent in *L. dispar* populations (Hajek et al. 2021). It was introduced to North America in 1910 or 1911 but never detected. However, in 1989 it was found causing high levels of infections in *L. dispar* populations in Connecticut (Hajek 1999). The details on the introduction of this fungus remain unclear, but most likely it was inadvertently introduced from Japan sometime between 1979 and 1989. Following the initial emergence of *E. maimaiga* in southern New England in 1989, the fungus rapidly spread across the range invaded by *L. dispar* (Hajek et al. 1995, 2021). Cool, wet springs are highly conducive for spread and proliferation of *E. maimaiga* spores, and the fungus is density independent (Reilly et al. 2014). *Entomophaga maimaiga* is ubiquitous in the infested areas and often results in the collapse of *L. dispar* populations (Hajek et al. 2015). Infected caterpillars hang head down in a vertical position on tree stems and branches, facilitating the spread of two spore types that can either re-infect the current population or remain dormant in the soil for up to a decade (Blackburn and Hajek 2018).

The use of semiochemicals has been a fairly recent management option for *L. dispar.* In 1972, Beroza and Knipling proposed the use of pheromones to suppress mating. However, transforming this concept into a practical tactic required many years of methods development. Thorpe et al. (2006) and Onufrieva (2023, this report) outline the development and operational use of mating disruption for low density populations. Hercon® Disrupt® II (Hercon Environmental, Emigsville, PA) was used predominantly in the National Slow the Spread (STS) Program and its pilot program from 1995 to 2017 (USDA FS 2021b). SPLAT GM and SPLAT GM-Organic (ISCA Technologies, Riverside, CA) was subsequently developed and used operationally from 1998 through the present (Coleman et al. 2023, this report page 45; USDA FS 2021b).

Silvicultural control has been implemented on public and private lands, but in recent years it has not been an area of focus for forest management on federal lands. The lack of silvicultural control may be attributed to the success of slowing the rate of spread of *L. dispar* at the advancing front and the changing management objectives on public lands. Gottschalk (1993) recommends silvicultural prescriptions that focus on reducing stand susceptibility and host vulnerability by increasing stand vigor, removing trees most likely to die, reducing *L. dispar* habitat and susceptible hosts, improving predator and parasitoid habitats, and regenerating stands that are close to maturity or understocked. Additional management options that have been considered but deemed ineffective, too costly, or inappropriate for large-scale integrated pest management (IPM) programs include inherited sterility or sterile insect technique, entomophagous nematodes, microsporidia, phytochemicals, and systemic insecticides (Doskotch et al. 1981, Kononchuk et al. 2021, Reardon et al. 1993, White et al. 1981, Xu et al. 2021).

Recent work on new *L. dispar* and *L. dispar asiatica* suppression tactics have focused on either gene silencing with RNA interference (RNAi) or DNA insecticides that block anti-apoptotic genes as biopesticides (Ghosh and Gundersen-Rindal 2017, Nyadar et al. 2016, Oberemok et al. 2019, Oberemok and Nyadar 2015, Oberemok and Skorokhod 2014, Wen et al. 2020). RNAi and DNA insecticides have the benefit of being potentially more species-specific to *L. dispar* than *Btk* and bypass resistance to insecticides and biopesticides (Nydar et al. 2016, Oberemok et al. 2019). Uptake of RNAi by caterpillar feeding (continuously) and absorption in the midgut is likely a promising method for an effective control strategy (Nyadar et al. 2016). Fogging applications have been proposed for use with DNA insecticides to thoroughly cover late-instar larvae in Asia (Oberemok et al. 2019). Reductions in body weight and egg masses, impaired development, and mortality have been observed in RNAi laboratory studies (Ghosh and Gundersen-Rindal 2017, Nyadar et al. 2016, Sun et al. 2022, Wen et al. 2020), and larval mortality (~47 percent) has been reported in tests with DNA insecticides (Oberemok et al. 2019). Terenius et al. (2011) report that RNAi has had varying levels of success in Lepidopterans. However, neither of these biopesticides has been field tested against *L. dispar* because of production costs, concerns about non-target impacts, and complications with delivery methods (Nyadar et al. 2016, Oberemok et al. 2019).

PEST MANAGEMENT PROGRAMS

The U.S. Department of Agriculture has had an active role in managing *L. dispar* since 1906, when Congress appropriated funds to manage an outbreak in Massachusetts and fund exploration and importation of natural enemies for *L. dispar* control (Forbush and Fernald 1896, McManus 2007). Ever since the passage of the Plant Quarantine Act in 1912, the USDA has implemented a quarantine aimed at limiting the spread of *L. dispar* in the United States by regulating the movement of plant material (Liebhold et al. 1992). Since the early 1900s, two barrier zone programs were implemented in the northeastern United States to actively stop the movement of *L. dispar:* the Barrier Zone (1923–1941) from Canada to Long Island along the Champlain and Hudson River Valleys, and the Gypsy Moth Appraisal Program (1953–1958) along the Adirondack mountains in New York to the Allegheny Plateau (Fig. 10). The Maryland Integrated Pest Management Project (MD-IPM Project, 1983–1987) was established in the southern part of that state. The Appalachian Integrated Pest Management Project (AIPM, 1988–1992) was modeled somewhat on previous IPM strategies and implemented in the Allegheny Mountains in Virginia and West Virginia. The Slow the Spread Pilot Project (1992–1999) continued one of the objectives of the AIPM project—to slow *L. dispar* spread—and demonstrated that an area-wide strategy was cost effective. Finally, the National Slow the Spread (STS) Program began in 2000 and implemented this strategy across eight states—Indiana, Illinois, Michigan, North Carolina, Ohio, Virginia, West Virginia, and Wisconsin—to reduce the rate of spread of *L. dispar* along the leading edge of the infestation (Fig. 10).

Previous *L. dispar* IPM programs helped provide a solid foundation for the STS Program. The barrier zone concept utilized in 1923 in New York was effective at reducing the rate of spread of *L. dispar,* even though the zone became generally infested in 1939, and funding and treatments were eliminated in 1941 when the United States entered World War II (Liebhold et al. 1992). The 1923 Barrier Zone implemented practices that remain part of USDA's current National Spongy Moth Management program, where individual states treated populations east of the barrier zone (i.e., suppression), and state and federal agencies treated in the transition zone (i.e., slow the spread). The 1953 Gypsy Moth Appraisal Program, involving New York, Vermont, and Connecticut, was initiated to prevent additional spread and damage from *L. dispar* and relied heavily on the application of DDT. These applications were heavily criticized, notably by Rachel Carson in the book "Silent Spring," published in 1962. Ultimately, the environmental effects associated with DDT led to its elimination. The barrier zone became infested, and the program ended.

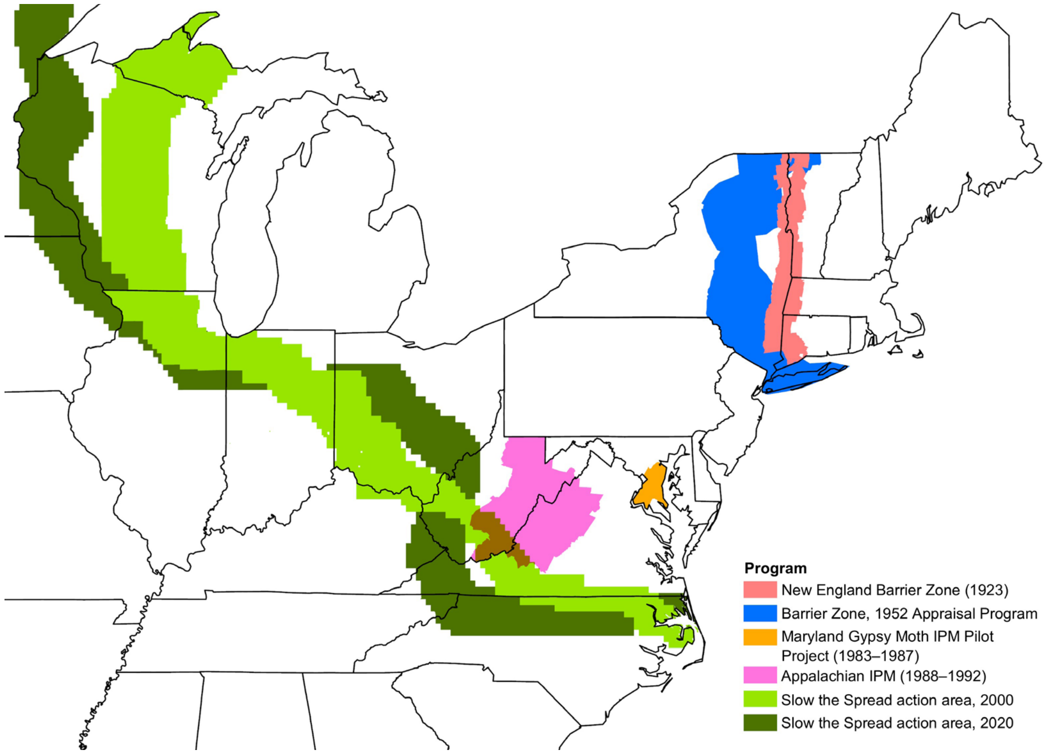

Figure 10.—Progression of *Lymantria dispar* management programs in the eastern United States. The program boundary from 2000 and 2020 for the National Slow the Spread Program highlights the success of the most recent integrated pest management program.

The two IPM programs that followed, the MD-IPM project and the AIPM project, initiated several activities that are still implemented in the STS Program. These include monitoring *L. dispar* populations along the leading edge with an extensive network of pheromone-baited traps, treating low-density *L. dispar* populations at a landscape scale with environmentally sensitive methods, and utilizing a centralized database to manage trap data and to inform land managers of potential trapping and treatment applications (McManus 2007, Reardon 1991, Reardon 1996, Reardon et al. 1993).

Maryland Integrated Pest Management (MD-IPM) Project

The MD-IPM Project was a five-year cooperative pilot project to determine the feasibility of managing *L. dispar* populations using an IPM approach over a diverse landscape (Reardon et al. 1993). The MD-IPM project was also used as a comparison to Maryland's current Gypsy Moth Cooperative Suppression Program. A project coordinator and technical committee were appointed to direct the project and develop a five-year plan, which was implemented by federal, state, county, and local agencies and organizations. The average annual budget for the MD IPM program was $441,200 and supported full-time (three entomologists) and seasonal staff (15 to 25 employees).

The program managed low- (<62 egg masses/0.4 ha) to moderate-density (<617 egg masses/0.4 ha) *L. dispar* populations in a 20,234 ha area that spanned five Maryland counties (Anne Arundel, Calvert, Charles, Howard, and Prince George's). Pheromone-baited milk carton traps monitored at 1 km grids, egg mass surveys in 1 km^2 cells, and tree banding provided population data, yearly trends, and phenological data. The project utilized decision making criteria (e.g., no action, preventive action, and suppressive action) to direct intervention techniques that relied on egg mass and male moth densities and trends, size and proximity of the infestation to other infestations, stand susceptibility, percent defoliation, environmental sensitivity, social and economic value, and land use (Reardon et al. 1993). Various techniques were tested or implemented alone or in combination with other techniques in the MD-IPM project, including ground (individual tree and broadcast applications) and aerial (*Btk,* Gypcheck) treatment techniques, inherited sterility (i.e., sterilized male and F1 sterile egg mass releases), ground applied mating disruption [i.e., Hercon® Luretape® GM (Hercon Environmental, Emigsville, PA)], augmentative and classical biological control with parasitoids and entomogenous nematodes, insect growth regulator (e.g., Diflubenzuron), contact insecticides (e.g., Bendiocarb), and systemic insecticides. Life stage and various other stand-specific data were used to evaluate treatment efficacy. Database management for the project was hosted at Virginia Polytechnic Institute and State University (VT), Blacksburg, Virginia, and VT staff assisted the decision-making process by developing computer-aided maps with population trend and density data. The MD-IPM project treated 3,203 ha (IPM area: 2,465 ha, comparison area: 739 ha) and 17 isolated, heavily infested individual trees during the five-year period using eight treatment methods. The majority of the treated area utilized aerial applications of *Btk* (Table 1). However, low population densities in both the IPM area and a comparison treatment area did not allow an efficacy assessment of the IPM work. Nevertheless, the program was instrumental for developing and testing biopesticides (*Btk* and Gypchek) against *L. dispar* because it demonstrated that an IPM program was feasible over a diverse landscape and provided the prototype for the AIPM Project.

Appalachian Integrated Pest Management (AIPM) Project

With support from Congress, the 5-year AIPM Project was implemented across 20 counties in West Virginia and 18 counties in Virginia, encompassing approximately 5.19 million hectares and playing a crucial role in the development of the framework ultimately adopted by the STS Program. Among its innovations, the AIPM program applied varying decision-making practices among different monitoring zones that were established to align with varying moth capture levels and management objectives. Decision-making tools helped guide trapping and treatment activities, and geospatial tools were developed to manage low-density populations (Reardon 1991).

The AIPM Project was established along the leading edge of the *L. dispar* invasion with four objectives: (1) to minimize the spread and adverse effects in the *L. dispar* project area; (2) to develop a prototype IPM structure consisting of standardized sampling protocols, decision matrices for intervention activities of low-level *L. dispar* populations, computer based geographical information systems (GIS), and an educational program; (3) to continue the development of intervention activities for the management of isolated low-density infestations; and (4) to assess the feasibility of implementing a coordinated federal and state program over a large area (Reardon 1996).

The project area was divided into four monitoring areas that spanned heavily infested areas (>500 male moths/trap) to low-density areas (<10 male moths average/trap), with each zone possessing its own intervention tactics. State and federal agencies monitored pheromone-baited traps at either a 2 or 3 km base grids, with delimiting surveys at smaller grids, and surveyed forest stands to assess defoliation and egg mass densities.

Table 1.—Treatment accomplishments from previous *Lymantria dispar* integrated pest management (IPM) programs

Project	Treatments	Area treated
A. MD-IPM Project (1983–1987)	Aerial application of *Bacillus thuringiensis* var. *kurstaki (Btk)*	2,342
	Aerial application of *Btk*/parasite release	768
	Ground application of *Btk*/Hercon® Luretape®	74
	Parasite release	2
	Aerial application of Diflubenzuron	14
	Ground application of Gypchek	4
	Ground application of Bendiocarb	0
	Ground application of Diflubenzuron	0
Total treated		**3,204**
	mean cost/trap: $13.35	
	mean *Btk* cost/0.4 ha: $62.07	
	mean Hercon® Luretape® cost/0.4 ha: $155.67	
	mean egg mass survey cost/0.16 ha: $7.00	
B. AIPM Project (1998–1992)	Aerial application of *Btk*	123,172
	Aerial application of Diflubenzuron	113,898
	Aerial application of Gypchek	2,648
	Aerial application of mating disruption	7,887
Total treated		**247,605**
C. STS Pilot Project (1992–1999)	Aerial application of *Btk*	58,386
	Aerial application of Diflubenzuron	1,412
	Aerial application of Gypchek	1,805
	Aerial application of mating disruption	28,594
Total treated		**90,196**

Notes: Data was compiled from Reardon et al. (1993), Reardon (1996), and VT (2021). Cost information for the MD-IPM Project was obtained from Reardon et al. (1993).

Project data (i.e., moth trap data, egg mass counts, defoliation data, proposed treatment areas, and forest cover types) were compiled in a geographical information system by VT to develop maps for project decision-makers and evaluate subsequent intervention methods (Liebhold et al. 1996). The AIPM Project focused suppression treatments on varying densities of *L. dispar* with aerial applications of *Btk*, Diflubenzuron, Gypchek, and mating disruption (Hercon® Disrupt® II) (Table 1). Reardon (1996) outlines the successes of the AIPM Project with technology development, evaluation of data, technology transfer, and their use in the STS Pilot Project.

Slow the Spread (STS) Pilot Project

As AIPM ended in 1992, the STS Pilot Project was initiated along the transition zone in 21 counties of Virginia, North Carolina, and West Virginia, and three counties in the Upper Peninsula of Michigan. The goal of the pilot program was to demonstrate that new and current technology could slow the rate of spread of *L. dispar* populations; assess the technological, economic, ecological, and environmental viability of implementing an operational STS program; and implement a plan for integrating STS technology into a national strategy for *L. dispar* management (McManus 2007). With an overall goal of reducing the rate of spread of *L. dispar* by approximately 50 percent, the pilot project had a mean annual funding of $2,678,636 (±643,454) for data available from 1993 to 1995. State and federal agencies along with a newly formed steering committee would implement the project, whereas a technical committee comprised of state, federal, and university scientists would provide expert recommendations (McManus 2007). Pheromone-baited traps were deployed in 1 km base grids with delimit-trapping at 250 m and 500 m grids in a 100 km wide action zone and in an adjoining evaluation zone. A centralized database remained at VT. During the pilot project, increases in federal funding allowed for an increase in treatment hectares, supporting the feasibility of a national program. Applications of *Btk,* Diflubenzuron, Gypchek, and mating disruption (Hercon® Disrupt® II) comprised the treatments, totaling 90,196 ha (Table 1). Continued spread and outbreaks of *L. dispar* threatened oak forests in the southern United States and provided justification for a *L. dispar* containment program. In 1995, federal agencies developed a memorandum of understanding to define responsibilities for the program; this document has since been updated but still directs *L. dispar* management in the United States (USDA FS and APHIS 2012a, 2012b). The USDA National Spongy Moth Management Program has provided a national strategy comprised of four components—suppression, slowing the spread, eradication, and regulatory—to reduce the rate of spread and lessen the impact of *L. dispar* (USDA FS and APHIS 2012b). A cost-benefit ratio of 2.78 for one-time impacts and 21.60 for yearly impacts for reducing the rate of spread by 60 percent justified the *L. dispar* containment strategy across the entire transition area for a national program (Leuschner 1991, Leuschner et al. 1996).

During the pilot program, Sharov and Liebhold (1998) conducted a study using a mathematical model to predict the efficacy of the STS Program. The spatially explicit model described spread via stratified dispersal (i.e., formation of isolated populations ahead of the invasion front that grow and coalesce). They parametrized the model for *L. dispar* spread using trap data from the AIPM and STS Pilot Project and predicted that a 100 km action area (where isolated populations are identified and treated) would cause a 54 percent reduction in spread, which closely approximated the observed 59 percent reduction in spread during these programs. These results, along with the economic analyses by Leuschner et al. (1996), provided further evidence that the STS strategy is viable and established a scientific basis for the program.

National Slow the Spread (STS) Program

The National STS Program was formally adopted in August 2000 with an updated goal of reducing the rate of *L. dispar* spread by 60 percent (from an unrestricted rate of spread of 19.6 km/yr to less than 7.8 km/yr). The steering committee of the pilot project was replaced with a board of directors and a non-profit foundation, the Slow the Spread

Foundation (Leonard 2007). Coleman et al. (2023, this report page 28) outline the roles of the three committees (operations, regulatory, and technical) and the general structure and workflow of the national program.

For 20 years, the National STS Program has successfully achieved its goal (Coleman et al. 2023, this report page 45), and the program represents one of the largest and most comprehensive IPM programs in the world (Liebhold et al. 2021). Sills (2008) compared the benefits of the reduced rate of spread and additional management and quarantine costs when *L. dispar* reaches outbreak populations, estimating a cost-benefit ratio at 1-to-3 for the STS Program and a net present value of $21 to $33 million from 2006 to 2026, depending on which benefits were included. A similar economic analysis conducted in British Columbia, Canada, determined that the expected annual benefits of a prevention program in the province ranged from 3.4 to 8.3 times the annual estimated cost of the program (Sun et al. 2019).

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Chapter 2

Coordination and Framework of a National Integrated Pest Management Program for *Lymantria dispar*

Tom W. Coleman, Christopher J. Foelker, and H. Mannin Dodd

Abstract

The National Slow the Spread (STS) Program represents the largest strategy to limit the impacts of the exotic spongy moth, *Lymantria dispar* L. (Lepidoptera: Erebidae, formerly known as the "gypsy moth"), in the United States. The STS Foundation, a non-profit organization, state and federal agencies, and university partners work collaboratively in three committees (operations, regulatory, and technical) to reduce the rate of spread of *L. dispar.* Since 2000, state agencies and the U.S. Department of Agriculture (USDA) Forest Service annually plan and implement trap and treatment activities, coordinating work through the non-profit foundation and gaining approval from the board of directors. Trap and treatment activities are planned and archived in a centralized database. From 2000 to 2020, mean annual funding directed to carry out trapping was $4.59 million, and $5.47 million was used for treatments.

Keywords: defoliator, geographical information system, gypsy moth, integrated pest management, invasive insect, spongy moth

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INTRODUCTION

The National Slow the Spread (STS) Program represents one of the longest running and most geographically expansive integrated pest management programs in the world (Sharov et al. 2002, Tobin and Blackburn 2007). The program's goal is to slow the rate of spread of spongy moth, *Lymantria dispar* L. (Lepidoptera: Erebidae, formerly known as the "gypsy moth"), by greater than 60 percent from its historical rate of spread (19.6 km/yr, an average of historical spread rates) in the United States (Liebhold et al. 1992). The Slow the Spread Foundation, a non-profit foundation, together with 12 states, two federal agencies, and two universities, have contributed to the success of the program since its inception in 2000. These groups work collaboratively throughout the year under the structure of three committees to successfully meet the goals of the program. In addition, the Slow the Spread Information Systems Group (STS-ISG) manages a centralized database and develops and maintains planning tools, archives project information, and manages the Slow the Spread decision algorithm (STS DA). A key component of the program, the STS DA defines program boundaries, objectively identifies newly established isolated *L. dispar* populations in the transition area, recommends management actions, and evaluates treatment success and moth spread (Tobin and Sharov 2007, Tobin et al. 2007a). This paper describes the framework for the STS Program, the roles and timing of work in the three support committees, and the funding trends for the national program, with the intention that this information can be used as a guide for future integrated pest-management programs that incorporate multiple agencies and span large landscapes.

PROGRAM PARTICIPANTS AND STRUCTURE

The Slow the Spread Pilot Project (1992–1999) began with four state partners: Michigan (MI), North Carolina (NC), Virginia (VA), and West Virginia (WV). The pilot transitioned into the national program in 2000 with the addition of Illinois (IL), Indiana (IN), Ohio (OH), and Wisconsin (WI) (Fig. 1) (McManus 2007). Kentucky (KY) joined STS in 2001, followed by Minnesota (MN), Iowa (IA), and Tennessee (TN) as the program boundaries moved into these states (Leonard 2007). In 2011 Michigan exited from the program because the entire state was generally infested, and trapping for the evaluation zone moved out of the state. No new states have joined the program since 2013; however, South Carolina and Missouri could be the next states to join STS because of their proximity to the program boundaries and *L. dispar* spread.

The program commonly separates the partnering states into three regions (southern, central, and northern) based on their similar land use and host composition. These regions also share similarities in spongy moth phenology and in how STS is implemented. The southern region is comprised of Kentucky, North Carolina, Tennessee, Virginia, and West Virginia; the central region is comprised of Illinois, Indiana, and Ohio; and the northern region is comprised of Iowa, Minnesota, and Wisconsin (Fig. 1). Across the three regions, Virginia, Ohio, and Wisconsin typically contain the majority of potential problem areas (PPAs), that is, isolated, low-density populations in the transition area (Tobin and Sharov 2007) and treatment blocks in the program, in part because the transition area bisects large areas in these states, where greater rates of spread can occur and because treatments tend to be aggressively implemented there. Although the STS Program is implemented uniformly across the three regions, variations in land cover, forest composition, and Allee effects (i.e., a decrease in per-capita fitness caused by a decrease in population size) cause some regions to treat populations more aggressively in the transition area. As such, the STS DA commonly does not recommend treatments for lower density populations (ca. five moths/trap) in the northern region; however local expertise encourages a more aggressive treatment approach than recommended by the STS DA, and catch or colony persistence indicates weaker Allee effects along the northern leading edge[1] (Tobin et al. 2007b, Whitmire and Tobin 2006).

The STS Foundation (comprised of a board of directors and an administrative officer) and three STS committees (operations, regulatory and technical) help coordinate the work of the program among state and federal agencies. The three committees work in close coordination with each other, and state and federal staff often hold multiple roles in each committee. The board of directors oversees the work of the operations and regulatory committees and coordinates their work through the STS Foundation.

OPERATIONS COMMITTEE

The operations committee represents the core decision-making in the STS Program; these decisions are planned and archived using the centralized STS database, which also facilitates summarization of trapping and treatment activities. The STS Foundation and federal and state partners comprise the operations committee and work closely together to meet the program's objectives.

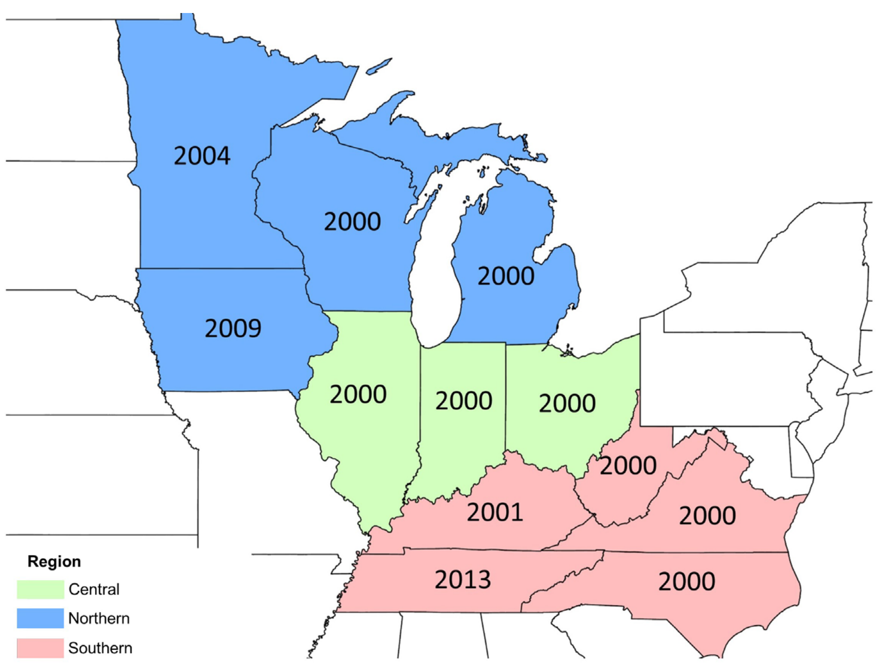

Figure 1.—State partners active from 2000 to 2020 in the National Slow the Spread Program. Years represent when each state joined the program. Michigan left the national program in 2011.

[1] See spread rates in Wisconsin, zones 2 and 3, in Coleman et al. 2023, this report page 45.

Slow the Spread Foundation

The framework for the STS Foundation, a non-profit organization, was structured similarly to the USDA Boll Weevil Eradication Program in the southern United States to address the cotton boll weevil, *Anthonomus grandis* Boheman (Coleoptera: Curculionidae). The primary function of the STS Foundation is to serve as the highest level of unified management across the member states, which solidifies ownership and accountability, promotes transparent planning and financial transactions, and standardizes operational materials and methods. The foundation has been staffed by one administrative officer since 2000, and the offices of president, vice-president/treasurer, and secretary have been filled by member states. The USDA Forest Service annually awards a grant to the STS Foundation early in the calendar year to support the trapping and treatment programs in each state, which the foundation distributes as subawards. Federal funding accounts for the majority of the program funding, and these funds are matched by state funding (Table 1). The administrative officer works closely with the STS program manager and the vice-president/treasurer for the STS board of directors to implement the trapping and treatment programs. The administrative officer awards subgrants to individual states for trapping and treatment work, submits grant and reimbursement requests, and maintains program files. Some participating states are unable to hire or contract trappers, in which case the STS Foundation directly contracts trappers and disperses payments after work is verified by state program managers. The foundation also manages grants for research and regulatory work, purchases the active ingredient for the mating disruption applications, supports spray calibration meetings, and reimburses travel for state cooperators. An outside accounting firm annually conducts an audit of the foundation's funds.

The STS board of directors is comprised of one person from each participating state, commonly the state's plant regulatory official or the state's STS program manager. Some states do not have a voting representative on the board due to state restrictions or limited involvement with the program. The president, vice-president/treasurer, and secretary are voted into office at the annual meeting of the board of directors (Table 1). At the annual meeting, the previous year's accomplishment report, the previous year's quality assurance-quality control (QA-QC) report, and the current year's plan of work are reviewed. The annual external audit report of the STS Foundation's expenses is also reviewed, along with other pertinent program issues from the USDA Forest Service (USDA FS), the USDA Animal and Plant Health Inspection Service (USDA APHIS), and the participating states. Conference calls are held monthly with the board of directors to inform members of recent program activities, budget allocations, and grant reimbursements, and to discuss new business topics.

State and federal STS collaborators plan and attend three meetings throughout the year to discuss program planning, annual accomplishments, aviation topics, and advancements in *L. dispar* research. These include a winter operations meeting, a summer operations meeting, and the Annual *Lymantria* Review Conference. The winter meeting reviews the previous year's accomplishment report, the current year's plan of work, and state and federal budgets. Coordination with the STS-ISG, advancements in trapping hardware and software, and trapping protocols are also planned and discussed at the meeting. The summer meeting provides an opportunity to review end-of-season accomplishments for all *L. dispar* treatments (i.e., states with suppression, eradication, and/or STS treatments); to discuss aviation issues, safety, and training; and to begin planning for next year's efforts. This meeting is planned by the National *Lymantria* Management Board (NLMB), which also plans the Annual *Lymantria* Review. The Annual *Lymantria* Review provides updates on recent research associated with *L. dispar* and other forest insect pests and an opportunity for the NLMB to meet and discuss recent activities.

Federal Cooperators and Roles

The USDA Forest Service has provided a National Program Manager, several entomologists, and technicians to support the annual work. These positions have been commonly stationed throughout the STS Program area (e.g., Asheville, NC; Morgantown, WV; and St. Paul, MN) to support participating states. The STS program manager coordinates annual trapping and treatment plans across all the states to meet current fiscal year funding levels. As the coordinator of this effort, the program manager procures annual trapping supplies from November to December from the USDA Animal and Plant Health Inspection Service through an interagency agreement (USDA APHIS places consolidated orders supplying both the STS Program and the *L. dispar* detection program in uninfested states) and then coordinates the delivery of traps, lures, and Dimethyl, 2, 3-dichlorovinyl phosphate insecticide strips in March to the states. USDA Forest Service funding supports the STS Foundation, the Information Services Group (STS-ISG) at Virginia Polytechnic Institute and State University (VT) and Michigan State University (MSU), and *L. dispar* technology development to improve trapping and mating disruption applications and increase our understanding of population spread (Onufrieva 2023, this report). The STS program manager plans and monitors the funding for each of these grants. USDA Forest Service entomologists and technicians have assisted the preparation and review of state environmental assessments for treatments in STS and routed these documents for approval. These positions also support mating disruption treatment planning, contracting, and applications and QA-QC for trapping. *Lymantria dispar* defoliation and treatment acres are tracked annually by the USDA Forest Service for suppression, eradication, and slow the spread projects (USDA FS 2021).

During the fall planning meetings, the program manager and state personnel review trap catches and PPAs from late September to early December to plan program boundaries, delimit-trapping grids, and treatment blocks for the upcoming year. These management decisions are guided both by the recommendations of the STS DA and by local expertise in each state (Table 1, Fig. 2). In the early years of the program, the STS program manager, database personnel, and support staff traveled to each state to hold annual fall planning meetings (Leonard 2007). These annual meetings became an integral part of the program planning and provided face-to-face interaction with state cooperators to plan the next year of work and were often referred to as “roadshow” meetings. As technology improved, these planning meetings were conducted by conference calls and in online meeting platforms.

Treatment blocks are commonly adjusted (i.e., treatment type changed, and/or blocks are reduced in size, deleted, or changed to a delimit-trapping grid) in several iterations to balance budget limitations prior to the STS board of directors meeting in mid-February. At that point, treatment blocks are finalized, and planning work transitions into a preparatory phase to implement the treatments. The STS program manager oversees the mating disruption applications under a USDA Forest Service contract. The applications are provided as a service to state treatment programs. The Forest Service contract was initiated in the early years of the program to develop and refine the application technology and to enhance coordination and standardization of the applications. It has been maintained as a federal contract to reduce the cost of applications by offering more work to contractors under a single contract (Appendix). The mating disruption contract must be awarded or renewed early in the calendar year (February to March) to meet Forest Service requirements (e.g., aircraft and pilot inspections/carding, aviation safety planning, and pre-operational planning meetings). Mating disruption applications commonly span from the first week of June to mid-July, with applications beginning along either the Atlantic Coastal Plain or piedmont of Virginia and North Carolina and ending in the northern regions of either Wisconsin or Minnesota near Lake Superior (Table 1).

Table 1.—Annual timeline of activities conducted by the partners, including state program managers and support staff (States), the Information Systems Group (STS-ISG), the STS program manager (PM), USDA Animal and Plant Health Inspection Service (USDA APHIS), USDA Forest Service (USDA FS), and *L. dispar* (Ld) private contractors/cooperators/researchers of the National Slow the Spread Program.

Activity	Timeline	Participants
Current season trap data finalized in STS database	Aug.–Nov.	States, STS-ISG
Review of trap catch data and pre-planning of next season's trapping and treatment work	Sept.–Dec.	States, PM
"Roadshow" planning meetings to discuss program boundaries, treatment blocks, delimit blocks, current issues	Oct.–Dec.	States, PM, STS-ISG
Annual *Lymantria* Review Conference	Early Nov.	States, USDA FS, Ld contractors/cooperators/researchers
Preliminary budget planning	Dec.–Jan.	States, PM
Winter Operations Committee meeting to review previous year's accomplishment report and discuss current season's actions and budgets	Mid-to-late Jan.	States, PM, STS-ISG
Technical Committee meeting to discuss knowledge gaps, review previous year's work, discuss and vote on new projects	Mid-to-late Jan.	States, PM, Ld researchers, USDA FS
Public scoping for treatment applications	Dec.–Apr.	States, USDA FS
STS Board of Directors meeting to finalize previous year's accomplishment report and current year's program of work, approve QA-QC report, review external audit	Mid-Feb.	Board of Directors, PM, USDA APHIS
Annual grants and treatment contracts awarded	Feb.–Mar.	States, PM, STS Foundation, STS-ISG, Ld researchers, USDA FS, USDA APHIS
Trap and treatment grants and research awarded to state programs	Feb.–Mar.	STS Foundation, States, Ld researchers
Preparation/review/approval of environmental analyses for treatment applications	Feb.–May	States, USDA FS
Larvicide applications	Apr.–May	States, Ld contractors
Trap placement, monitoring, quality assurance/quality control	Mar.–Oct.	States, Ld contractors
Mating disruption applications	June–mid-July	States, PM, USDA FS, Ld contractors
Summer Operations Committee meeting to discuss end of the year accomplishments, aviation issues, begin planning for next season	Early Aug.	States, USDA FS, Ld contractors

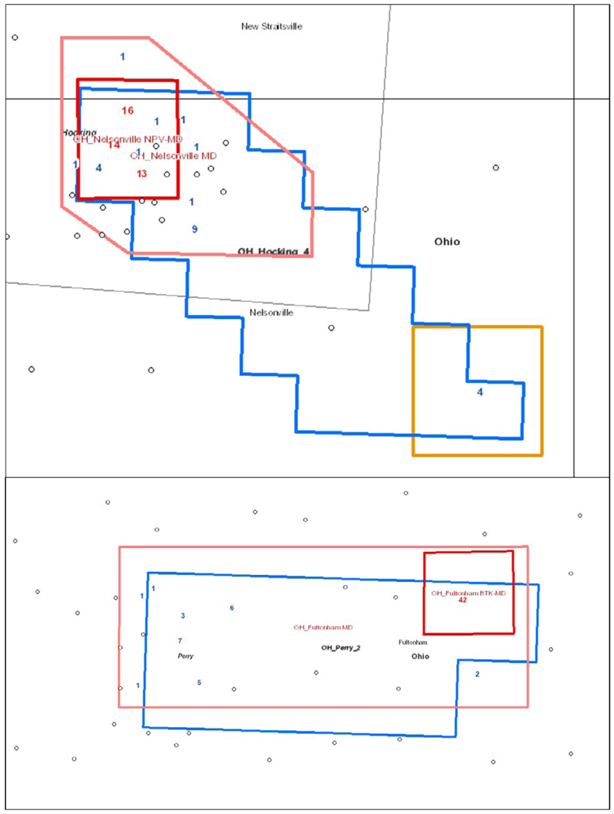

Figure 2.—Examples of delimit-trapping grids (yellow polygon) and larvicide (red polygons) and mating disruption (pink polygons) treatment blocks planned around *Lymantria dispar* trap catches (numbers and white circles represent zero trap catches) and potential problem areas (blue polygons) in the centralized database. The National Slow the Spread Program decision algorithm identifies isolated, low-density populations in the transition area as potential problem areas.

State Cooperators and Roles

In 2020, the STS Program partnered with 11 state cooperators, including several departments of agriculture (IA, MN, NC, OH, VA, WV, and WI), two departments of natural resources (IN and IA), a state entomology office at the University of Kentucky (Lexington, KY), and a division of forestry (TN) (Fig. 1). Most state cooperators in STS are, or have been, representatives from department of agriculture offices due to their regulatory authority. The Michigan Department of Agriculture was a cooperator during the pilot project, but their participation was terminated early in the operational program because the *L. dispar* transition area moved out of their state. Even so, Michigan continues to assist the program by annually certifying the calibration of spray booms for aerial larvicide applications, and a limited amount of *L. dispar* trapping still occurs in the southern part of the state to assist population growth and spread models that are monitored by the STS-ISG.

State program managers direct the STS programs within their respective states with input and assistance from the national program manager and have two primary objectives: (1) to coordinate and implement state trapping programs and (2) to contract and implement larvicide pesticide applications for higher density *L. dispar* populations (>60 moths/trap or presence of immature life stages) and assist with mating disruption applications. Planning for trapping and treatment programs begins as early as October, soon after final trap catches are reviewed and finalized in the centralized STS database (Table 1). Following the recommendation of the STS DA and local expertise, each state delineates draft treatment and delimit-trapping plans in the database prior to a planning meeting with the national program manager (Fig. 2). Following completion of annual planning at the winter operations meeting in January, treatment blocks are finalized, and from December to April, state personnel solicit public comments for environmental assessments (Table 1). Public scoping for environmental assessments includes mailing landowners in and adjacent to treatment blocks (<1.6 km or less); press releases; local, county, state, and federal government mailings; public meetings; online and social media content; and discussions with local government officials. States submit environmental assessments from March to April to the USDA Forest Service for review and approval to satisfy National Environmental Policy Act of 1969 requirements for federal funding. State programs and aerial applicators also coordinate treatment blocks with local federal safety district offices of the Federal Aviation Administration for flight plans in congested areas.

To implement trapping and treatment activities, state programs typically receive federal funding from the STS Foundation early in the calendar year (February through April). Federal funding can support program staff, establish contracts for pesticide applications, and hire seasonal trappers (Table 1). State programs define trapping territories (i.e., bid units) from February to March in the centralized STS database, and seasonal trappers are hired and trained soon after this period. Trappers receive electronic trapping hardware (e.g., GPS, phones, and computer tablets) and trapping supplies (e.g., delta and milk carton traps, staplers, gloves, wire, lures, and pest strips) for the current field season and are required to upload trapping information to the centralized database regularly. The STS Program commonly employs approximately 175 seasonal trappers per year. Teachers, college students, retirees, outdoor enthusiasts, and state staff are commonly employed as trappers, and many return year after year. Trap placement begins in the southern region of the program by late March and can extend into July in the northern region of the program. Traps are retrieved from August to October across the range of the program. State program managers and lead trappers coordinate workloads, train new trappers, and conduct QA-QC of traps. State programs conduct annual QA-QC inspections of their trapping programs (at least 10 percent) in a year. Quality assurance-quality control for trap monitoring annually has met program expectations (Coleman et al. 2023, this report page 45), providing a constant and reliable data stream to plan and evaluate treatment programs (Table 2). The STS database provides an annual QA-QC report that is reviewed by the board of directors at their annual meeting.

State program managers solicit larvicide treatment contracts from January to April for the upcoming treatment season. State program managers possess operational control for all treatments blocks in the state and follow accepted guidelines for applications (Appendix). Larvicide contracts are awarded or renewed as early as March to ensure applications occur during the appropriate treatment application window (i.e., biowindow). Timing of work objectives varies across the program, with most work generally occurring first in the southern region, second in the central region, and last in the northern region as *L. dispar* phenology progresses over a season (Table 1). Work in higher elevations of North Carolina, Virginia, and Tennessee are typically delayed from other regions in the state to better align with *L. dispar* phenology.

REGULATORY COMMITTEE

The regulatory committee regulates, inspects, and educates public and private groups about *L. dispar* for the STS Program. The USDA Animal and Plant Health Inspection Service (APHIS) has funded regulatory activities in several STS states via the STS Foundation to increase industry and public awareness; to reduce the human-facilitated spread of *L. dispar;* to identify, monitor, and establish compliance agreements with high-risk facilities (e.g., lumber yards, nurseries, holiday tree lots); and to document and evaluate regulatory activities. This work represents the main focus of the regulatory committee activities in the STS Program. Since 2017, regulatory work has been focused in Illinois, Minnesota, Virginia, West Virginia, and Wisconsin. The committee is co-chaired by USDA APHIS and a state partner (Leonard 2007).

TECHNICAL COMMITTEE

The STS technical committee is made up of university, federal, and state personnel with experience in *L. dispar* biology and management, population ecology, biological invasions, and invasive species spread. The technical committee analyzes emerging issues, provides technical and expert information, and recommends changes to the program (e.g., changes to the STS decision algorithm) as well as annual technology development projects to the entire STS Program. The technical committee has been chaired by a USDA Forest Service scientist and a university scientist (Leonard 2007). Examples of projects supported by STS can be found in Onufrieva (2023, this report). The committee holds an annual technical meeting, usually in coordination with the operations' committee winter meeting.

CENTRALIZED DATABASE

A centralized STS database has been managed by STS-ISG, the information services group comprised of geospatial developers and information technology (IT) specialists, since the conception of the program in the Departments of Entomology at VT and MSU (Ziegler and Roberts 2007). Aspects of the database were initially developed during the Maryland Integrated Pest Management Project (MD-IPM), Appalachian Integrated Pest Management Project (AIPM), and STS Pilot Project, which were also managed by VT (MD-IPM and AIPM) and MSU (AIPM only). The STS-ISG develops and implements the STS Program's geospatial strategy and provides the foundation for all information management and product distribution. The STS-ISG provides development and operations support in the following functional areas: information technology infrastructure and data management, analytics and decision support, design and planning, field mobility and monitoring, and information sharing and collaboration.

Information Technology Infrastructure and Data Management

All STS trapping, treatment, analysis, and planning data are managed in ESRI (Redlands, CA) ArcGIS server geodatabases integrated with Oracle relational databases. These datasets of current and historical program data are shared through the STS ArcGIS Online (AGOL) organization (ESRI), which enhances cooperator access for sharing and editing STS data in a web environment. Over time, the information system resources required to support the STS Program's operations have increased, migrating from a single FTP server to a robust array of virtual servers and web hosts. This server array provides STS developers with development, staging, and production environments to allow for continuous integration and easier deployment of new features and applications. System administrators have created redundant backup and replication processes for the virtual servers and implemented strong security protocols and firewall rules to protect the server array. Program data continue to be collected, organized, and maintained in an Oracle relational database with the spatial components managed by ESRI's ArcGIS Enterprise software suite. Database managers maintain current versions of the database and geographic information system (GIS) software to allow developers access to the latest tools and environments. As commercial, off-the-shelf web GIS and mobile data collection applications have matured, STS-ISG has migrated most mapping and data visualization products to an ArcGIS Online system and developed a new trapping data collection workflow using the ArcGIS Collector mobile application. To take advantage of the centralized environment provided by ArcGIS Online, STS-ISG has migrated the STS website into two integrated ArcGIS Hub initiatives: one publicly available STS Program Hub and one password-protected STS Operations Hub (VT 2021).

Field Mobility and Monitoring

Trap location and catch information are the core of all STS data, providing input for analysis and mapping the spread of *L. dispar.* To facilitate trapping data collection in the field and provide QA-QC processes, the STS-ISG began developing a custom mobile software application (Trapper Gadget, G1) in 2002. Trapping software and hardware have been updated throughout the life of the STS Program to address advancements in technology and improve the user interface to reduce errors (Table 2). After trapping areas are finalized in mid-February (Table 1), the STS-ISG creates trap sites (nodes) and target circles (areas around each node where traps may be placed) for the coming season (Roberts and Ziegler 2007), and state personnel begin designing bid units (trapper territories) to apportion the trap placement and monitoring work within their state. Since the beginning of the national program, GIS software has been used to aid in the design and planning process. Initially paper maps were created and mailed to state cooperators ahead of in-person "roadshow" planning meetings. Next, STS-ISG developed custom GIS tools to facilitate planning data entry and validation, and state personnel used GIS software on their own computers to create trapping and treatment plans. The current version of the STS planning editor is a web-based GIS application that allows state and federal cooperators to plan activities without needing any additional software on their computers (Table 3). The STS-ISG has developed and maintained additional editing software (e.g., STS Bid Unit, Field Data Collector, Treatment Application Planning, and Regulatory Sites) to plan and implement the STS Program (Table 3).

Table 2.—Trapping software and hardware developed and updated by the Slow the Spread-Information Systems Group (STS-ISG) to facilitate the data collection of tens of thousands of traps monitored by the National Slow the Spread Program

Trapping Software	Year	Hardware and language
G1	2002	Pocket personal computer personal digital assistant (PDA), Visual C++
G2	2009	PDA, Javascript/HTML/CSS
G3	2014	Mobile devices (phones, tablets), C#.NET
External mapping support	2016	ArcGIS Collector (ESRI, Redlands, CA)
G4	2020	Mobile devices, collector for ArcGIS, supporting processes in C# and Python (piloted in 2019 and expanded to four states in 2020, and implemented program-wide in 2021)

Table 3.—Software developed and maintained by the Slow the Spread-Information Systems Group (STS-ISG) to facilitate the planning and implementation of the National Slow the Spread Program (STS)

Software	Purpose
STS Planning	Allows cooperators to create and update trapping and treatment grids and provides summary reports from a web-based GIS application
STS Bid Unit	Provides tools and reports to help design trapper territories and manage trapping work
Field Data Collector (mobile data-collection application)	Allows field personnel to record *L. dispar* life stage locations, local vertical hazards, and restricted areas associated with planned treatments
Treatment Application Planning (collection of applications, including military training routes and aeronautical charts)	Supports treatment program and aims to improve application safety
Regulatory Sites	Allows cooperators to manage their USDA Animal and Plant Health Inspection Service (APHIS) regulatory trap sites to be incorporated into the STS trapping workflow

Analytics and Decision Support

The STS-ISG maintains the STS decision algorithm (STS DA), which analyzes trap catch data and provides management recommendations, representing the foundation of the Program, (Tobin and Sharov 2007). The results of the STS DA analysis are used to plan the next season of work and are available as GIS layers in STS planning applications. Since 2007, the STS DA has been updated numerous times to address PPA updates; to integrate with the STS database and GIS layers; to re-write the computer language from ASP.NET to C#; to change STS regions from four to three; to develop a one region kriged (spatially interpolated) trap catch layer; to expand phenology analyses; and to develop a long-term spread rate and trap-based treatment evaluations.

PROGRAM FUNDING

One of the earliest challenges of the STS Program was the ability to expand the STS Pilot Project area to a larger, multi-state area. As a result, trapping and treatment programs increased during the latter years of the pilot program and at the beginning of STS to demonstrate that the program could function at a national scale. The pilot project demonstrated the feasibility of a national program, and a cost-benefit analysis helped support the national program (Leuschner et al. 1996).

In 2000, the National STS Program was launched and allocated \$8.3 million in federal dollars from the USDA Forest Service. Funding was increased to \$10 million in the first several years of the program and was earmarked by the U.S. Congress (Fig. 3). Total STS funding from 2000 to 2020 was \$238,171,952 with a mean (±SE) annual total funding of \$11,341,521 (±311,441). Total USDA Forest Service contributions were \$182,606,674 during this time, and state contributions totaled \$52,366,072. From 2000 to 2020, the mean annual federal funding allocated to STS was \$8,695,556 (±267,349), whereas the mean annual state funding during this same period was \$2,493,622 (±169,806). Peak federal funding occurred in 2004 at \$11 million (Fig. 3). Since 2011, federal funding has been in a general decline, with the lowest annual funding (\$7 million) allocated in 2018. Mean annual monitoring costs from 2000 to 2020 were approximately \$4.59 (±0.11) million, whereas mean annual treatment costs were \$5.47 (±0.29) million. Mean annual technical development and mean annual indirect costs were \$0.22 (±0.01) and \$0.94 (±0.04) million, respectively. Regulatory committee work has been supported annually by USDA Animal and Plant Health Inspection Service funds and had a mean annual funding level of \$208,300 (±25,651) (data obtained from 2000–2005 and 2017–2020).

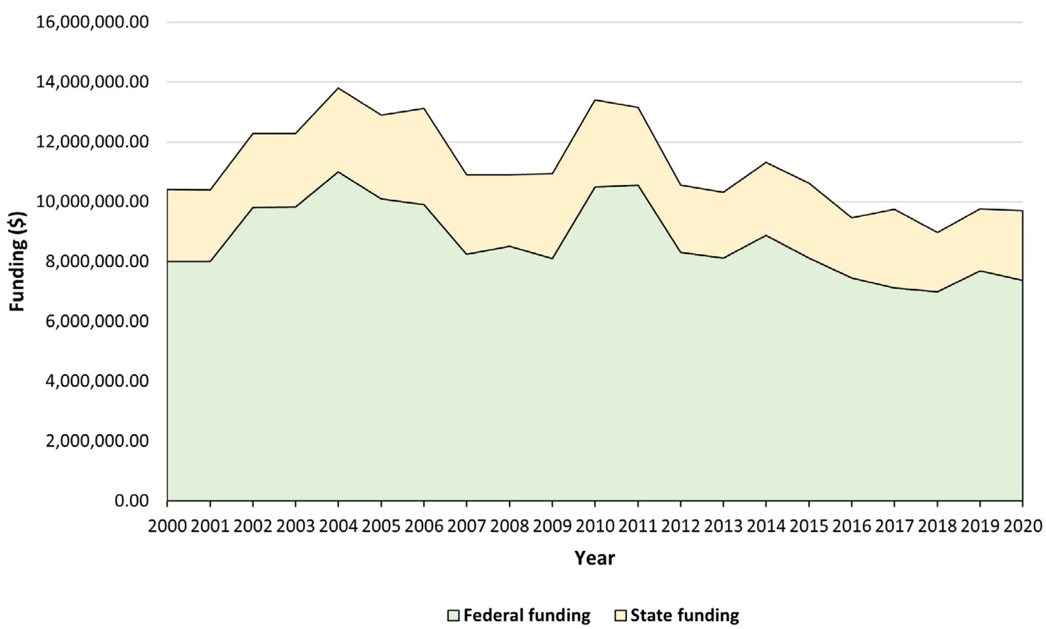

Figure 3.—Federal and state funding from 2000 to 2020 utilized for the National Slow the Spread Program.

The STS Program strives to balance federal funding between trapping and treatment programs, targeting an approximate 50:50 allocation. Generally, the program has succeeded in balancing this work (Fig. 4). For the comprehensive budget data available (2005–2020), trapping programs accounted for 44 percent (±0.84) of the annual program budget, database management accounted for 9 percent (±0.38), treatments accounted for 45percent (±1.19), and technical work accounted for 2 percent (±0.17) of the annual federal funding (Fig. 4). However, recent declines in federal funding and increased base program costs have shifted the program closer to a 60:40 allocation between trapping and treatment programs. In recent years, approximately $4 million has been required to fund the trapping program (i.e., state trapping programs and the centralized database), which is the foundation for all the program's work.

Delays in awarding annual federal funds to the STS Foundation continue to cause significant hurdles for the program, since *L. dispar* is an early-season defoliator. Annual budget planning numbers are needed by December, or as early as possible, to facilitate budget and environmental planning, initiate new grants, solicit contracts for trapping and treatment activities, and hire personnel. The general decline in federal funding primarily reduces the number and size of treatment blocks. Since 2018, 24,000 to 40,000 treatment hectares have been cut from the STS Program due to budget limitations. However, the program has still been able to meet its main objectives of reducing the rate of spread of *L. dispar* by greater than 60 percent (Coleman et al. 2023, this report page 45, VT 2021), thereby delaying the negative ecological and economic impacts associated with *L. dispar* outbreaks (Coleman 2023, this report).

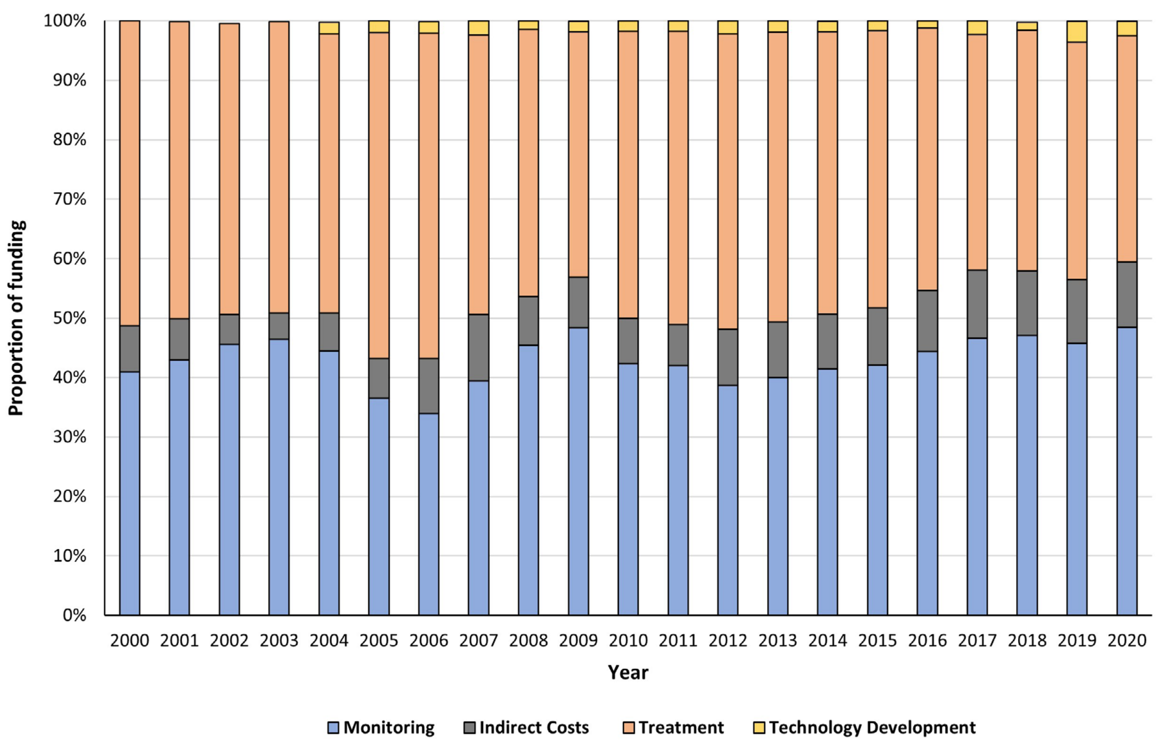

Figure 4.—Federal and state funding from 2000 to 2020 allocated to trapping and treatment activities, indirect costs, and technology development for the National Slow the Spread Program. The program has strived to maintain a 50:50 balance between trapping and treatment programs.

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APPENDIX

The following are standard protocols for implementing aerial applications for larvicide and mating disruption applications in the National Slow the Spread Program. The guidelines are updated and adapted from the Proposed Format for Technical Specifications for Aerial Application Contracts (AASC 2015).

	Treatment application	
Parameter	**Larvicide**	**Mating disruption**
Number of applications	1 or 2 (second application 7–10 days after first application)	1
Timing of application	Mix of 1st instars (50%) and 2nd instars (50%) for *Bacillus thuringiensis* var. *kurstaki* (*Btk*) and *Lymantria dispar* nucelopolyhedrosis virus (NPV, Gypchek) 3rd instars for Dilflubenzuron (Dimilin 4L) 1st to 3rd instars for Tebufenozide (Mimic 2LV)	7–10 days prior to moth flight
Temperature	<65° F [primarily for *Btk*]	No application <50° F
Humidity	Preferred >60% (primarily for *Btk*)	No specification
Swath width	Varies by aircraft; ranges from 100–150 ft for helicopter and 100–200 for fixed-wing aircraft	100 ft for fixed-wing aircraft
Spray height	50–100 ft above the forest canopy	100–200 ft above the forest canopy
Nozzles or application equipment	Rotary atomizers or flat-fan/hollow-cone nozzles	Specially designed application pods
Wind restrictions	No application >6 mph (primarily for *Btk*)	No application >20 mph
Droplet sizes (volume median diameter, VMD)	124–145 microns for *Btk* (Foray 48B) 80–100 microns for *Btk* (Foray 76B) 200 microns for Dilflubenzuron (Dimilin 4L) 200 microns for *Lymantria dispar* nucelopolyhedrosis virus (Gypchek) 100–125 microns for Tebufenozide (Mimic 2LV)	Droplets (SPLAT GM-Organic) ranging from 100 to >1,500 microns
Insecticides and standard doses	*Btk* (Foray 48B, 24 (2x applications) and 36 (1x applications) CLU/ac) *Btk* (Foray 76B, 25 CLU/ac) Dilflubenzuron (Dimilin 4L, 2 oz/ac), Tebufenozide (Mimic 2LV, 4 oz/ac) *Lymantria dispar* NPV (Gypchek, 33.3 g/ac)	Hercon® Disrupt® II (6 g and 15.2 g/ac) and sticker SPLAT GM-Organic (6 g and 15.2 g/ac)

Chapter 3

A 20-Year Synthesis of the *Lymantria dispar* Slow the Spread Program

Tom W. Coleman, Christopher J. Foelker, and Travis Perkins

Abstract

For 20 years, the National Slow the Spread (STS) Program has successfully slowed the rate of spread of the non-native spongy moth, *Lymantria dispar* L. (Lepidoptera: Erebidae, formerly known as the "gypsy moth"), to a mean rate of 2.6 km/yr, an 87 percent reduction from its historical rate of spread and surpassing the program's goal of a 60 percent reduction. Because the program has been so successful and the location of the population front has remained in the same general area, state partners have remained fairly consistent during the course of the program. Much of the program focuses on the use of pheromone-baited traps to locate isolated populations along the invasion front, to measure spread, and to adjust program boundaries annually. From 2000 to 2021, a total of >9 million male moths were captured. Annually, a mean of 730 new, low-density, isolated *L. dispar* populations (i.e., "potential problem areas") were detected in the transition area, but only 13 percent were recommended for treatment. The STS Program has treated >3.76 million hectares with mating disruption and larvicides. Ohio, Virginia, and Wisconsin represent the states with the greatest treatments. Mating disruption treatments accounted for 88 percent of the total treatment hectares. Treatment blocks intersected with federal lands and urban areas on 10 and 9 percent of the total hectares, respectively.

Keywords: *Bacillus thuringiensis* var. *kurstaki*, gypsy moth, integrated pest management, mating disruption, pheromone-baited trap, spongy moth

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Citation

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INTRODUCTION

Since 2000, a broad network of collaborators has implemented the National Slow the Spread (STS) Program to reduce the rate of spread of *Lymantria dispar* L. (Lepidoptera: Erebidae, or spongy moth, formerly known as the "gypsy moth") in the eastern United States (Fig. 1) (Sharov et al. 2002b). These collaborators include 12 state agencies, the U.S. Department of Agriculture, the USDA Forest Service (USDA FS) and Animal and Plant Health Inspection Service (USDA APHIS), university partners, and the Slow the Spread Foundation, a non-profit organization with a board of directors. The USDA National Spongy Moth Management Program incorporates four strategies to reduce to the impact of *L. dispar*; the STS Program is a key component of that national strategy. The 12 participating states comprise three regions [southern region: Kentucky (KY), North Carolina (NC), Tennessee (TN), Virginia (VA), and West Virginia (WV); central region: Illinois (IL), Indiana (IN), and Ohio (OH); and northern region: Iowa (IA), Michigan (MI), Minnesota (MN), and Wisconsin (WI)] to plan and implement STS trapping and treatment programs along the *L. dispar* transition zone (invasion front), which encompasses invaded and uninvaded areas. This paper synthesizes the history of the program boundaries, output from the STS decision algorithm (STS DA) that guides program boundaries and trapping and treatment activities, trapping and treatment accomplishments, and the rate of spread achieved by the STS Program. In instances where complete datasets were unavailable for the full duration of the program, summaries based on partial timelines are provided.

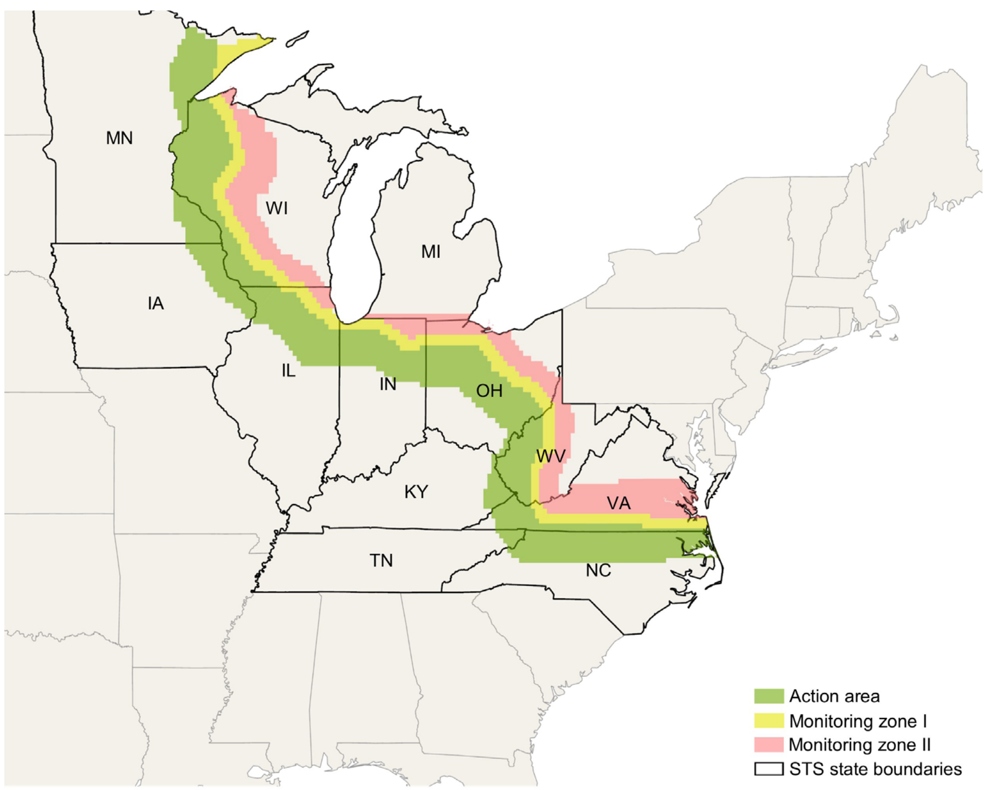


Figure 1.— State partners active in the National Slow the Spread Program in 2020 and the location of the program boundaries: the action area, monitoring zone I, and monitoring zone II.

PROJECT BOUNDARIES

Three distinct monitoring areas (action area, monitoring zone I, and monitoring zone II), each with a network of base trapping grids, comprise the STS project boundaries (Roberts and Ziegler 2007). The action area boundary shifts annually to stay approximately 10 km ahead of the 10-moth line (i.e., the boundary corresponding to where spatially interpolated values of trap capture equal 10 moths/trap) and along the leading edge of the uninvaded area (i.e., the transition zone). Both monitoring zones reside in quarantined, invaded areas. These base trapping grids are annually planned and implemented to detect new populations in the action area and to measure *L. dispar* population growth and spread in the monitoring zones. Additional trapping grids are monitored mostly in the action area to identify new populations, to delimit the extent of these new populations (for the purpose of planning for treatment boundaries), and to evaluate treatment efficacy. Slow the Spread trapping and treatment programs are concentrated in those states (IL, IN, OH, VA, WV, and WI) that reside in the proximal portion of the action area (80 to 100 km wide) (Fig. 2). These states also include a monitoring zone in the generally infested area, which is assessed at two base trapping grid densities: monitoring zone I (approximately 30 to 40 km wide with 5 km trap spacing) and monitoring zone II (approximately 40 to 50 km wide with 8 km trap spacing) (Fig. 2). The two monitoring zones are jointly referred to as the evaluation area. States in the distal portion of the action area (IA, KY, MN, NC, and TN) generally catch and treat fewer *L. dispar* populations because of the predominantly natural, short-distance spread [i.e., stratified dispersal model (Hengeveld 1989, Liebhold et al. 2007)] of *L. dispar* populations from generally infested areas. Due to the success of the program, the STS Program boundaries remain within most of the original state partners (IL, IN, NC, OH, VA, WV, and WI) (Fig. 2). The only state to exit the STS Program has been Michigan, which left when the transition area moved through the Upper Peninsula into northern Wisconsin. No new states have joined since Tennessee in 2013 (Coleman et al. 2023, this report page 28).

The National STS Program was initially implemented as optimized (Sharov and Liebhold 1998). At the start, implementation included a 100 km wide action area with a base trapping grid at 2 km spacing and a 70 km wide evaluation area with more widely spaced traps. In response to the first decline in federal funding of approximately $1.7 to $1.9 million (Coleman et al. 2023, this report page 28), the program responded by shifting the boundary between the action and evaluation areas to decrease the area included in the action area. The width of the action area was decreased to 90 km in 2007, 80 km in 2008, and back to 90 km in 2009, and the width of the evaluation zone was increased to reflect the lost width of the action area (Tobin 2008). These reductions reduced the total number of traps deployed and reduced overall costs (Table 1). In 2010, the action area width was expanded to the original 100 km because increased rates of spread were documented in the portions of the action area that had been excluded from treatment activities. From 2012 to 2013, when federal funding declined again, a different strategy was used. During that season, the base grid trap spacing in the action area was increased from a 2 km to a 3 km spacing (Table 1), but the wider trap spacing was ineffective for detecting newly established populations. As a result, in 2014 the base grid trap spacing was reverted to 2 km in the proximal 50 km of the action area and 3 km in the distal 50 km to facilitate detecting new populations and to address increasing monitoring costs. Ultimately, the 50:50 split of the base grid trap spacing has eliminated approximately 15,000 traps in the action area, saving the program approximately $1.17 million annually in monitoring

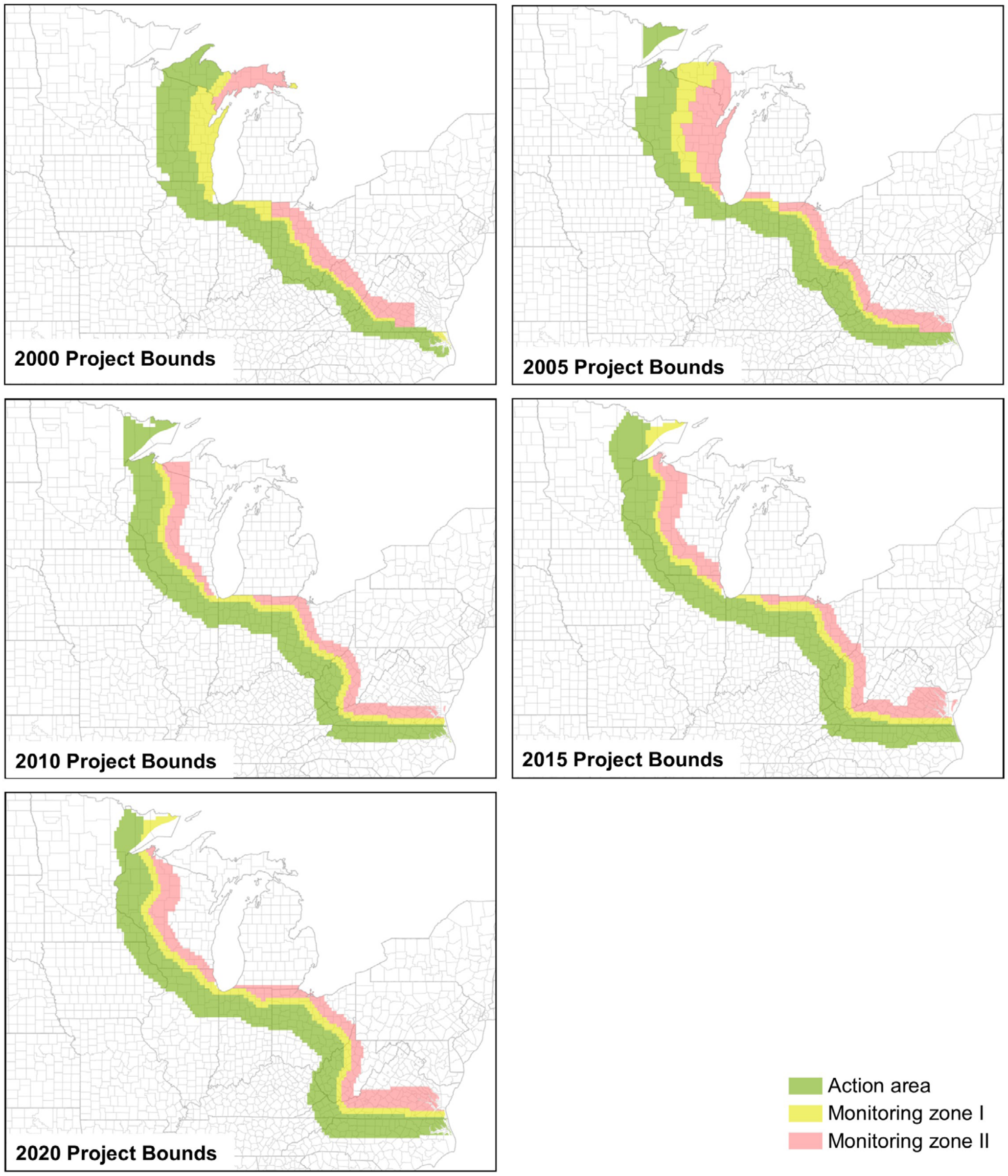


Figure 2.— Program boundaries: the action area, monitoring zone I, and monitoring zone II, of the National Slow the Spread Program in five-year increments from 2000 to 2020.

costs while not measurably impacting the efficacy of the program. The proximal edge of the action area increased in length from 2,157 km in 2000 to 2,771 km in 2020, representing a 27 percent change in advancements and retractions along the infested front (Fig. 2). The trap spacing grid of the evaluation zone (either 5 km or 8 km spacing) has not changed since the start of the program (Table 1). Some states use the equivalent English measurement in the action area, monitoring zones, and delimit-trapping grids to better align with roads for trap placement.

Table 1.—National Slow the Spread Program boundaries (action area, monitoring zone I, and monitoring zone II) planned from 2000 to 2020

Year	Action area width (km)	Action area trap spacing (km)[a]	Monitoring zones I and II width (km)	Monitoring zone I trap spacing (km)	Monitoring zone II trap spacing (km)
2000–2006	100	2	70	5	8
2007	90	2	80	5	8
2008	80	2	90	5	8
2009	90	2	80	5	8
2010	100	2	70	5	8
2011	100	2	70	5	8
2012	100	3	70	5	8
2013	100	3	70	5	8
2014–2020	100	2, 3[b]	70	5	8

[a] Equivalent English system used for trap spacing in Wisconsin, Minnesota, and Illinois. Some states have used narrower trap spacing in urban areas and as base trapping grids in the action area (i.e., 2 mile action area in Wisconsin and 1 km spacing in some Minnesota urban areas).

[b] The base trapping grid in the action area was split in half with traps in the proximal 50 km spaced at 2 km and traps in the distal 50 km spaced at 3 km in the second 50 km with the tighter trap spacing toward the quarantine area.

TRAPPING

Between 2000 and 2020, the STS Program has planned 1,487,460 traps (base trapping grids and delimits) across its boundaries and placed a total of 1,436,972 traps (97 percent). The program has monitored a mean (±s.e.) of 67,755 (±3,553) traps annually, with the highest number of traps monitored in 2005 (86,250) and the lowest in 2013 (46,403) (Fig. 3). The variations in these trap numbers correspond to periods of peak program funding and changes in the base trapping grid spacing, respectively (Table 1). In the evaluation zone (monitoring zones I and II), 5,386 (±531) traps were monitored annually. Total trap numbers since 2000 were 1,323,866 (2001–2020) for the action area and 113,106 (2001–2020) for the monitoring zones. Seven states (IA, IN, IL, OH, NC, KY, and VA) use the STS protocols and the centralized database to collect and monitor data from *L. dispar* detection traps deployed in the uninfested area for detection purposes. Positive trap catch data from the uninfested area were provided either to the USDA Forest Service or Animal and Plant Health Inspection Service for additional delimiting and potential eradication efforts. Although these data are displayed on the STS website, they are not included in this assessment because they are outside of the STS Program.

From 2000 to 2020, the mean annual number of pheromone-baited traps [(+)-disparlure, (7R,8S)-cis-7,8-epoxy-2-methyloctadecane, Scentry Biologicals Inc., Billings, MT)] monitored by the STS Program was similar among the three regions [southern: 22,153 (±1,369); central: 26,000 (±1,520); and northern: 25,737 (±1,411)]. The mean annual count of base grid traps monitored in the action area from 2001 to 2020 was also comparable across the three regions [mean southern: 15,198 (±1,404); central: 17,139 (±1,472); and northern: 17,115 (±1,297)], whereas the total count of base gird traps in the action area was comparable only in the central (342,784) and northern (342,317) regions and much

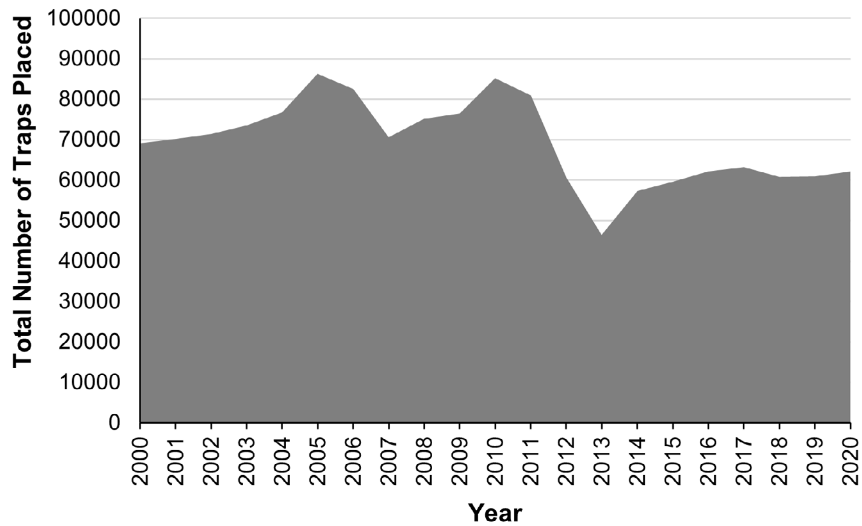


Figure 3.—Total number of traps placed annually from 2000 to 2020 in the National Slow the Spread Program.

lower in the southern region (303,974). The same trend was observed for the mean annual count of delimiting-traps monitored across the three regions [central: 3,768 (±253); northern: 5,001 (±337); and southern 1,712 (±214)]. These differences may be attributed to the fact that few potential problem areas (PPAs), that is, new, low density, isolated populations in the transition zone (Tobin et al. 2007), identified by the STS DA have been found in the southern region, and only a limited number of treatments have been conducted there (KY, NC, TN, and WV). However, Ohio and Wisconsin annually address numerous PPAs in the central and northern regions. To delimit newly detected, low-density, isolated populations, additional traps were placed in a 1 km grid spacing (185,956) or in a 500 m grid spacing (99,321) or in 250 m grid spacing (6,354). Evaluation area traps (monitoring zones I and II) were more prevalent in the southern [5,094 (±846)] and central regions [5,031 (±819)] than the northern region [3,351 (±528)]. This difference can likely be attributed to the larger geographical area covered by the central (three states with evaluation areas) and southern (two states with evaluation areas) regions when compared to the northern region (one state with an evaluation area).

From 2001 to 2020, a total of 9,746,980 male moths were captured in traps in the STS Program, with the majority of moths (92 percent) caught in milk carton traps and 8 percent obtained from delta traps (Scentry Biologicals Inc., Billings, MT). Milk carton traps are the standard in the evaluation area and certain delimit-trapping grids. Capable of catching hundreds of moths, these traps are used in areas with high trap catches. Because the efficiency of delta traps deteriorates in trap captures >12 males (Elkinton 1987), delta traps are generally used in areas where either low trap catches are expected (<12 moths) or <5 moths were caught the previous year. Delta traps are used primarily in the base trapping grids in the action area and most delimits. On average, from 2010 to 2020 a total of 60,771 (±15,017) moths were trapped annually in the action area, 95,535 (±18,020) moths were trapped annually in the monitoring zone I, and 123,086 (±10,926) moths were trapped annually in the monitoring zone II. During this period, a mean of 0.80 (±0.22) moths/trap/year were collected in the action area, 19.7 (±2.01) moths/trap/year were collected in the monitoring zone I, and 76.3 (±4.74) moths/trap/year collected in the monitoring zone II.

Counties in central Wisconsin, northeastern Illinois and Indiana, southcentral Ohio, southern West Virginia, and western Virginia had continually high *L. dispar* trap catches in either the action area or evaluation area (Fig. 4). Although counties with high trap catches contained areas with more contiguous forest canopy cover and a higher proportion of host composition, and forest composition was incorporated into the decision-making process for the Maryland Integrated Pest Management Project (MD-IPM) (Reardon et al. 1993), additional confirmation studies are needed. Counties with higher trap densities located in southcentral Ohio represent formerly *L. dispar*-invaded areas, where STS treatments have successfully eliminated the populations and caused the transition zone to retreat from this area (Fig. 4). Counties located within the action area since the start of the STS Program generally show lower levels of total trap catches (10 to 5,000). However, *L. dispar* has been trapped in all counties in the STS Program and in many adjacent counties (Fig. 4), highlighting its ability to disperse into diverse landscapes (e.g., agricultural, urban, and forested). The capture of males in some of these areas may not indicate the local presence of reproducing populations but rather dispersal of males into these regions (Tobin and Blackburn 2008).

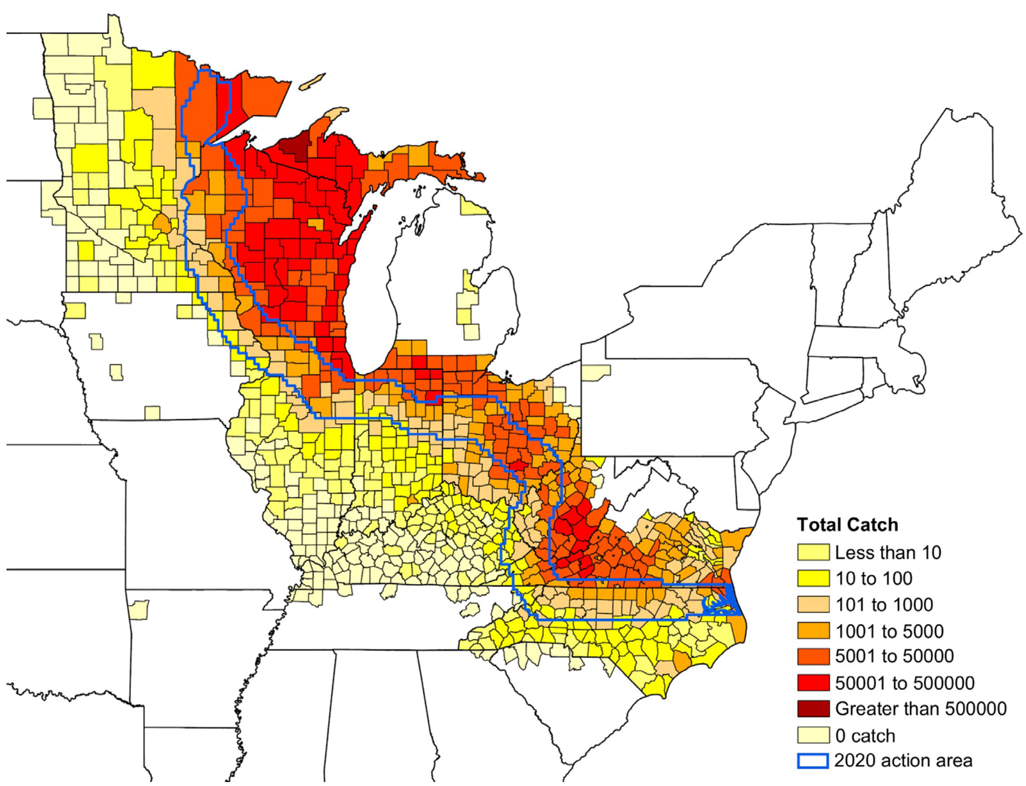
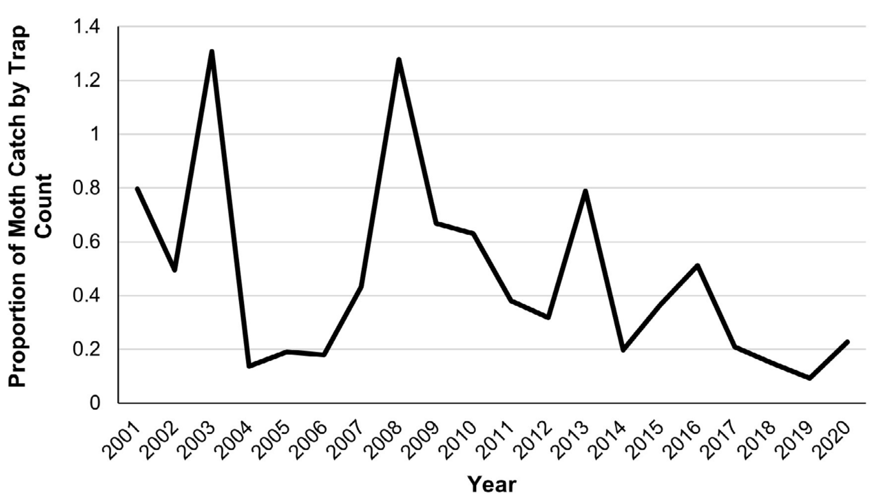


Figure 4.— Cumulative *Lymantria dispar* trap catch by county in the National Slow the Spread Program.

Across all monitoring areas, mean trap catch for milk carton traps was 32.1 (±3.51), and mean trap catch for delta traps was 0.45 (±0.08). The count of male moths caught per trap per year was variable from 2001 to 2020 for the action area and the evaluation area (Fig. 5A, B). The collection of male moths/trap/year peaked during three periods (2003, 2008, 2013) for both trap types, but these peak periods of trap catch do not correspond to extensive *L. dispar* outbreak years in infested areas (Fig. 5C) (USDA FS 2021). The number of male moths/trap has been in a general decline in the program from 2001 to 2020.

A



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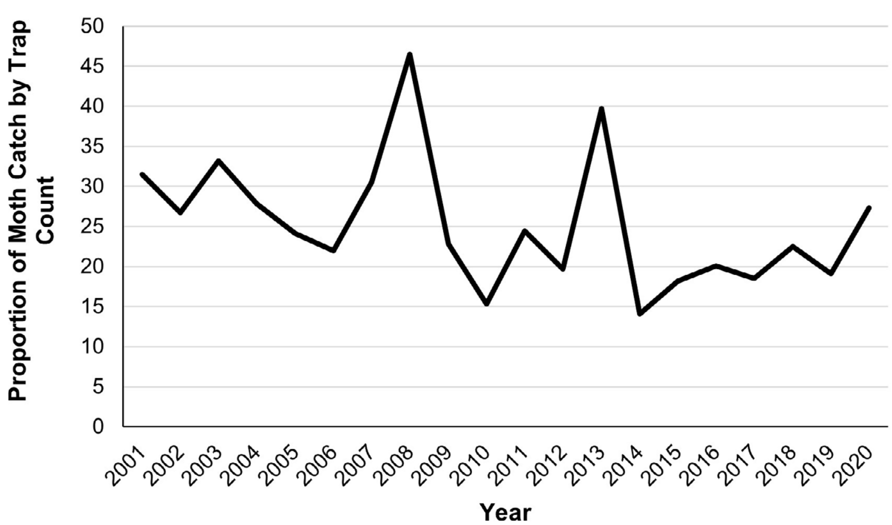

C

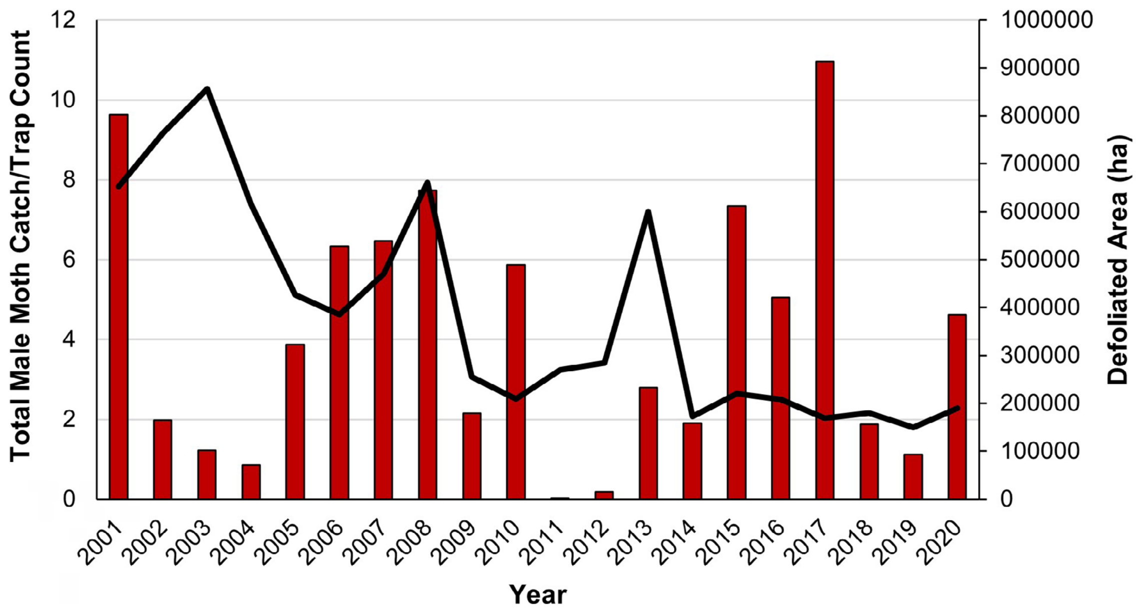

Figure 5.— Proportion of *Lymantria dispar* male moth catch by trap count from 2001 to 2020 for delta traps (A), milk carton traps (B), and both trap types (C). *Lymantria dispar* defoliation data (ha) recorded from aerial detection surveys was added for both trap types (USDA FS 2021).

The mean cost of setting a trap, potentially conducting a mid-season check on a trap, and retrieving a trap, including project overhead and costs associated with the centralized database, from 2000 to 2020 was $66.96 (±2.93). Trapping costs generally increased during the two decades of work, with the lowest trap cost occurring in 2001 ($47.00) and the highest trapping cost occurring in 2020 ($101.42). Annually, there are approximately 200 trap leaders and trappers to implement the program. Monitoring costs continue to account for nearly 60 percent of the annual budget (Coleman et al. 2023, this report page 28).

Trapping data are the foundation of the STS Program and guide management activities. As a result, quality assurance-quality control (QA-QC) standards for the trapping program were implemented and have been assessed annually since 2001 (Roberts and Ziegler 2007). Lead trappers and program managers conduct QA-QC checks on traps and use the STS trapping software to upload information into the centralized database (Coleman et al. 2023, this report page 28). An annual report is developed by the STS Information Systems Group and submitted to the board of directors.

The program strives to account for 100 percent of the planned trapping locations in the database as deleted, omitted, or placed. From 2001 to 2020, a mean of 0.03 (±0.01) percent traps were unaccounted for in the database. The number of unaddressed trapping nodes in a year ranged from 0 to 95 traps over the two decades of work. A mean of 2,506 (±291) traps were omitted annually, representing a 3.38 (±0.30) percent omission rate and surpassing the program goal of setting 95 percent of planned traps. The predominant reasons for omitting traps were the following: the site was too wet; an obstacle prohibited access to the site; rough, steep terrain; thick vegetation; no structure for a trap; or a landowner denied access. The program also strived to inspect at least 10 percent of the traps in a state, with QA-QC checks conducted by state and federal personnel. Annually, 8,869 (±357) traps or 12.9 (±0.50) percent of the traps were evaluated following QA-QC guidelines. Trap inspections had an exceptionally high passing rate [mean of 98.8 (±0.14) percent]. The primary reasons traps failed inspections were the following: the trap information was not recorded correctly on the trap; the trap was assembled incorrectly; the trap was too far from the node; directions to the trap location were wrong; the record was filled out, but no trap was set; or the trap was hung too low.

From 2009 to 2020, QA-QC assessments included an evaluation of traps placed within a defined distance of a trapping node, trap placement and removal dates, and compliance with the STS DA. Over 12 years, a mean of 91.7 (±1.17) percent of traps were placed within the target distance of a trapping node, falling short of the 95 percent goal. However, the goal of placing traps within a certain target circle was achieved from 2018 to 2020, surpassing 95 percent for traps in the target circle. Technological advances and adoption of trapping protocols (i.e., all states moved to a digital platform) across the entire program likely led to the improved trap set accuracy. Traps were placed outside the defined target circle in the greatest numbers in 2012 (15.5 percent were outside the target circle). Trap placement and removal aligned 97.2 percent (±1.62) of the time with the period of moth flight predicted by BioSIM, a *L. dispar* phenology model linked with raster climatic data (Régnière et al. 2017). BioSIM projections have been used to help plan trap deployment, trap retrieval, and treatment timing since 2008 (Fig. 6). Alignment between the STS DA recommendations and actual management action taken for treatments and delimits was 86.2 percent (±2.74) and 87.5 percent (±3.64), respectively, indicating the STS DA is a useful model in guiding and prioritizing decision-making processes.

DECISION ALGORITHM

The STS DA assists program managers in identifying new, isolated *L. dispar* populations (i.e., PPAs) located in the transition zone and providing a recommendation for a management action (e.g., do nothing, delimit, post-treat delimit, or treat) using a geospatial and trap catch based assessment process (Tobin and Sharov 2007). The total number of PPAs identified since 2000 was 15,348 with a mean annual number of 730 (±43.8). The northern region [mean 311 (±32.5), 6,541 total] had more PPAs than the central [mean 252 (±9.29), 5,299 total] and southern [mean 167 (±10.6), 3,508 total] regions. The mean number of PPAs across the three regions has been in a general decline since 2011, with the highest number of PPAs occurring from 2009 to 2011 (Fig. 7). The STS DA was altered in 2012 to address PPA geometry (i.e., smooth the action area along the transition zone), to end the creation of independent action PPAs, and to correct issues with priority indices, which may account for some of the reductions in PPA numbers.

The STS DA has detected PPAs across the entire STS Program (Fig. 8); however, certain areas have experienced *L. dispar* population growth that has been particularly intense. These include areas near central and southern Wisconsin; urban areas near Ft. Wayne, Indiana and Columbus, Ohio; southern Ohio; and western and southcentral Virginia. The intense population growth has often resulted in additional trapping and treatments that have reduced *L. dispar* population growth and also slowed moth spread. Recommendations of “do nothing” from the STS DA were higher (44 percent) when compared to other PPA recommendations [delimit (27 percent), independent (6 percent), post-treatment delimit (9 percent), and treat (13 percent)] (Table 2). In the early years of the program, managers added management actions into the database independent of the STS DA decision-making process. These independent recommendations are no longer used or tracked in the database.

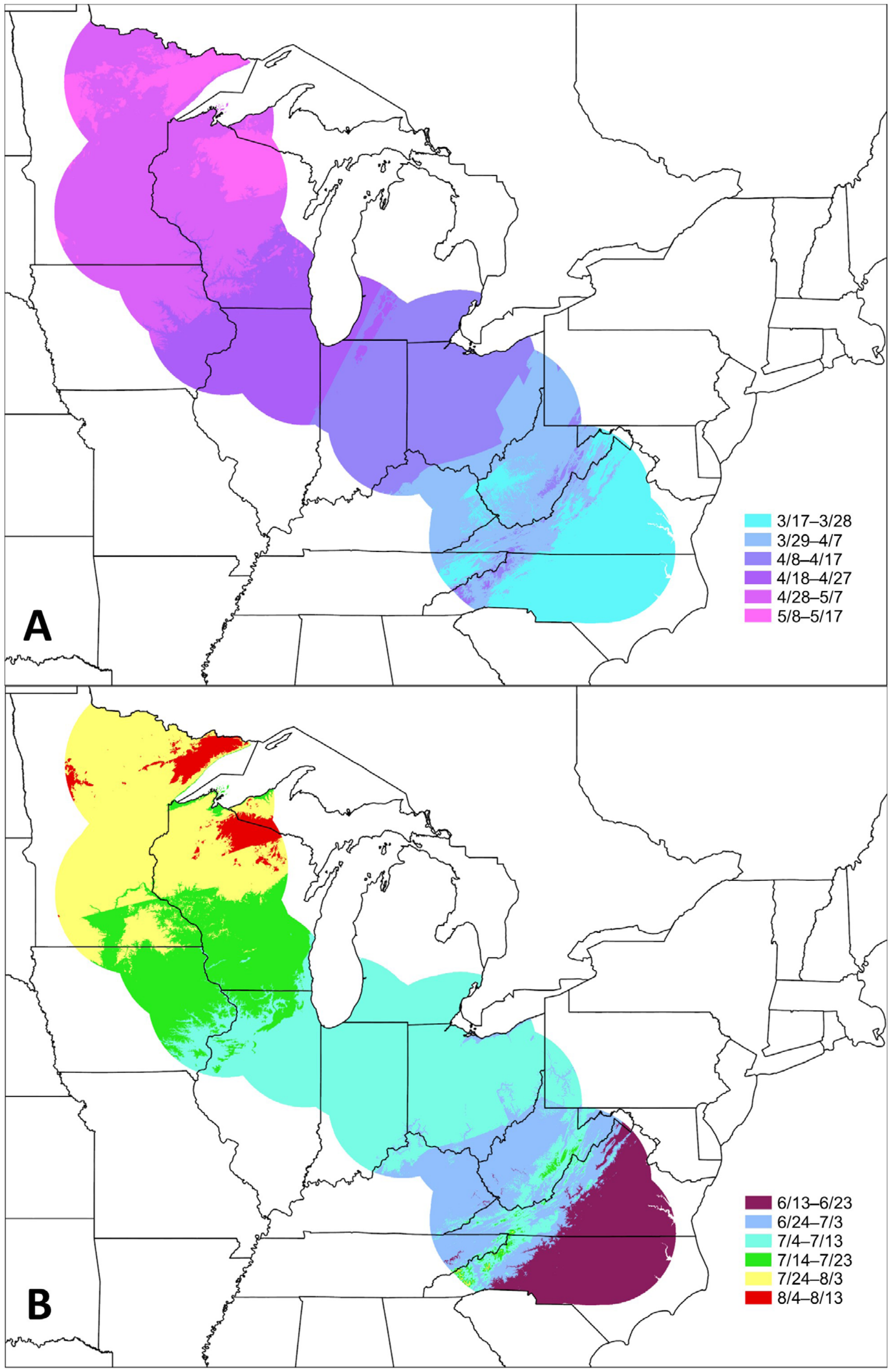

Figure 6.— BioSIM model projections (30-year average) for egg hatch (5 percent, A) and adult male moth flight (5 percent, B) for the National Slow the Spread Program (Régnière et al. 2017).

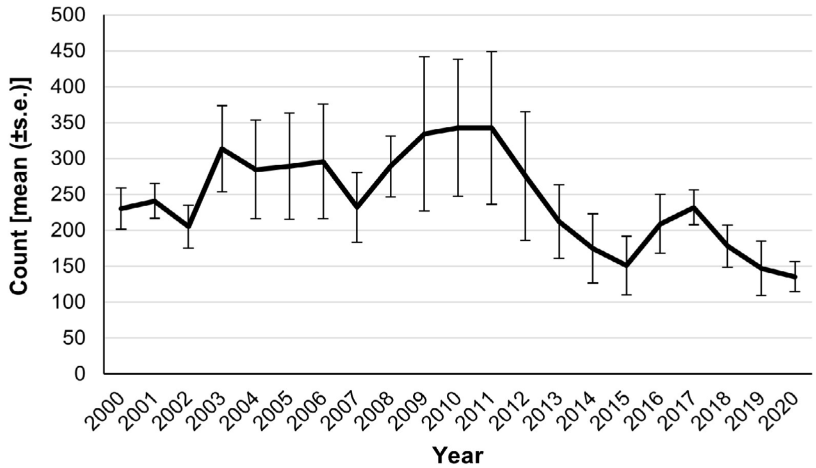

Figure 7.— Mean (±s.e.) count of potential problem areas (PPAs) from 2000 to 2020 across the three regions in the National Slow the Spread Program.

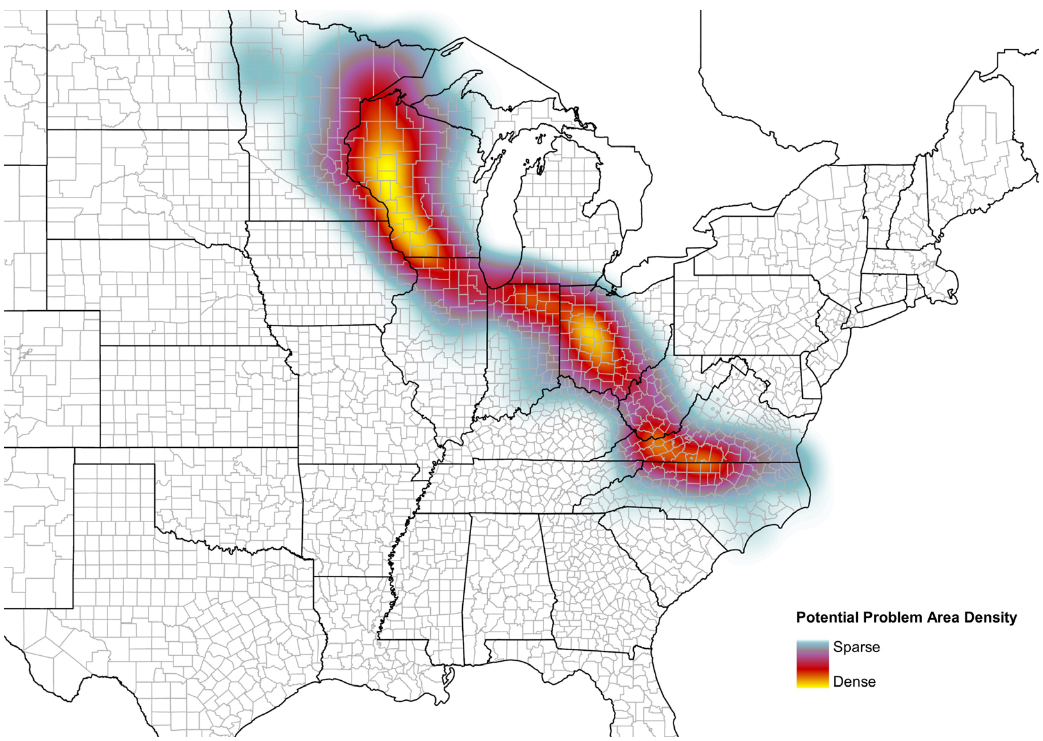

Figure 8.— Smoothed density of potential problem areas (PPAs) from 2000 to 2020 defined by the National Slow the Spread Program decision algorithm. These areas are identified by higher percentile of trap catches than the surrounding area and incorporate four indices. Potential problem areas represent isolated, low-density populations in the transition area.

Table 2.—Mean (±s.e.) count, distance from infested area, maximum previous year trap catch, and current year trap catch for recommended management actions from 2000 to 2020 by the National Slow the Spread Program decision algorithm

Management recommendation	Count	Distance from infested area (km)	Maximum previous trap catch	Maximum current trap catch
Delimit	147 (±10.6)	43.0 (±2.81)	28.2 (±3.81)	42.2 (±4.68)
Do nothing	362 (±31.6)	18.4 (±3.64)	16.6 (±2.01)	28.2 (±2.82)
Independent	179 (±26.4)	86.8 (±2.51)	4.36 (±0.58)	0.89 (±0.18)
Post-treatment delimit	62.6 (±11.7)	30.6 (±3.46)	6.01 (±4.59)	0 (±0)
Treat	66.2 (±3.53)	45.2 (±2.59)	48.0 (±6.28)	91.6 (±7.30)

Table 3.—Mean (±s.e.) count (A), maximum previous year trap catch (B), and maximum current year trap catch (C) for management recommendations from the decision algorithm in the three regions of the National Slow the Spread Program from 2005 to 2020; percentages represent proportion of management recommendations by region

Parameter	Management recommendation	Southern region	Central region	Northern region
A. Count	Delimit	36.2 (±3.43) 28%	56.3 (±2.35) 27%	54.8 (±6.86) 22%
	Do nothing	84.1 (±11.7) 42%	127 (±8.99) 45%	152 (±23.3) 42%
	Independent	16.9 (±5.14) 6%	34.3 (±5.57) 6%	131 (±34.8) 22%
	Post-treatment delimit	14.1 (±2.37) 7%	32.8 (±5.43) 9%	29.2 (±7.16) 6%
	Treat	20.3 (±2.24) 17%	27.9 (±1.61) 13%	18.0 (±2.05) 8%
B. Maximum previous trap catch	Delimit	40.1 (±8.17)	31.1 (±6.51)	21.3 (±8.12)
	Do nothing	24.3 (±6.48)	17.7 (±3.03)	13.5 (±2.02)
	Independent	7.64 (±6.29)	3.12 (±1.79)	4.37 (±0.43)
	Post-treatment delimit	10.8 (±8.45)	5.35 (±4.03)	1.77 (±1.17)
	Treat	54.8 (±12.4)	58.8 (±7.92)	25.4 (±6.96)
C. Maximum current trap catch	Delimit	47.7 (±9.22)	52.5 (±8.06)	31.0 (±8.43)
	Do nothing	39.1 (±5.53)	25.9 (±2.77)	26.8 (±4.33)
	Independent	0.65 (±0.22)	0.44 (±0.56)	1.09 (±0.06)
	Post-treatment delimit	0 (±0)	0 (±0)	0 (±0)
	Treat	83.9 (±16.3)	111 (±12.5)	79.2 (±22.2)

Across the three regions, the mean count of recommendations was greatest for "do nothing" in each region (Table 3A). Recommendations of "delimit" ranged from 22 to 28 percent across the three regions, and "treat" ranged from 8 to 17 percent. Delimit-trapping grids from 2000 to 2020 extended across the transition area, with lower numbers of delimit grids along the Illinois and Indiana border, eastern West Virginia, and eastern Virginia and

North Carolina (Fig. 9). The border of Illinois and Indiana is dominated by agriculture, and suitable hosts are sparse and highly fragmented. *Lymantria dispar* populations rarely establish and are comparatively easy to contain if detected in these highly fragmented landscapes. In eastern West Virginia, many hypotheses have been proposed for the lack of increasing populations (e.g., lack of preferred host type, increased summer temperatures, rolling topography), although none have been adequately tested. A higher number of delimit-trapping grids occurred in central and southern Wisconsin; the metropolitan areas of Duluth and Minneapolis, MN; Chicago, IL; Ft. Wayne, IN; southern Ohio, including Columbus; and western and southcentral Virginia. Although the southern region had the least number of PPAs compared to the central and northern regions, the distribution of the recommendations was comparable across the three regions (Table 3A). The northern region had generally lower maximum previous year and current year trap catches in PPAs when compared to the other regions (Table 3B, C). Program managers have often taken a more aggressive approach against populations in Wisconsin when compared to the other regions because low trap catches have a higher likelihood of persisting in subsequent years (Whitmire and Tobin 2006). The program continues to discuss adjusting the STS DA to address this issue, but changes have not yet been implemented.

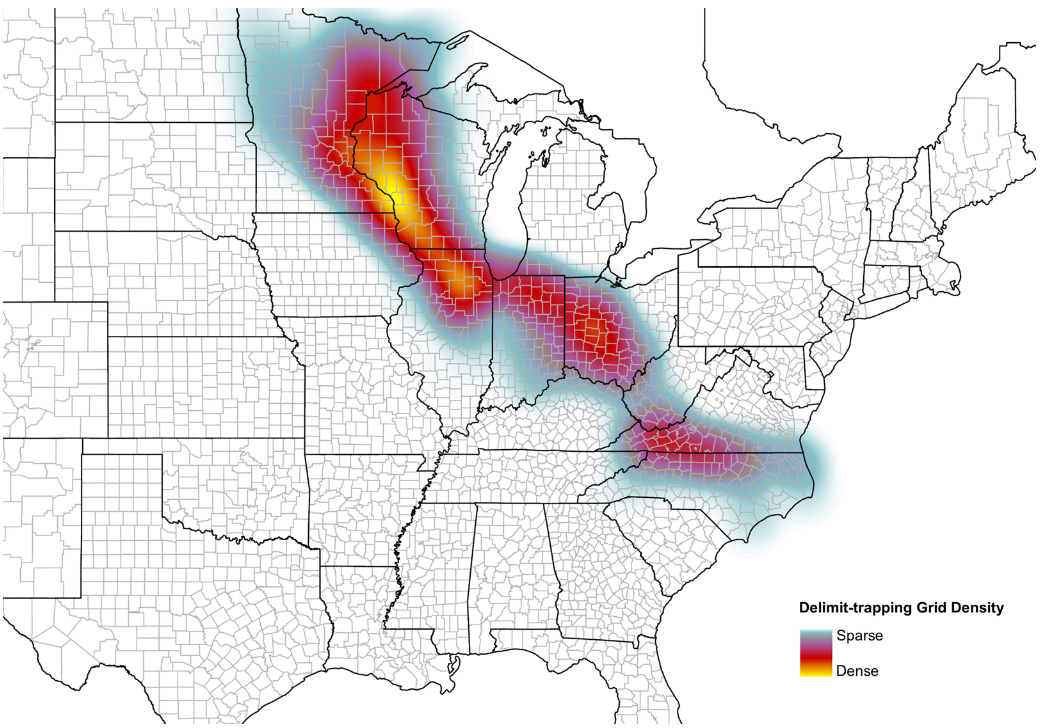

Figure 9.—Smoothed density of delimit-trapping grids monitored from 2000 to 2020 in the National Slow the Spread Program. Traps located to the west and south of the program area represent *Lymantria dispar* detection traps for eradication efforts.

TREATMENTS

The STS Program has treated 3,760,681 ha since 2000 (Table 4). An additional 90,194 ha were treated during the STS Pilot Project (Coleman 2023, this report), bringing the total to 3,850,793 ha for STS programs. Mean annual planned treatment hectares [163,018 (±8,475) from 2006 to 2020] was lower than the mean annual accomplished treatment hectares by 9 percent [178,818 (±10,778) from 2000 to 2020]. This increase in treatment area generally resulted from underestimating the treatable forested area in mating disruption blocks. The most treatment hectares were accomplished in 2004 (268,695) and the least in 2019 (120,201). The mean area covered by the STS action area from 2000 to 2020 was 23,206,212 (±536,837) ha. Each year, treatments targeted newly established populations in the transition area and covered only a mean 0.8 percent of the STS action area land area.

Table 4.—Area treated (ha), primarily by aerial applications, from 2000 to 2020 by the National Slow the Spread Program

	Biological pesticides		Insect growth regulator		Mating disruption			
Year	*Bacillus thuringiensis* var. *kurstaki (Btk)*	Nucleopolyhedrosis virus (Gypchek)	Diflubenzuron	Tebufenozide	Hercon® Disrupt® II[a]	SPLAT[b]	Hercon Bioflakes	Total
2000	34,082	0	0	0	37,890	0	0	71,972
2001	25,252	0	263	0	86,170	0	0	111,685
2002	11,617	0	1,594	0	219,587	0	0	232,798
2003	28,519	2,760	0	0	224,391	0	0	255,670
2004	53,129	3,331	0	0	212,241	0	0	268,701
2005	43,954	6,910	320	0	116,507	0	0	167,692
2006	38,794	2,834	4,975	0	172,456	0	0	219,058
2007	23,278	1,533	39	0	147,674	0	0	172,524
2008	18,311	45	0	0	140,703	8,288	0	167,348
2009	14,636	123	0	0	114,059	40,805	0	169,623
2010	23,880	1,884	0	0	140,328	49,267	0	215,359
2011	17,376	1,043	0	0	185,631	8,854	0	212,903
2012	12,646	1,152	0	0	202,189	4,346	0	220,333
2013	11,132	1,818	0	26	153,272	0	0	166,248
2014	8,531	1,945	0	0	157,952	9,756	0	178,184
2015	8,989	849	0	0	188,108	9,993	1,214	209,153
2016	9,521	413	0	7	150,744	18,187	4,128	183,000
2017	13,790	0	0	0	152	137,523	0	151,465
2018	11,072	151	0	0	0	135,431	0	146,655
2019	15,526	45	0	0	0	104,633	0	120,204
2020	9,636	409	0	0	0	110,061	0	120,106
Total	433,671	27,245	7,190	33	2,650,056	637,144	5,342	3,760,681

[a] Hercon® Disrupt® II and Bioflakes® (Hercon Environmental, Emigsville, PA)

[b] SPLAT (ISCA Technologies, Riverside, CA)

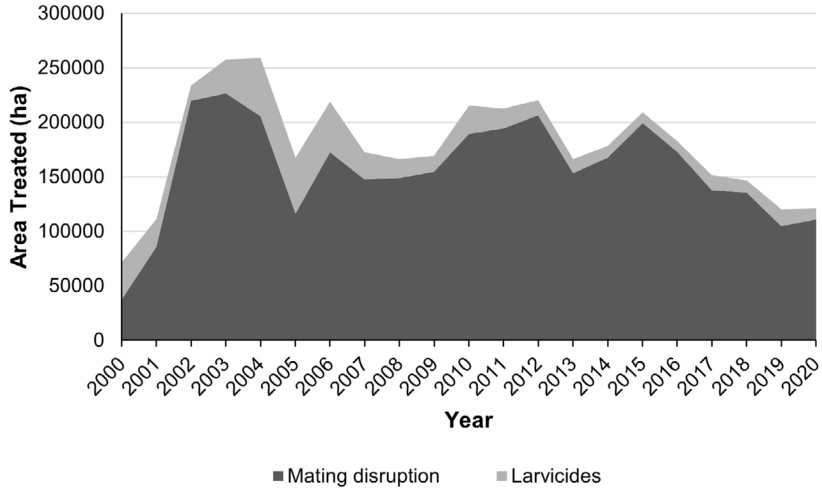

Figure 10.— Total area (ha) treated by the National Slow the Spread Program. Larvicide applications have remained fairly consistent since 2012. Mating disruption hectares have declined since 2015.

Overall, STS treatments have been in a modest decline since 2015 (Fig. 10). The annual decreases are due primarily to reductions in funding from the federal government for the STS Program, and each winter an estimated $100,000 to $300,000 of planned treatments have been eliminated in order to balance the annual program budget. Ultimately, these reductions do not appear to have severely affected the program's success. The program annually treated a mean 22,292 (±3,089) ha with larvicide treatments [*Bacillus thuringiensis* var. *kurstaki* (*Btk*), nucleopolyhedrosis virus (NPV, Gypchek), and insect growth regulators]. Peak larvicide treatment hectares occurred in 2004 (56,458 ha), and the lowest larvicide treatment hectares occurred in 2015 (9,838 ha) (Table 4). The hectares of larvicide applications often include two applications on the same treatment block footprint. In addition, the program annually treated a mean of 156,784 (±10,423) ha with a mating disruptant. The most mating disruption hectares occurred in 2003 (226,685 ha), and the fewest occurred in 2000 (37,888 ha) as the program was transitioning to a national program (Table 4). Mating disruption applications are always applied as a single application per treatment block.

Larvicide applications (468,139 ha) accounted for 12 percent of the total treatments. Mating disruption applications (3,292,542 ha) represented 88 percent of the total. These treatments were overwhelmingly applied aerially by either fixed- or rotary-wing aircraft. The fraction of treatment areas that used larvicide applications has been in a general decline since 2004 and likely results from the advancement, reduced cost, and efficacy of mating disruption applications (Onufrieva 2023, this report), as well as declining program budgets and more effective treatment planning. For 2001 and 2006 through 2020, the mean treatment block size was 241 (±14.5) ha for *Btk* (double applications), 180 (±21.8) ha for *Btk* + mating disruption blocks, 124 (±91.9) ha for Diflubenzuron blocks (double applications), 10.9 ha for Tebufenozide (double applications), 6.9 (±0) ha for Tebufenozide + mating disruption, 167 (±23.1) ha for NPV (double applications), and 162 (±54.2) ha for NPV + mating disruption. The mean treatment block size was 2,029 (±113) ha for mating disruption applications (single application). The larvicide + mating disruption treatments represented a single application of each with the larvicide typically applied to a dense population core. Current management guidance suggests using larvicide applications in areas with either >60 moths/trap or where other *L. dispar* life stages (e.g., egg masses, pupae, pupal cases) are detected. Mating disruption applications are implemented in areas with <60 moths/trap and are preferred over larvicide applications because of the specificity to *L. dispar.* Hercon® Disrupt® II (Hercon Environmental, Emigsville, PA) was the primary mating disruption product used in the operational blocks from 2000 to 2016 (Table 4). However, SPLAT GM-Organic (ISCA Technologies, Riverside, CA) replaced the use of Hercon® Disrupt® II because it is biodegradable and certified organic by the USDA, and because it has an easier loading and application process. SPLAT GM-Organic has been used exclusively in the program operational treatment blocks since 2017. Hercon Environmental developed a biodegradable mating disruption flake formulation, Hercon® Bioflakes®, that was approved for program use (Onufrieva 2023, this report) but only had limited use (2015–2016) before the product registration was discontinued (Table 4).

A total of 3,174 low-density, isolated populations, or PPAs, were treated since 2000. The mean annual number of PPAs treated were 151 (±8.48), which is 1.3 times greater than the mean number of "treat" recommendations from the STS DA (Table 2). The STS Program treated the largest number of populations in 2004 (210) and the lowest (98) in 2008. The northern region had the greatest annual total treatment hectares [88,234 (±8,181) ha], followed by the central [45,749 (±4,719) ha] and southern [45,092 (±5,000) ha] regions (Fig. 11). The same trend was observed for larvicide applications across the three regions [northern: 14,069 (±2,034) ha; central: 5,112 (±989) ha; and southern: 3,111 (±868) ha] and mating disruption treatments [northern: 74,165 (±8,074) ha; southern: 41,982 (±10,350) ha; and central: 40,637 (±4,537) ha]. All states have conducted larvicide and mating disruption applications except Kentucky, which has never had treatments in the STS Program (Fig. 11). This is mostly attributable to the state's location in the distal part of the STS action area, away from quarantined areas, and to the success of the adjacent states. Mean annual treatment application costs were $12.96 (±0.95)/0.04 ha for all treatments.

Aerial applications were made in urban areas 709 times, representing 22 percent of the total number of applications and 9 percent of the total treatment area (Fig. 12). Applications in urban areas occurred mostly in the metropolitan areas of Chicago (IL), Columbus and Dayton (OH), Duluth (MN), and Ft. Wayne (IN). The majority of aerial applications occurred on nonfederal lands (1,939 applications, 61 percent). Aerial applications occurred on federal and tribal lands 1,235 times (39 percent). On federal lands, tracts managed by the USDA Forest Service; Department of Interior, National Park Service and U.S. Fish and Wildlife Service; Department of Energy; U.S. Army and Air Force; and Department of Defense, Army Corps of Engineers in southeastern Ohio, eastern Illinois, northern Indiana, northern Minnesota, central and western Virginia, and northern Wisconsin received the most treatments, representing 10 percent of total treatment area (Fig. 13). The Cherokee, Chequamegon-Nicolet, George Washington-Jefferson, Wayne, Pisgah, and Superior National Forests have had STS treatments. Tribal lands, including Bad River, Red Cliff, St. Croix Reservation, and Lac Courte Oreilles-Off Reservation Lands in Wisconsin and Grand Portage Reservation in Minnesota also have had STS treatments on their lands. Additional national forests and National Park Service lands in the southern Appalachian Mountains, including Chattahoochee, Daniel Boone, Nantahala, Blue Ridge Parkway, and Great Smoky Mountains, are anticipated for future treatments due to the increased spread in this region and the abundance of susceptible host species.

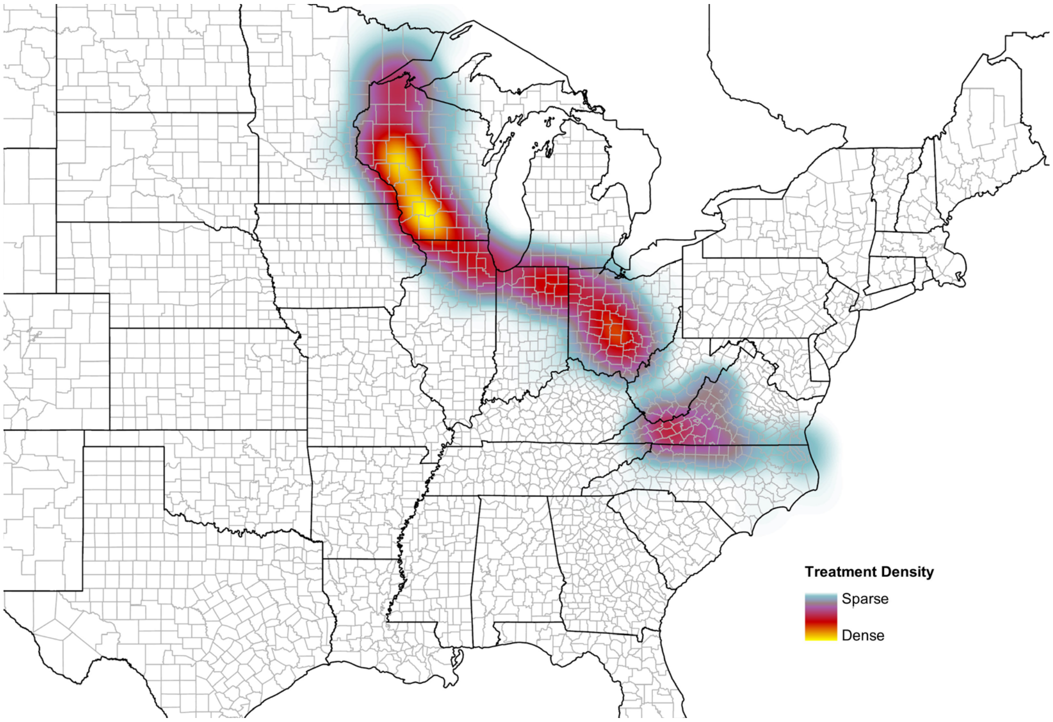

Figure 11.— Smoothed concentration of treatments from 2000 to 2020 in the National Slow the Spread Program. Note the lack of treatments in eastern Virginia and West Virginia.

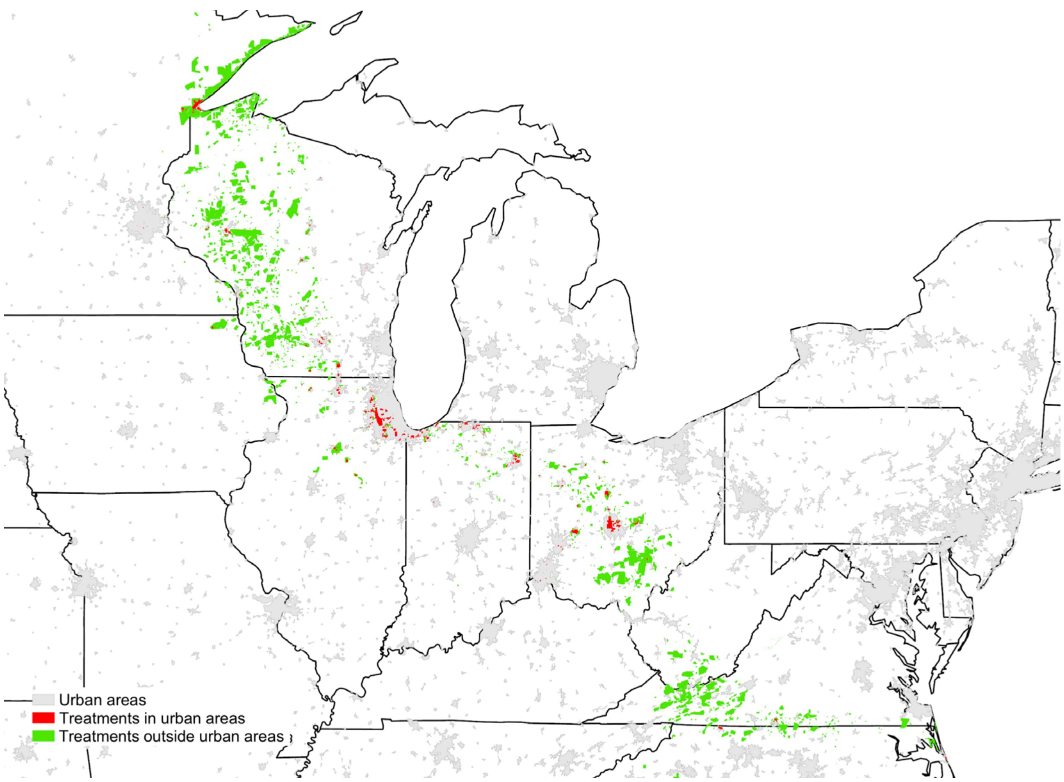

Figure 12.— Treatment in urban areas and outside urban areas by the National Slow the Spread Program. Aerial applications of a mating disruptant and *Bacillus thuringiensis* var. *kurstaki* dominated the treatments from 2000 to 2020.

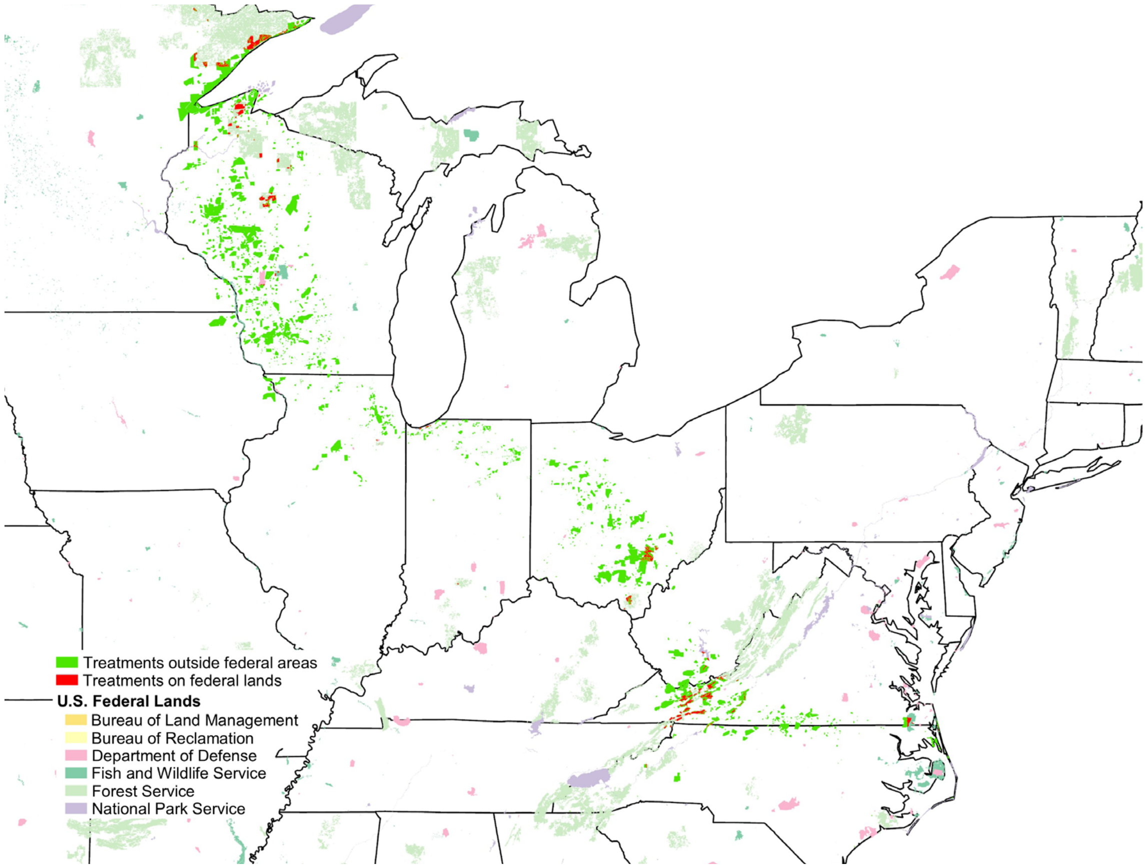

Figure 13.— National Slow the Spread Program treatments conducted from 2000 to 2020 that encompassed federal lands and nonfederal lands.

Post-treatment delimits were implemented following all treatment applications, either in the current year (larvicide applications) or the following year (mating disruption applications). Mean success of larvicide applications from 2002 to 2020 was 81.2 percent (±1.89), including full and partial success as defined by the *T* statistic (Sharov et al. 2002a), a trap catch-based metric that analyzes proportional changes in population density before and after treatment (Tobin et al. 2007). Mean mating disruption success (pooled full and partial successes represented as a percentage) from 2002 to 2020 was 91.4 percent (±0.87) (*T*+1-value). The STS Program has had a consistently high level of treatment success, and treatment success has increased since the start of the program (Walter et al. 2021). The lowest treatment success (64 percent) was reported in 2008 for larvicide applications, whereas the lowest mating disruption success was in 2004 (84 percent).

RATE OF SPREAD

Over the past two decades, the STS Program has surpassed its goal of slowing the rate of spread of *L. dispar* by greater than 60 percent from the historical rate of spread (19.6 km/yr), which is the average of two mid-range estimates (Liebhold et al. 1992, Sharov and Liebhold 1998). Mean spread across the program area from 2000 to 2020 was 2.6 km/yr (±1.8), with a goal of below 7.8 km/yr. Spread was highest in the northern region [9.62 (±4.13) km/yr], followed by the southern region [1.63 (±2.36) km/yr] and the central region [-2.31 (±2.26) km/yr]. The program area uses 12 zones to measure population spread (Fig. 14). The program has successfully pushed back the transition area and halted the rate of spread from Illinois to Ohio and in eastern and central Virginia and North Carolina (Table 5). The program boundaries have shifted westward in Wisconsin and southwestern in Virginia along the Appalachian Mountains, where moth spread has been the fastest. However, the central region, driven primarily by program activity in Ohio, slow spread rates, and sparse, disjunct host habitat, has successfully reversed the expansion of the proximal edge of the action area approximately 90 km into quarantined counties, delaying the advancement of *L. dispar* into Kentucky and causing a retreat of populations from previously invaded counties. Peak spread rates occurred in 2008, with 18.0 km/yr, which was only a 10 percent decrease when compared to the historic rate of spread (an average of spread rates across different regions and habitats) (Fig. 15) and coinciding with large outbreaks in quarantined counties (USDA FS 2021). There have been only five years since 2000 when the program has not achieved its goal of slowing the rate of spread by >60 percent (Fig. 15) and three years where the 3-year average spread rate elevated above the target spread rate. In 2008, spread rates were fastest in Wisconsin and Illinois (zones 3-8), ranging from 24.9 to 74.4 km/yr. In 2004, the rate of spread was its lowest at -9.66, causing populations to retreat in several zones from Wisconsin to Ohio (zones 2-5) and in West Virginia and Virginia (zones 10-12). Since 2013, the STS Program has consistently met its annual goal, despite reductions in treatment blocks due to a declining or flat federal budget. Without the STS Program, the current projected distribution of *L. dispar* would likely encompass all of North Carolina, Ohio, Indiana, Virginia, and Wisconsin and most of Illinois, Iowa, Minnesota, and Tennessee; and the distribution would likely include Missouri, Georgia, and South Carolina (Fig. 16). Liebhold et al. (1997) reported that Georgia, Minnesota, and Missouri have some of the highest concentrations of extremely susceptible forest type (preferred host species comprise >80% of the stand basal area on >1 million acres).

Table 5.—Mean (±s.e.) rates of spread of *Lymantria dispar* projected from 2000 to 2020 across the 12 zones (see also Fig. 14) in the National Slow the Spread Program

Zone	Region1	Rate of spread
1	Upper Peninsula of MI	12.2 (±8.96)
2	Northern WI, MN	14.5 (±7.17)
3	Central WI, MN	8.48 (±4.49)
4	Southern WI, northern IA	11.1 (±3.89)
5	IL	-4.39 (±5.24)
6	IN	-0.85 (±2.55)
7	Western OH	-1.64 (±3.33)
8	Eastern OH, KY	-3.02 (±3.70)
9	WV, KY, eastern TN, and western VA	4.23 (±1.74)
10	Central VA, NC	3.03 (±2.51)
11	Eastern VA, NC	1.03 (±4.73)
12	Appalachian Mountains in NC, TN, WV, VA	5.67 (±1.70)

Note: State abbreviations in order of appearance are MI (Michigan), WI (Wisconsin), MN (Minnesota), IA (Iowa), IL (Illinois), IN (Indiana), OH (Ohio), KY (Kentucky), WV (West Virginia), TN (Tennessee), VA (Virginia), NC (North Carolina).

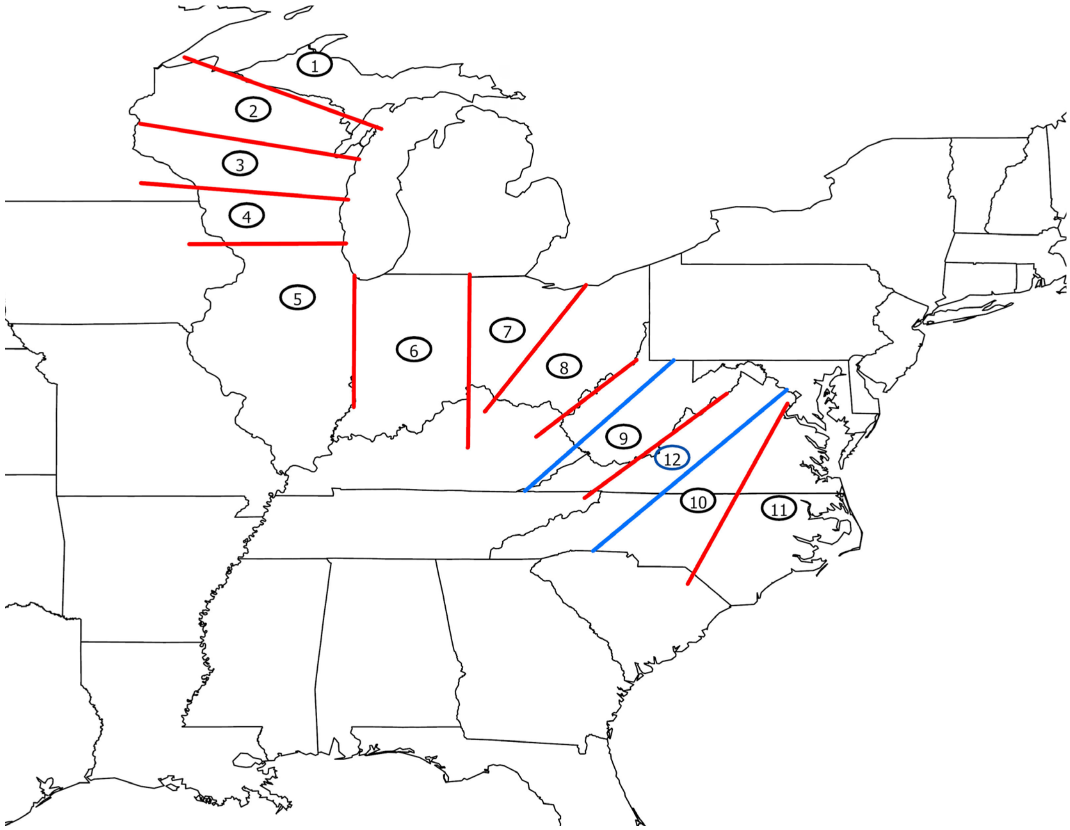

Figure 14.— The 12 zones used by the National Slow the Spread Program to calculate annual rates of spread. Zone 12 is noted by the blue boundary lines.

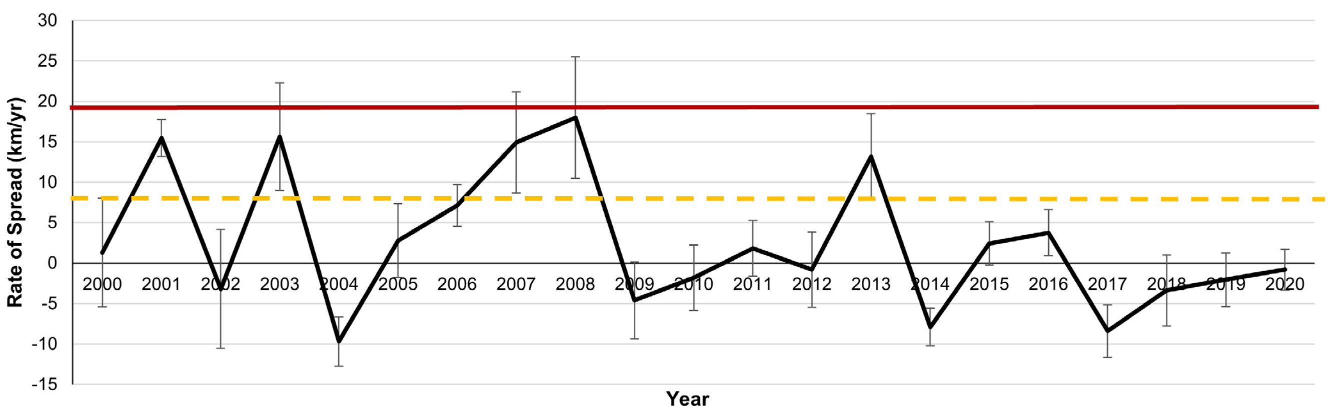

Figure 15.— Mean (±s.e.) rates of spread of *Lymantria dispar* from 2000 to 2020 across the 12 zones in the National Slow the Spread Program. The historical rate of spread (19.6 km/yr) and the 60 percent reduction in the historical rate of spread (7.8 km/yr) is noted by the red line and the dashed yellow line, respectively.

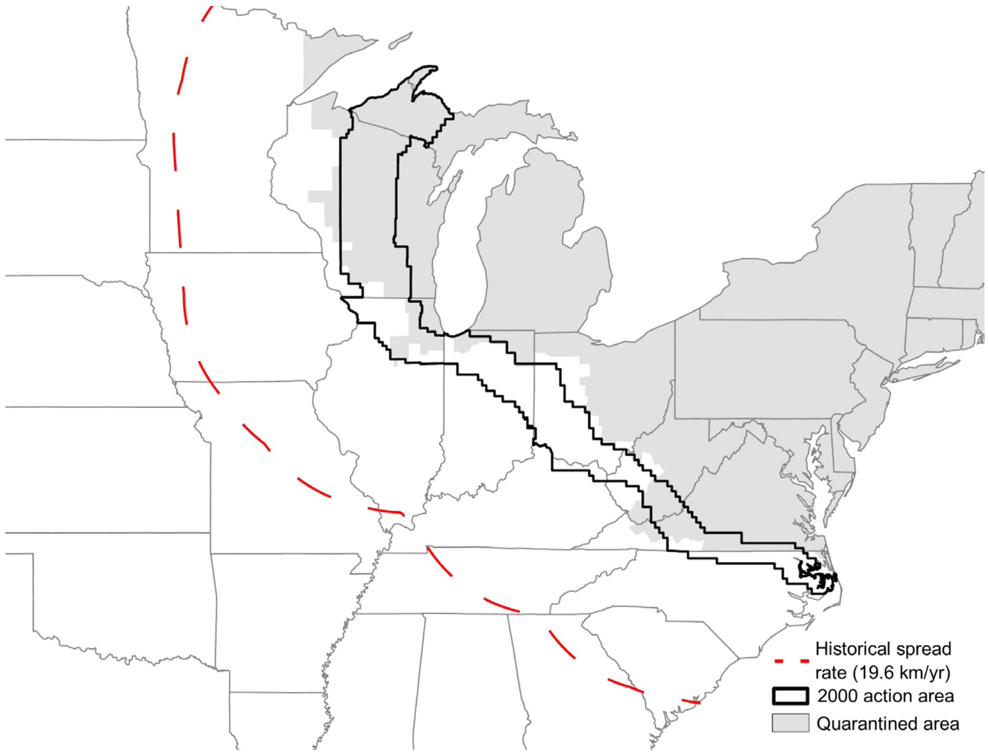

Figure 16.— The projected spread of *Lymantria dispar* from the 2000 action area, using the historical rate of spread (19.6 km/yr), had the National Slow the Spread (STS) Program never existed. The gray area (quarantined counties) represents the current distribution of *L. dispar* and the black boundaries represent the location of the STS Program in 2000.

FUTURE OF THE PROGRAM

Since *L. dispar's* introduction, the STS Program represents the longest running, most expansive, and most successful management program against this non-native defoliator in the United States (McManus 2007, Liebhold et al. 2021). Previous area-wide management programs were discontinued due to reductions in funding, limited program success, environmental concerns, and short-term program objectives (Coleman 2023, this report). In principle, some of these same issues could ultimately contribute to the end of STS. However, strong cross-collaboration among the USDA Forest Service, USDA Animal and Plant Health Inspection Service, and state government agencies has sustained and prioritized the program throughout its duration. The remarkable success of the STS Program, which generates data-driven, science-based management decisions using environmentally safe tactics, has been key to the program's longevity. Furthermore, without the additional supporting strategies of the USDA National Spongy Moth Management Program, specifically regulatory efforts and eradication treatments that target outlier populations in uninvaded areas, the STS Program would become ineffective. It is imperative for the STS Program to continue to delay the impacts of *L. dispar* on timber, recreation, and residential areas in currently uninfested areas (Leuschner et al. 1996).

Many of the trapping and treatment technologies utilized in STS were developed in previous management programs. In addition, years of research conducted by STS and collaborators have developed inexpensive, environmentally low-risk suppression strategies against low density *L. dispar* populations that are ideal for targeting isolated populations in the expansive transition area. The STS Program continues to advance trap data collection procedures and mating disruption treatment techniques to improve the program's efficacy and reduce costs. As a focus of forest integrated pest management programs in the United States, STS must continue to evaluate and implement new trapping and treatment methodology.

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Chapter 4

Recent Developments in *Lymantria dispar* Spread

Jonathan A. Walter and Andrew M. Liebhold

Abstract

The spread of spongy moth, *Lymantria dispar* L. (Lepidoptera: Erebidae, formerly known as the "gypsy moth"), in North America arguably represents the best-studied biological invasion in the world, due in part to extensive monitoring data from the USDA National Slow the Spread (STS) Program. In this paper, we focus on recent research on spread, with particular emphasis on findings since the publication of Tobin and Blackburn (2007). Recent advances in understanding *L. dispar* spread generally fall into three categories: (1) the role of mating success and Allee effects, (2) the effects of geographical variation in climate, and (3) the genetic adaptation of local populations. Some studies have quantified how the strength of the demographic Allee effect varies regionally and interannually, due in part to differences in climate, topography, and landscape structure. Recent observations suggest that climatic suitability of the cold and warm extremes of *L. dispar*'s North American range are higher and lower, respectively, than earlier predictions, and for reasons that are not yet fully clear. Furthermore, data indicate that *L. dispar* has adapted to local climatic conditions, with convincing evidence of adaptation in traits allowing life stages to tolerate hot spring and summer temperatures in warmer parts of their range. Despite these advances, several opportunities for future research and operationalization of current knowledge remain. One area of future work of potentially high importance is the development of a realistic model of *L. dispar* spread that could be used for optimizing the STS Program decision algorithm.

Keywords: Allee effect, climate suitability, gypsy moth, local adaptation, spongy moth

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INTRODUCTION

Once invading species found initial populations, they tend to expand their range until they have saturated the novel habitat. This phase of biological invasions, called "spread," is one of the most studied but incompletely understood ecological processes (Hastings et al. 2005, Parry et al. 2013). A manifestation of two population processes—population growth and population dispersal—invasion spread has attracted the attention of mathematical investigators as well as applied ecologists. Their work has yielded a variety of mathematical models of invasion spread that vary from simple to complex. But like much theoretical ecology research, most of these models remain untested, largely due to a lack of rich datasets and detailed understanding of population processes necessary to evaluate nuanced population behaviors.

The invasion of North America by spongy moth, *Lymantria dispar* L. (Lepidoptera: Erebidae, formerly known as the "gypsy moth"), and management efforts have created unparalleled amounts of data on spread as well as detailed knowledge of factors affecting invading populations. Between the USDA National Slow the Spread (STS) Program and surveillance programs carried out in the uninvaded states, more than 200,000 pheromone traps are deployed annually, and data from these traps represent a unique resource from which the spatial dynamics of invading populations can be deduced. Analyses of trap capture data have yielded significant insights into the mechanisms behind the spread of this species, and these findings have important implications for understanding the spread of other organisms (Grayson and Johnson 2018). For example, analyses of historical *L. dispar* trap data have identified important influences of both stratified dispersal (i.e., the combination of local diffusion and long-distance transport) (Fig. 1) and Allee effects on *L. dispar* spread, and these analyses have served as a model system for a general understanding of invasion spread (Liebhold et al. 2007, Sharov and Liebhold 1998, Tobin et al. 2009).

The uniquely detailed knowledge of *L. dispar* spread has played a crucial role in the development of the STS Program, a science-based approach to managing *L. dispar* spread in the United States. Quantification of the stratified dispersal phenomenon has allowed for the identification and optimization of an overall strategy of the STS Program, one that focuses on surveillance for the presence of isolated populations which are then suppressed (Sharov and Liebhold 1998, Sharov et al. 1998). Additional analyses of historical spread have also yielded information that has been crucial to developing the STS decision algorithm (STS DA) and solving operational problems encountered during the course of the program (Tobin et al. 2004).

Liebhold et al. (2007) summarized the state of knowledge on *L. dispar* spread using information and data analyses of *L. dispar* spread both prior to the STS Pilot Project (1900–1995) and during the STS Pilot Project (1996–1999). Since the implementation of the National STS Program and the publication of Tobin and Blackburn (2007), considerably more research has been conducted on *L. dispar* spread. Our objective here is to summarize this more recent research and discuss its relevance toward improving the efficiency of the STS Program.

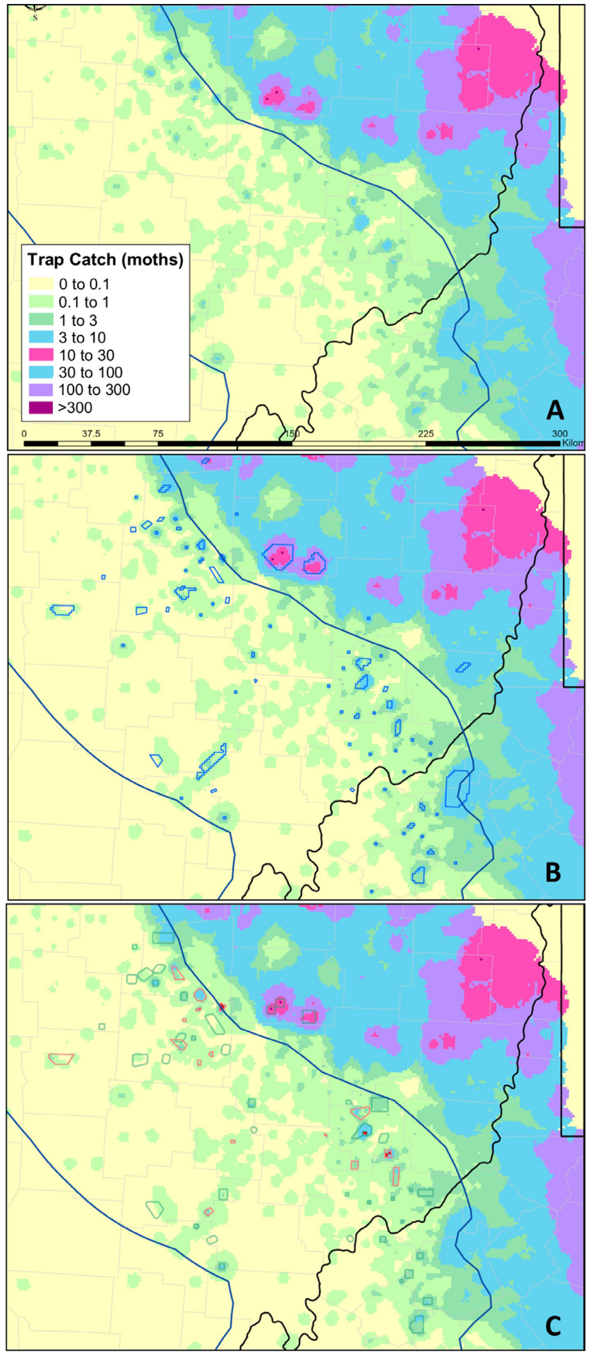

Figure 1.— Results of stratified diffusion of *L. dispar* in West Virginia and Ohio and STS response. (A) Interpolated trap catch densities show isolated low-density populations ahead of the invasion front resulting from long-distance transport; if allowed to persist, these will coalesce through local diffusive spread. (B) Blue polygons correspond to potential problem areas (PPAs) identified under the STS decision algorithm. Note that many "hotspots" ahead of the invasion front are identified as PPAs for possible population delimitation or treatment. (C) Areas treated: mating disruption (pink), larvicides (red), and delimited (blue). Dark blue lines indicate the projected bounds of the STS action area.

IMPORTANCE OF MATE-FINDING FAILURE AND ALLEE EFFECTS

A key topic since the publication of Tobin and Blackburn (2007) is the importance of mate-finding failure in low-density populations to *L. dispar* population establishment and spread. In eastern North America, where *L. dispar* is descended from the European strain of *L. dispar* (Wu et al. 2015), females are flightless and attract flying males using a sex pheromone. Successful reproduction, therefore, depends on a free-flying adult male locating a receptive female. The various behavioral components of *L. dispar* mate-location and their dependencies are reviewed in Cardé (1981). Sharov et al. (1995) provided the first report that *L. dispar* mating success is low in low-density, newly invaded populations. Recent developments have shed light on how the failure to find mates translates to critical population dynamic patterns that can be exploited to help manage *L. dispar* spread (Tobin et al. 2011) and how interactions between *L. dispar* biology and environmental conditions shape rates of mate-finding, and thus invasion dynamics.

Population density is the most important factor affecting mate-finding rates. Where there are many moths in an area, the likelihood that any female is successfully mated is higher than where the number of moths is fewer. In empirical field studies, Sharov et al. (1995) and Contarini et al. (2009) demonstrated that the probability of experimentally deployed *L. dispar* females being mated increased with the background population density, as measured from pheromone-baited trap catch. These studies also revealed mate-finding failure in *L. dispar* to be an important cause of Allee effects, a population dynamic phenomenon causing slow growth and extinction in small or low-density populations (Allee 1931, Courchamp et al. 1999). *Lymantria dispar* experiences strong Allee effects, which are characterized by a threshold below which populations are likely to become extinct in the absence of immigration (Tobin et al. 2009). Allee effects can be caused by a variety of mechanisms, and those effects in *L. dispar* may result from a combination of multiple factors, including mate-finding failure (Contarini et al. 2009; Robinet et al. 2007, 2008; Sharov et al. 1995; Walter et al. 2015, 2016) and predation (Bjørnstad et al. 2010, Haynes et al. 2009, Tobin et al. 2009). The empirical evidence in the cited studies on the role of mate-finding failure in driving Allee effects in *L. dispar* was foundational to research and management alike.

The key implication of strong mate-finding failure Allee effects for *L. dispar* management is that the moth's spread can be mitigated, not necessarily by driving population density to zero, but by driving population density below the Allee threshold (Liebhold and Bascompte 2003, Liebhold and Tobin 2008, Tobin et al. 2012). Once below the Allee threshold, the population is likely to decline to zero without further intervention, particularly when the population is isolated and receives few or no immigrants to supplement it (Taylor and Hastings 2005). That mate-finding failure is a key mechanism of Allee effects also affirms the value of mating disruption treatments for slowing *L. dispar* spread. Reducing rates of mate-finding effectively shifts the Allee threshold to higher densities (Liebhold and Tobin 2008; Walter et al. 2015, 2017), causing populations remaining below the elevated Allee threshold to decline toward extinction.

The strength of Allee effects in *L. dispar* populations has been found to vary across the invasion front (Tobin et al. 2007b, Walter et al. 2020), meaning that the threshold population density that determines whether a population will persist and increase in abundance or become extinct without supplementation from immigrants differs from place to place. These differences are due to variation in environmental conditions that influence key population processes; chief among these are reproductive phenology, male flight, and mortality (Robinet et al. 2007).

The timing, or phenology, of reproductive development differs between male and female *L. dispar* and within and among *L. dispar* populations (Gray 2004). These differences are partly responsible for differences in mating success and Allee effects across the invasion front. This species exhibits protandry, in which males in a population tend to emerge as reproductive adults earlier than females, typically by a few days (Robinet et al. 2007). Additionally, within a population, individuals of each sex reach maturity over a period of days to weeks, rather than in perfect seasonal synchrony. Both the amount of protandry and the length of the period over which adults emerge are partly controlled by temperature and therefore vary across the invasion front (Gray 2004, Robinet et al. 2007, Walter et al. 2015). The degree of reproductive asynchrony (i.e., the mismatch in timing of reproductive maturation between an individual and potential mates in a population), translates to differences in mating success and Allee effects. All else being equal, increasing the mismatch between males and females in a population and spreading out the distributions of reproductive maturation dates over a longer timespan reduces mating success and strengthens Allee effects (Robinet et al. 2007, 2008; Walter et al. 2015).

Because female *L. dispar* in eastern North America are flightless, successful mating depends on male flight. Adding to studies that have shown the general positive effect of male moth density on mating success (Contarini et al. 2009, Sharov et al. 1995), recent research has investigated how characteristics of the landscape shape male flight and mating success. Since the landscape encountered by spreading populations is a mosaic of different habitat types, some suited to *L. dispar* and others inhospitable due to lack of host resources, one focal area has been how landscape structure, such as the composition and arrangement of habitat types on the landscape, influences male flight, mating success, and spread. In a series of field experiments involving the release of laboratory-reared adult male *L. dispar,* Walter et al. (2016) found that male moths dispersed similar distances in search of mates in forested versus open field habitats but were unlikely to cross forest edges into open fields, at least in the absence of a pheromone cue from the open field. Relatedly, in an experiment where "calling" females were present in both the field and the forest, Thompson et al. (2016) observed higher mating success just inside forest edges, which could be explained by directionally unbiased mate-searching movements combined with resistance to leaving forest patches. Anecdotal evidence suggests that adult male *L. dispar* moths are visually attracted to dark colors,[1] which could be the mechanism behind the observed behavioral preference for forest habitats. A biologically detailed model simulating *L. dispar* spread used by Walter et al. (2016) showed that the proportion of forest in the landscape and the degree to which the forest was connected across the landscape strongly influenced the strength of Allee effects and the rate of spread through that landscape. Less connected forest meant stronger Allee effects and slower spread. Simulation results were consistent with historical patterns of spread in Virginia and West Virginia, but the model also indicated that the most important cause of this effect was that larvae dispersing into unforested areas perished.

While strong Allee effects due to mating failure fundamentally shape *L. dispar* spread and management, the tendency for populations subject to strong Allee effects to decline

[1] Unpublished observation, Kyle Haynes, University of Virginia, 2019.

to extinction, provided they are below the Allee threshold, assumes that immigration is absent or minimal. While this assumption seems to hold more often than not, especially for isolated nascent populations targeted by STS, there are exceptions. Although larvae typically disperse between 10 and a few hundred of meters from the hatch site (Mason and McManus 1981), and adult males disperse similar distances (Robinet et al. 2008, Walter et al. 2016), specific meteorological conditions can result in a "blow-in" of male moths from established, higher-density areas to newly colonized areas, providing an influx of immigrants that facilitates population establishment and growth (Fig. 2) (Tobin and Blackburn 2008). Although the direction of spread is largely opposite that of prevailing winds, there is evidence that the rapid invasion by *L. dispar* of eastern Wisconsin was facilitated by storm events blowing east to west, across Lake Michigan (Frank et al. 2013). Similar long-distance, blow-in events are generally thought to be less common in other regions, but their true prevalence is unknown.

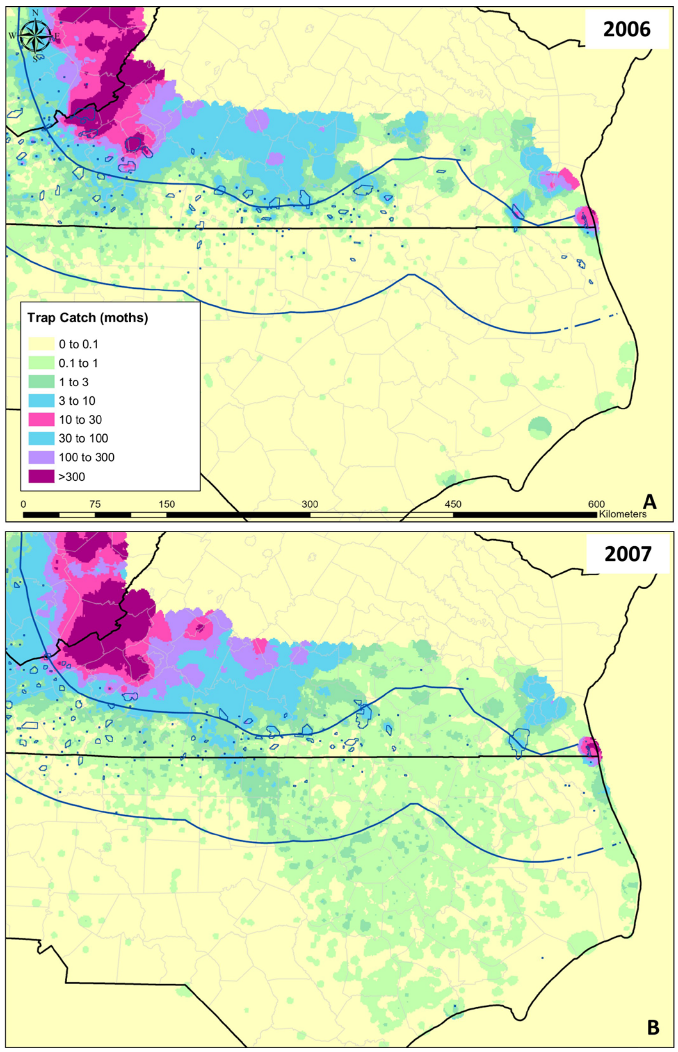

Figure 2.—Patterns of male *L. dispar* moth trap catch (interpolated trap catch density) suggestive of a blow-in event in the North Carolina piedmont. Note the rapid expansion of populations with very low average trap catch densities that are distributed relatively evenly and randomly over a large area in 2007 (B) compared to 2006 (A). Dark blue lines indicate the projected bounds of the STS action area in 2006.

It has also been shown that a pattern of pulsed (intermittent) advance and retreat of the *L. dispar* range boundary is related to population outbreaks (Fig. 3) (Johnson et al. 2006, Walter et al. 2015). A study focusing on spread in Virginia and West Virginia found pulsed advances of the *L. dispar* range boundary in years following outbreaks taking place up to 100 km (approximately 60 miles) behind the range boundary (Walter et al. 2015). That invasion pulses tended to lag outbreaks by a year suggests that egg masses were transported inadvertently by humans from outbreaking populations to the invasion front, where adult males arising from them were detected the following year. If invasion-front populations experienced an influx of larval or adult life stages during outbreaks, then the invasion pulse should be detected in the same year as the outbreak. Regardless of the manner in which immigrants arrive—whether blown in on storms or by accidental human transport—these inputs of immigrant moths to local, nascent populations raise local population densities, increase mating success, and enable populations to exceed the Allee threshold, become established, and facilitate further spread.

GEOGRAPHICAL VARIATION IN CLIMATE AFFECTS *LYMANTRIA DISPAR* SPREAD

Across the range boundary, from North Carolina to Minnesota, rates of *L. dispar* spread vary widely on regional scales (Grayson and Johnson 2018; Tobin et al. 2007a, 2007b) and finer scales (Grayson and Johnson 2018; Walter et al. 2015, 2016). Climatic differences are one of the major drivers of spread rate variation, even at relatively fine spatial scales. It has long been known that temperature is an important factor shaping whether *L. dispar* can persist in an area (Gray 2004, Nunez-Mir et al. 2022, Sharov et al. 1999); however, some recent spread patterns have accorded poorly with earlier predictions and led to new insights into how climate shapes *L. dispar* spread.

At the southwestern edge of the expanding range front, spread appears to have slowed or stopped as a result of high summer temperatures. Tobin et al. (2014) documented range retractions in the coastal plain ecoregion of eastern Virginia and North Carolina and associated these retractions with "supraoptimal" hot temperatures, that is, those that exceed optima for growth and development. A dedicated program of research subsequently determined the likely physiological basis for this pattern, finding that extreme warm temperatures reduce egg viability, impair larval development, and lead to mortality. It has been shown for traits associated with tolerance to hot temperatures that *L. dispar* has adapted to local climate conditions, such that life stages originating from places that commonly experience hot temperatures are more tolerant of them (Banahene et al. 2018; Faske et al. 2019; Thompson et al. 2017, 2021).

At the other end of the range, *L. dispar* has expanded its northwestern range into areas predicted to have low climatic suitability due to cold temperatures (Fig. 4). One contributing factor may be the role of snowpack in insulating egg masses from extreme cold air temperatures (Streifel et al. 2019), but further research is needed to examine this and other mechanisms that potentially allow *L. dispar* to persist in areas previously thought to be too cold, whether due to lethal extreme cold temperatures or insufficient warmth to complete development. Tests of geographic variability in tolerance to cold temperatures are forthcoming (Hafker et al. 2021). Adaptation of *L. dispar* to local climates will be discussed further in the next section.

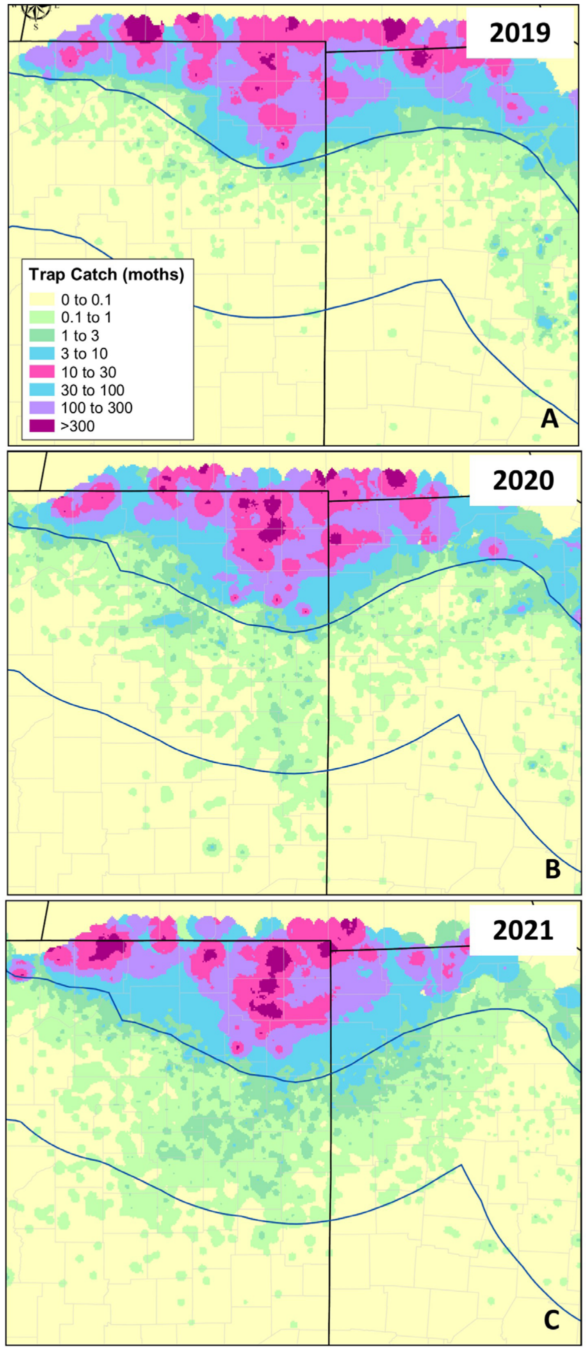

Figure 3.— The *L. dispar* invasion front can surge forward, creating a pulsed invasion dynamic, particularly when populations in established areas behind the invasion front are high and there is substantial defoliation. Low-density populations surged forward between 2019 (A) and 2020 (B), and in 2021 (C) were largely persistent and had expanded somewhat from their 2020 distributionin Indiana and Ohio. Dark blue lines indicate the projected bounds of the STS action area.

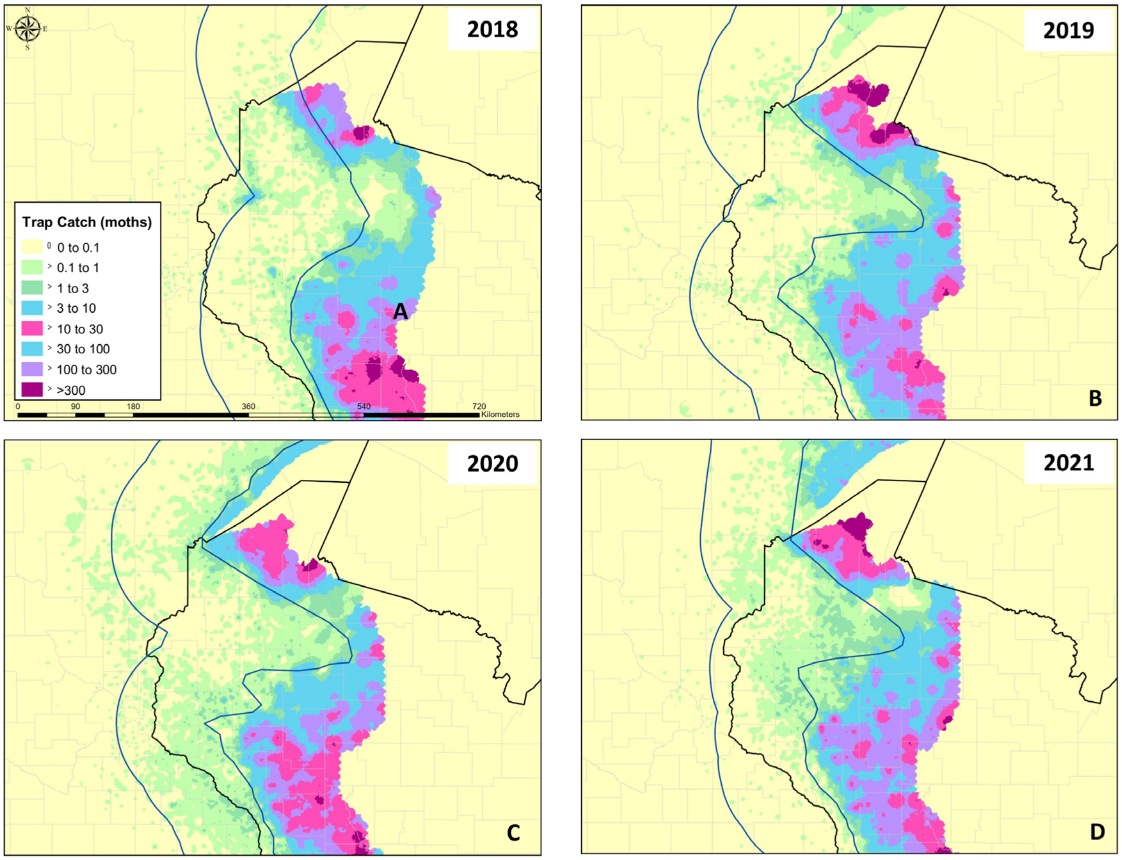

Figure 4.— Models of *L. dispar* development (Gray et al. 2004) predict low climatic suitability for *L. dispar* in northernmost Wisconsin and the arrowhead region of Minnesota, but from 2019 to 2021 (A, B, C, and D), populations became established and reached high densities in these areas. Dark blue lines indicate the projected bounds of the STS action area.

More subtly, temperature also influences the degree of reproductive asynchrony in a population. Walter et al. (2015) found that temperature creates different levels of reproductive asynchrony and mating success across broad climatic zones encompassed by the invasion front as well as locally with changes in elevation. In colder climates, the interval between the emergence of adult males and adult females (i.e., protandry) is longer, and the distribution of maturation dates for each sex is broader. In other words, the effective population density is smaller because as a population's reproductive maturation extends over a longer period and *L. dispar* also perish, a smaller fraction of the total population is reproductively mature at any given time. This strengthens Allee effects and slows population growth and spread. Although subtler than regional differences in reproductive asynchrony, the authors found that effects of climate on reproductive asynchrony and mating success are substantial enough that populations at different elevations can experience differences in mating success, and populations in areas of high topographic variability may have reduced mating success due to increased reproductive asynchrony.

GENETIC ADAPTATION OF INVADING *LYMANTRIA DISPAR* POPULATIONS

Changes in the genetic composition during the spread phase is a phenomenon observed in many different invading species (Baker and Stebbins 1965, Keller and Taylor 2008). These changes may result from stochastic effects (e.g., founder effects), selection unique to the establishment of populations at the invasion front, or long-term selection acting upon established populations. Despite the enormous economic importance of *L. dispar* and its presence in North America for more than 150 years, relatively little is known about genetic changes that have occurred during its invasion. Part of the reason for this lack of evidence of genetic changes during the *L. dispar* invasion of North America is the general lack of genetic variation within the North American population, presumably a result of a genetic bottleneck occurring during initial establishment (Wu et al. 2015).

Recently, Friedline et al. (2019) investigated genetic variation as a result of divergent selection. The authors compared phenotypic and genetic variation among six North American populations with varying dates of initial invasion. Among phenotypic traits tested, geographical variation in larval developmental time was strongest, with relatively little variation found in either pupal mass or pupal duration. The authors also made genome-wide analyses (based on single nucleotide polymorphisms, or SNPs) to investigate the genetic basis for each trait and to search for evidence of selection on those genes. Evidence indicated a polygenic architecture for each trait. Similar to other studies, the authors found low levels of genetic structure across the North American range as well as evidence of bottlenecks occurring during historical range expansion. They also found evidence of historical divergent natural selection on larval developmental time and pupal mass with strongest signals of such selection present in relatively new populations at the range margin. The authors conclude that local adaptation has contributed to the ability of *L. dispar* to spread and establish in new regions of North America that differ in climate and other environmental characteristics. However, the question of how such adaptation has affected rates of spread and how this adaptation might affect the success of the STS Program remains an open question.

As described in the preceding section, *L. dispar* has encountered highly divergent climatic conditions as it has expanded its North American range, and there is ample evidence that this climatic variation has translated into variable rates of spread across the range. A good example of this effect is seen in the markedly slower rate of spread (i.e., zero spread or retraction) in the coastal plain of Virginia (Tobin et al. 2014). Faske et al. (2019) conducted transplant experiments using insects collected both inside and outside of this region, which were reared simultaneously inside and outside of the same regions. Similarly, Thompson et al. (2017) simulated transplant experiments by rearing populations sourced in different regions under different temperature regimes. Faske et al. (2019) found that all populations exhibited lower fitness when reared in the coastal plain, supporting the hypothesis that climatic conditions in the coastal plain adversely affect *L. dispar* performance and spread. Thompson et al. (2017) found that northern populations exhibited greater larval mortality and that eggs collected from populations in the coastal plain region survived at higher rates than other populations when reared in the coastal plain climate. These results provide more evidence for local adaptation of *L. dispar* to climatic extremes that they encounter as they expand their range.

AREAS OF FUTURE RESEARCH

Even though the invasion of *L. dispar* is better understood than that of most non-native species, many aspects remain unclear. Improved understanding of spread holds potential for increasing the effectiveness and cost efficiency of the STS Program.

The STS DA currently applies criteria for decision-making that are largely constant across the entire action area (i.e., the *L. dispar* transition zone). However, environmental factors such as climate, forest composition, and human activities vary across the invasion front and likely influence local *L. dispar* reproduction and spread, and how they do so is not completely understood. Deeper knowledge of these influences could potentially be used to prioritize trapping and treatments in certain areas, which could potentially lead to cost savings and increased effectiveness of the STS Program.

A largely unknown aspect of *L. dispar* spread is the role of natural enemies (predators, parasitoids, and pathogens) in influencing patterns of spread. Results from one study (Hajek and Tobin 2011) indicated that the pathogens *L. dispar* nucleopolyhedrovirus (LdNPV) and *Entomophaga maimaiga* Humber, Shimazu, and R.S. Soper (Entomophthorales: Entomophthoraceae), as well as the parasitoid *Compsilura concinnata* Meigen (Diptera: Tachnidae) are present in populations near the expanding *L. dispar* population front. However, it is not clear how these agents are affecting host populations and ultimately how these effects are influencing rates of spread. Less is known about how populations are affected directly after initial colonization; unfortunately, low population densities preclude meaningful sampling of larval populations that exist at the time of initial colonization. Even less is known about the effects of predators on spread. Studies within the generally infested area indicate that predation by small mammals is the largest source of mortality in low-density populations, yet almost nothing is known about impacts of predators on spread. Predator population densities are known to vary considerably among different forest types, and this variation potentially could influence spread rates. Knowledge of geographical predator variation could potentially be incorporated into the STS DA.

Even though the STS Program is designed to find and suppress isolated populations ahead of the expanding population front, little information exists about the principal pathways responsible for the founding of these isolated populations. In one study, Bigsby et al. (2011) examined statistical correlates of the presence of isolated *L. dispar* populations for counties falling in the transition zone. They found that the use of wood for home heating was positively correlated with the occurrence of new isolated populations, suggesting that accidental movement of life stages (e.g., egg masses) with firewood is a likely invasion pathway that facilitates local spread. Other studies of *L. dispar* establishment in more distant uninfested areas (e.g., California) indicate the importance of accidental transport of life stages with household moves as a key invasion pathway (McFadden and McManus 1991). A refined understanding of important invasion pathways in the transition area as well as identification of mitigative procedures could ultimately lead to greater effectiveness of the STS Program, in particular the regulatory component.

The STS Program relies on the use of pheromone-baited traps to locate isolated colonies that are targeted for treatment. In most cases, this approach works well; however, data show that in certain areas and in certain years, large numbers of adult males disperse long distances from outbreak areas into STS trapping grids, and their presence in the grids may obscure the presence of locally reproducing isolated populations. Evidence for this phenomenon can be found in reports of captures of males in STS trapping grids during times other than the seasonal period of locally developing adult males (Régnière and Sharov 1998, Tobin et al. 2009). Unfortunately, the phenomenon of mass migration by *L. dispar* males is poorly understood, although one study (Frank et al. 2013) found that such long-distance transport events may be associated with specific meteorological conditions. More work that clarifies the identity of these conditions and explains why the phenomenon is more common in certain regions would be useful. In addition to obscuring the detection of isolated populations in trapping grids, these mass dispersal events may strongly influence *L. dispar* spread. Considerable evidence indicates that *L. dispar* spread is limited by the failure of males to find females for mating at low densities; however, dispersal of large numbers of males into distal portions of the transition area may greatly elevate mating success in these areas and cause increases in spread rate. More work is needed to clarify this situation.

Predictions of *L. dispar* phenology (i.e., the timing of insect development) are used for various purposes in the STS Program. For example, the timing of trap placement and recovery as well as the timing of mating disruption treatments are all based on predictions of the timing of the *L. dispar* adult developmental periods. This information comes from *L. dispar* phenology models that are linked with raster climatic data in the BioSim model (Régnière et al. 2014). This approach is quite effective, although evidence suggests that phenology predictions are less accurate in more northerly portions of the STS action area. Thus, there is a continuing need to improve phenology models for use across a diversity of climatic conditions. Furthermore, incorporation of information about local adaptation of *L. dispar* populations to climate (Faske et al. 2019, Thompson et al. 2017) may also contribute to more accurate phenology predictions.

Since the beginning of the STS Pilot Project and through the operational program to the present, the STS DA has been continually modified. The initial decision algorithm was very simple, and most aspects of decisions were made based on visual assessment of trap data. Over time, refinements of the algorithm have improved its capacity to better mimic these assessments, thereby reducing subjectivity and increasing consistency. However, aside from the initial selection of the width of the action area (Sharov and Liebhold 1998), none of the refinements of the STS DA have been made based on evidence that they will increase the effectiveness of the program. This is because it has not been possible to test the efficacy of modifications relative to a counterfactual. To make such comparisons, there would be value in the development of a very realistic model of *L. dispar* spread that incorporates treatment impacts. Such a model would likely have to be spatially explicit and account for the stochastic nature of *L. dispar* spread dynamics. With such a model in hand, it would be possible to test various modifications to the STS DA and optimize its performance.

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Chapter 5

Analyses of *Lymantria dispar* Mate-Finding Behavior in Support of Management in the STS Program

Ksenia S. Onufrieva

Abstract

The National Slow the Spread (STS) Program for spongy moth, *Lymantria dispar* L. (Lepidoptera: Erebidae, formerly known as the "gypsy moth"), is a science-based program. In this paper, we provide a brief description of research funded by the STS Program with the goal of optimization and improvement of *L. dispar* management tactics. Recent research developments include evaluation of new pheromone formulations for their abilities to disrupt mating in *L. dispar* populations and their persistent effects in the environment; development of methods for ground application of pheromone and for improved evaluation of research results and their implementation in the operational STS Program; and improved understanding of the effects of climate, insects' age, and population density on mating success and mating disruption in *L. dispar* populations. Although research sponsored and conducted by the STS Program is specific to *L. dispar,* results of this work could be useful for development of tactics against other existing or future pests.

Keywords: gypsy moth, mating disruption, pheromone, pheromone formulation, spongy moth, trapping

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INTRODUCTION

The National Slow the Spread (STS) Program of spongy moth, *Lymatria dispar* L. (Lepidoptera: Erebidae, formerly known as "gypsy moth"), is a science-based, integrated pest management program (Tobin and Blackburn 2007, Tobin et al. 2007). Since its implementation as a pilot project in 1992, the STS Program has maintained a concurrent research program aimed at improving *L. dispar* management through better understanding of *L. dispar* population ecology and optimization of control tactics against this insect. A technical committee within the STS Program is charged with conducting research and providing expert recommendations. Since 2000, research funded by the STS Program has produced a total of 34 peer-reviewed papers. (Published findings that received funding are noted with an asterisk in the literature cited section of this paper.)

Chaired by a research scientist, the STS technical committee is composed of experts from the U.S. Department of Agriculture, Forest Service (USDA FS) and Animal and Plant Health Inspection Service (USDA APHIS), universities, and other state agencies. The committee meets once a year and has responsibility for (1) reviewing the operational plans relative to compliance with existing project standards and protocols; (2) identifying problem areas where the standards and protocols are not working or are not followed; and (3) identifying, prioritizing, planning, and budgeting for technology development projects needed to address problems. The chair of the technical committee provides regular updates and moderates discussions with another STS committee, the operations committee, to facilitate technical needs and updates of the STS Program. The chair of the technical committee also interacts directly with the STS program manager and the STS Foundation board of directors.

The goal of the STS Program is to reduce the rate of *L. dispar* spread by >60 percent of the historic average across the United States by identifying and managing isolated populations beyond the leading edge of the *L. dispar* population front. In STS, the primary method of *L. dispar* control is mating disruption (see Coleman et al. 2023, this report page 45), which is based on the idea of adding artificial pheromone sources to the environment at levels that interfere with the ability of flying males to find flightless females. Several mechanisms of mating disruption have been proposed, including sensory fatigue, camouflage of the natural plumes, sensory input imbalance, false trail following, and leaving the pheromone treated area (Cardé and Minks 1995, Richerson et al. 1976a, Richerson et al. 1976b, Sanders 1997). Recent studies concluded that failure of males to locate calling females is largely attributed to false trail following (Miller and Gut 2015). *Lymantria dispar* pheromone, disparlure, was identified as (+) enantiomer of Z-7,8-epoxy-2-methyloctadecane and synthesized in the laboratory (Bierl et al. 1970). Currently the synthetic (+) enantiomer of disparlure is used as a lure in traps to detect new infestations, assess densities of existing populations, and evaluate the success of control efforts. Although (+) disparlure is a better attractant than racemic disparlure (mixture of (+) and (-) enantiomers) (Miller et al. 1977, Plimmer et al. 1977), it is the 50:50 racemic disparlure that is used for mating disruption treatments because it is less costly and is sufficiently effective in disrupting mating (Kolodny-Hirsch and Schwalbe 1990). The (-)-enantiomer is known to inhibit the response of *L. dispar* males to (+)-disparlure (Cardé et al. 1977, Miller et al. 1977, Plimmer et al. 1977, Yamada et al. 1976), and therefore may also contribute to the mating disruption effect (Sharov et al. 2002b).

Mating disruption was proven to be more effective against low-density *L. dispar* populations than *Bacillus thuringiensis* var. *kurstaki* (*Btk*) treatments in a comprehensive, large-scale study (Sharov et al. 2002a). Direct comparisons between efficacies of mating disruption and *Btk* aerial treatments were made in 266 blocks, totaling 188,064 hectares. The conclusion was based on the analysis of treatment success and the need for consecutive treatments in the same area. Mating disruption also has the advantage of having no known adverse effects on nontarget species, and even the target species are not killed (USDA FS and APHIS 2012).

For successful mating disruption, synthetic pheromone must be present in the air in sufficient quantities for the duration of adult moths' activity season (approximately six weeks), which is achieved by encapsulation of a pheromone in a controlled-release matrix. A number of controlled release pheromone formulations were evaluated during the STS Pilot Project (Thorpe et al. 2006), but most of them did not release disparlure efficiently, produced inconsistent results, and were incompatible with the aircraft spray systems available at the time. From 1983 to 2009, Hercon® Disrupt® II plastic laminated flakes (Hercon Environmental, Emigsville, PA) was the only formulation available for operational use (Coleman et al. 2023, this report page 45; Reardon et al. 1998, Thorpe et al. 2006). Early mating disruption trials revealed that (1) a direct dosage-response relationship exists for disruption of mating communication and mating success (Webb et al. 1988), (2) the degree of mating is inversely related to male population density (Webb et al. 1988), and (3) a peak in mating success occurs during peak male flight (Kolodny-Hirsch and Schwalbe 1990). Mating disruption trials from 1999 to 2005 also resulted in the development of a standard protocol for evaluating efficacy of a formulation in the field using laboratory-reared *L. dispar* males and females and a list of criteria for a successful formulation (Thorpe et al. 2006), which are still utilized by the STS Program.

A standard study plot used for efficacy evaluation of an aerially applied pheromone treatment is 500 by 1,000 m separated by at least 700 m to prevent treatment interference (Sharov et al. 2002b). One plot is treated with an experimental formulation, one plot in each block is left untreated and used as control, and one plot is treated with an operational formulation and used as a positive control. Due to the large size of the experimental plots and the large distance between them, usually two blocks of plots are used, and each treatment is therefore replicated two times. Study plots are usually treated by the same contractor at the same time as the operational plots. Treatments are applied according to the STS Program contract specifications in nonoverlapping 30.5 m swaths by a fixed-wing aircraft (Air Tractor, Olney, TX) flying at 30.5 to 60.1 m above the canopy at a speed of 193 km/h.[2]

Following treatment, mating success is monitored within a core area of 350 by 350 m containing three male moth release points 180 m apart (Fig. 1). Trees in a 50 m radius circle around the central release point are used for female deployment. Virgin *L. dispar* females are protected from predation by a band of Nixalite Tanglefoot bird repellent (East Moline, IL) (Fig. 2A) (Thorpe et al. 2007a) and left on tree boles for 24 hours, after which females are collected and kept in the laboratory to deposit egg masses. Egg masses are kept for at least 60 days to allow for embryonation, after which they are examined under the microscope to determine their fertilization status. Each week, females are deployed on four consecutive days. Each set of females is recovered after 24 hours, with the final collection made on day 5.

[2] Personal communication from T.W. Coleman.

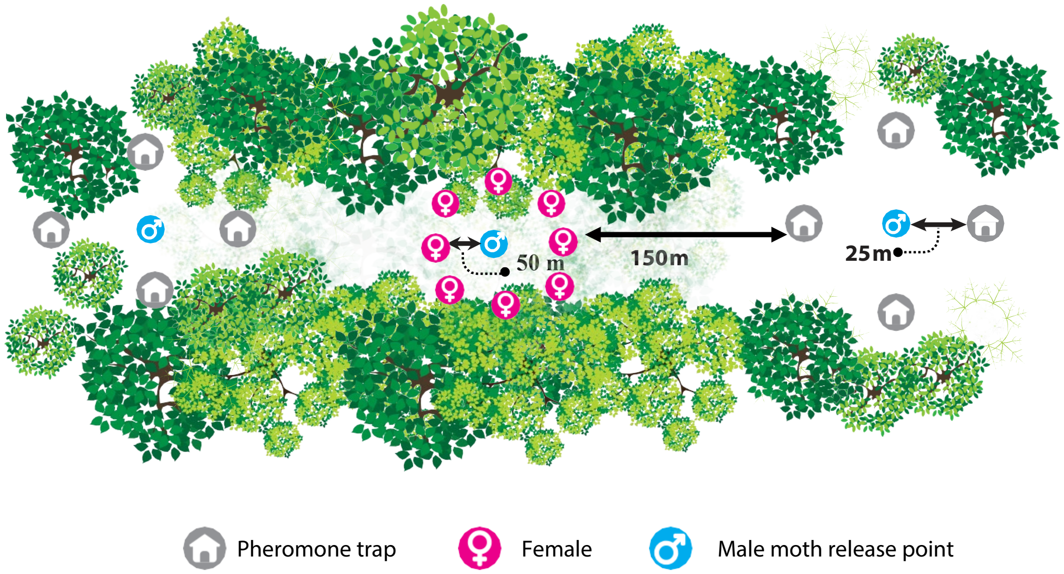

Figure 1.—Layout of pheromone-baited traps, male moth release points, and tethered females in the 300 by 300 core sampling area of an experimental forest plot. (Figure courtesy of Michael J. Stamper, Data Visualization Designer and Lecturer at the University Libraries, Data Services, at Virginia Polytechnic Institute and State University.)

Each of the two peripheral release points is surrounded by four standard USDA milk-carton pheromone traps baited with 500 µg of (+)-disparlure in twine dispensers (Scentry Biologicals, Inc, Billings, MT) (Fig. 2B). Pheromone-baited traps are checked and emptied at the time of each release. Only laboratory-reared, released males are used in statistical analyses.

To appropriately model background populations managed by the STS Program, the same number of lab-reared and marked male moths (50 to 200) are released twice a week from each of the release points (Onufrieva et al. 2019b, Onufrieva and Onufriev 2018). Releases are made by hand counting out the exact number of males at each release point to ensure equal releases among all release points in all study plots. *Lymantria dispar* pupae are supplied by the USDA APHIS, Pest Survey Detection and Exclusion Laboratory, OTIS Air National Guard Base, Buzzards Bay, MA, and reared to adults in the field lab just prior to release. A solvent red 26 dye (Royce International, Paterson, NJ) is added to the larval diet at the rearing facility. The dye is expressed in adults and is used to differentiate between released and feral male moths (Fig. 2C). The use of laboratory-reared insects ensures similar population densities among study plots and allows researchers to extend the time period during which the data can be collected.

In the STS Program, a formulation is considered suitable for operational use if it suppresses male moth catches in pheromone-baited traps and mating success of females by 90 and 95 percent, respectively, for at least eight weeks to cover the entire period of *L. dispar* flight (up to six weeks) and to provide a safety margin for uncertainties associated with the logistics of treatment planning and with *L. dispar* phenology (Thorpe et al. 2006).

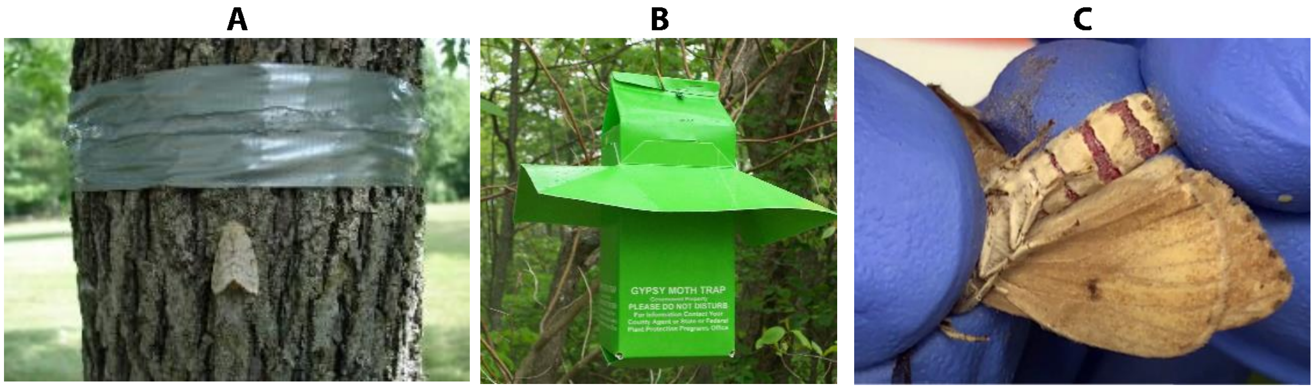

Figure 2.—A *Lymantria dispar* female deployed for mating success assessment in the center release point (A), USDA milk carton pheromone-baited trap used in the two peripheral release points (B), and an *L. dispar* male with the red dye from artificial diet used for rearing expressed in the body (C).

Since 1983, Hercon® Disrupt® II has remained the only formulation approved for operational use in the STS Program, despite efforts to develop others (Table 1) (Thorpe et al. 2006). Several experimental formulations were developed, evaluated, and compared to the efficacy of Hercon® Disrupt® II; however, none of them satisfied the STS Program criteria and could not be approved for operational use. Several attempts were also made to develop a ground pheromone treatment application to treat smaller areas that were not suitable for aerial treatment applications (Thorpe et al. 2006). Hercon® Luretape® applied at an overall dosage of 15 g AI/ha reduced mating success to the levels acceptable in the STS Program. However, Hercon® Luretape® is noticeable, takes many years to degrade, and requires removal at the end of the *L. dispar* flight season, necessitating additional funds. SPLAT GM (ISCA, Riverside, CA), formulated as paintballs and applied using a paintball gun, also demonstrated promising efficacy results (Thorpe et al. 2006), but this formulation never became commercially available.

Additional significant aerial application findings included a reduction of the operational dosage of Hercon® Disrupt® II from 75 to 37.5 and 15 g AI/ha (30.4 to 15.2 and 6 g AI/acre) (Tcheslavskaia et al. 2005b); the discovery of the effects of pheromone reaching 250 to 600 m beyond treated area boundaries (Sharov et al. 2002b); the persistence of aerial Hercon® Disrupt® II treatments beyond one year of application, thus reducing potential trap catch by 56 percent in the following year (Thorpe et al. 2007b); and the development of a skipped-swath method of pheromone application (Tcheslavskaia et al. 2005a). Still, some questions have remained unanswered, including the mechanisms underlying the persistence effect of pheromone treatments in the environment.

Finally, extensive research was conducted to relate mating success of females to the daily feral male moth catches in pheromone-baited traps and to confirm that releases of laboratory-reared *L. dispar* males in the study plots were adequate to simulate population densities treated by the STS Program (Sharov et al. 1995, Tcheslavskaia et al. 2002, Thorpe et al. 2006). However, the relationship between mating success of females and season-long trap catches as well as the relationship between male moth recaptures in experimental plots and season-long trap catches observed in the operational STS Program remained unknown.

In this paper, we report the advancements of mating disruption application techniques since the publication of Thorpe et al. (2006). All studies were conducted using the aforementioned standard procedures adopted previously by the STS Program.

Table 1.—Pheromone formulations designed for aerial mating disruption treatments against *Lymantria dispar* (produced in the United States unless otherwise noted)

Formulation	Manufacturer	Years tested	Results	EPA registration
Hollow plastic fibers	Conrel, Inc., MA	1971–1989	Inefficient release of pheromone in the field; application problems	No
Gelatin microcapsules	National Cash Register, Co., Penwalt Co., Philadelphia, PA	1971–1989	Inefficient release of pheromone in the field; application problems	No
Plastic laminated flakes Hercon® Disrupt® II	Hercon Environmental, Emigsville, PA	1971–2020	Efficacious, yet problems with application and uneven deposition	Yes
Bead formulation	AgriSense, Fresno, CA	1990	Too fast and inconsistent release rate; application problems	No
Sprayable microcapsules	3M Canada, London, Ontario	2000–2004	Release rate too fast; product withdrawn	Yes
Liquid sprayable formulation	Shin-Etsu Chemical Co., Tokyo, Japan	2002, 2005	Release rate too fast	No
Modified plastic laminated flakes	Hercon Environmental, Emigsville, PA	2003	Release rate too fast	No
Micro-flakes	Hercon Environmental, Emigsville, PA	2003	Release rate too fast	No
Hollow fibers	Scentry Biologicals, Inc., Billings, MT	2003	Release rate too fast	No
Granules	Valent BioSciences, Libertyville, IL	2003	Release rate too fast	No
BioFlakes	Hercon Environmental, Emigsville, PA	2008–2009, 2015	Efficacy similar to plastic flakes	Yes
BioGM+	Hercon Environmental, Emigsville, PA	2016–2017	Efficacy similar to plastic flakes	No
SPLAT GM	ISCA, Riverside, CA	2005–2011	Efficacy similar to plastic flakes	Yes
SPLAT GM-Organic	ISCA, Riverside, CA	2010–2021	Efficacy varies due to problems with formulation consistency	Yes

EXPERIMENTAL FORMULATIONS

Liquid Formulations

Efficacy of Aerial Applications of SPLAT GM (2006–2008)

SPLAT GM is an emulsion formulation developed by ISCA (Riverside, CA) that is designed for both aerial and ground application (Fig. 3). SPLAT is a non-Newtonian, thixotropic fluid whose viscosity decreases under stress (e.g., stirring or pumping) and increases again when the stress is removed (Mafra-Neto et al. 2013). The formulation contains 13.0 percent racemic disparlure and is applied with specially developed application systems pressurized either by positive displacement pumps, gas cylinders, or a combination of both.

SPLAT GM was tested in study plots in 2006 at 37.5 and 15 g AI/ha in Appomattox-Buckingham (ABSF) (Appomattox and Buckingham Counties) and Cumberland (CSF) (Cumberland County) State Forests, Virginia, and in 2007 in the Goshen Wildlife Management Area (GWMA) (Rockbridge County, Virginia). The results of the study indicated that SPLAT GM reduced trap catches and mating success of females by >90 percent and >99 percent, respectively, for at least 10 weeks, meeting the threshold for a successful application (Figs. 4 and 5) (Onufrieva et al. 2010).

A B

Figure 3.—SPLAT GM-Organic formulation designed for aerial (A) and ground (B) application for *L. dispar* mating disruption.

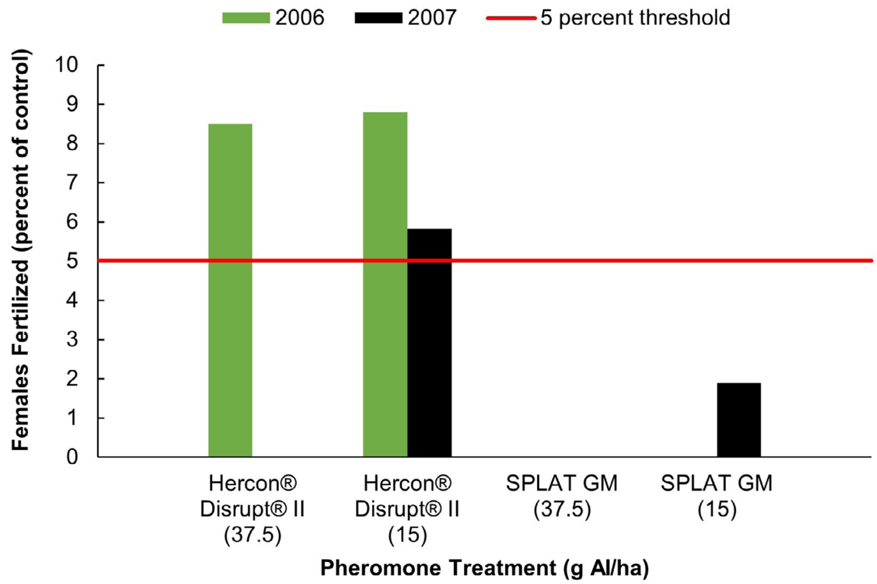

Figure 4.—Female mating success reduction in plots treated with Disrupt® II and SPLAT GM at 37.5 and 15 g AI/ha in Appomattox-Buckingham and Cumberland State Forests, VA, and in 2007 with Disrupt® II and SPLAT GM at 15 g AI/ha in Goshen Wildlife Management Area, VA. To satisfy the National Slow the Spread Program criteria, bars should be below the red line. Mating success of females in plots treated with SPLAT at 37.5 g AI/ha was reduced by 100 percent in both years.

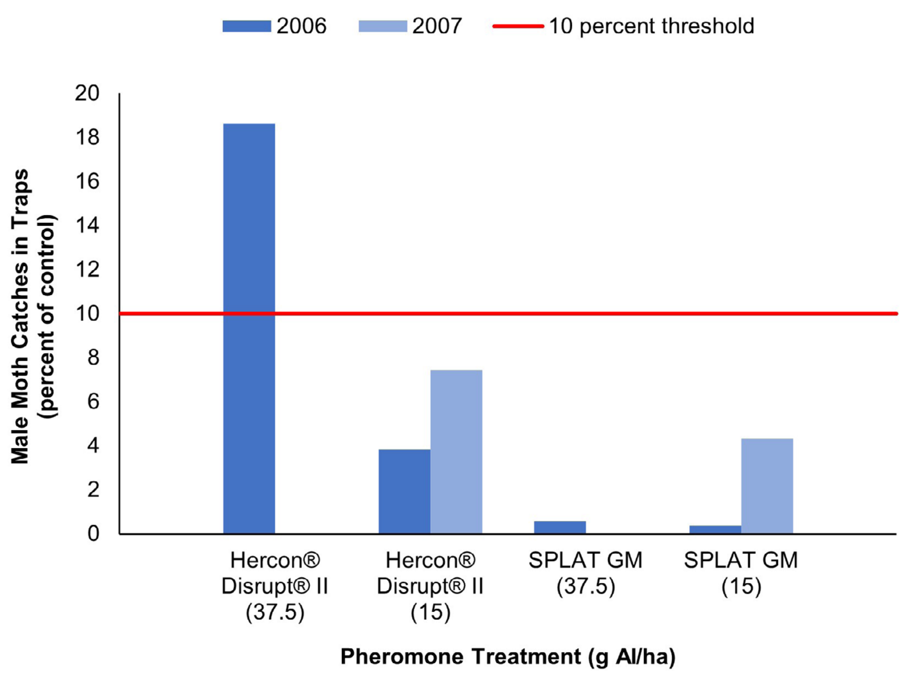

Figure 5.—*Lymantria dispar* males captured in plots treated in 2006 with Disrupt® II and SPLAT GM at 37.5 and 15 g AI/ha in Appomattox-Buckingham and Cumberland State Forests, VA, and in 2007 with Disrupt® II and SPLAT GM at 15 g AI/ha in Goshen Wildlife Management Area, VA. To satisfy the National Slow the Spread Program criteria, bars should be below the red line.

Until 2009, Hercon® Disrupt® II was the only formulation approved for operational use. Bringing a second formulation on the market reduced treatment prices through competition between formulators and applicators. As a direct result of this competition, in 2009 the STS Program was able to treat 5 percent more hectares with the same budget than it would have prior to SPLAT GM being on the market (Onufrieva et al. 2010).

In 2008, we conducted a dosage-response study to determine the lowest dosage of SPLAT GM that effectively disrupts mating. The dosage of 7.4 g AI/ha appeared to be as effective as the operational dosage of 15 g AI/ha and lasted greater than eight weeks (Fig. 6) (Onufrieva et al. 2010).

Efficacy of SPLAT GM-Organic (2010–2020)

In 2010, ISCA (Riverside, CA) developed a new liquid SPLAT GM-Organic formulation, which was approved by the USDA to meet National Organic Program standards for use in organic certified farms. Organic formulation is safer for the environment and therefore helps reduce public concern and resistance to aerial mating disruption treatment applications. In 2010, due to calibration errors, SPLAT GM was applied at 11.5 g AI/ha and SPLAT GM-Organic was applied at 22.6 g AI/ha. In 2011, calibration issues were resolved and both formulations were applied at an operational dosage of 15 g AI/ha. The results of a 2-year field trial (2010 and 2011) demonstrated that the SPLAT GM-Organic formulation was as effective as SPLAT GM and Hercon® Disrupt® II when applied at similar dosages, and that it reduced mating success, as measured by male moth catches in pheromone-baited traps, by >90 percent compared to untreated control plots for 10 weeks (Figs. 7 and 8).

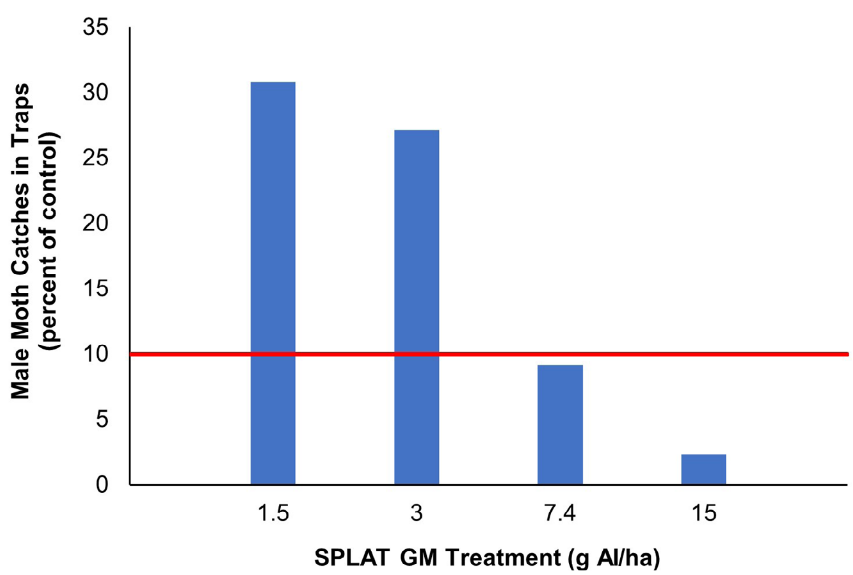

Figure 6.—*Lymantria dispar* males captured in plots treated in 2008 with various dosages of pheromone formulated as SPLAT GM in Goshen Wildlife Management Area, VA. To satisfy the National Slow the Spread Program criteria, bars should be below the red line.

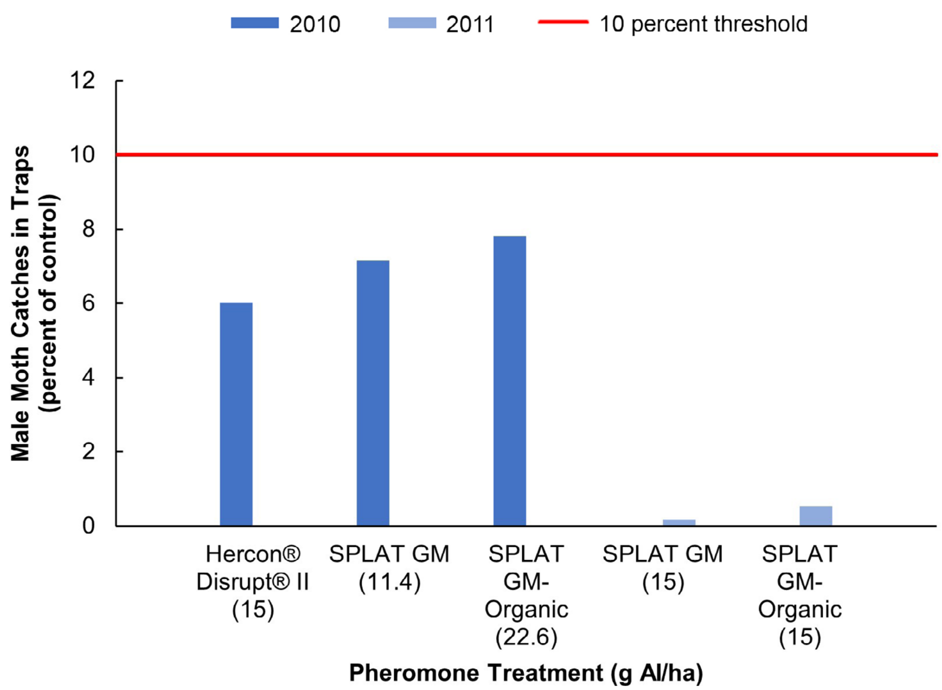

Figure 7.—*Lymantria dispar* males captured in plots treated in 2010 and 2011 with various dosages of pheromone formulated as SPLAT GM and SPLAT GM-Organic in Goshen Wildlife Management Area, VA. To satisfy the National Slow the Spread Program criteria, bars should be below the red line.

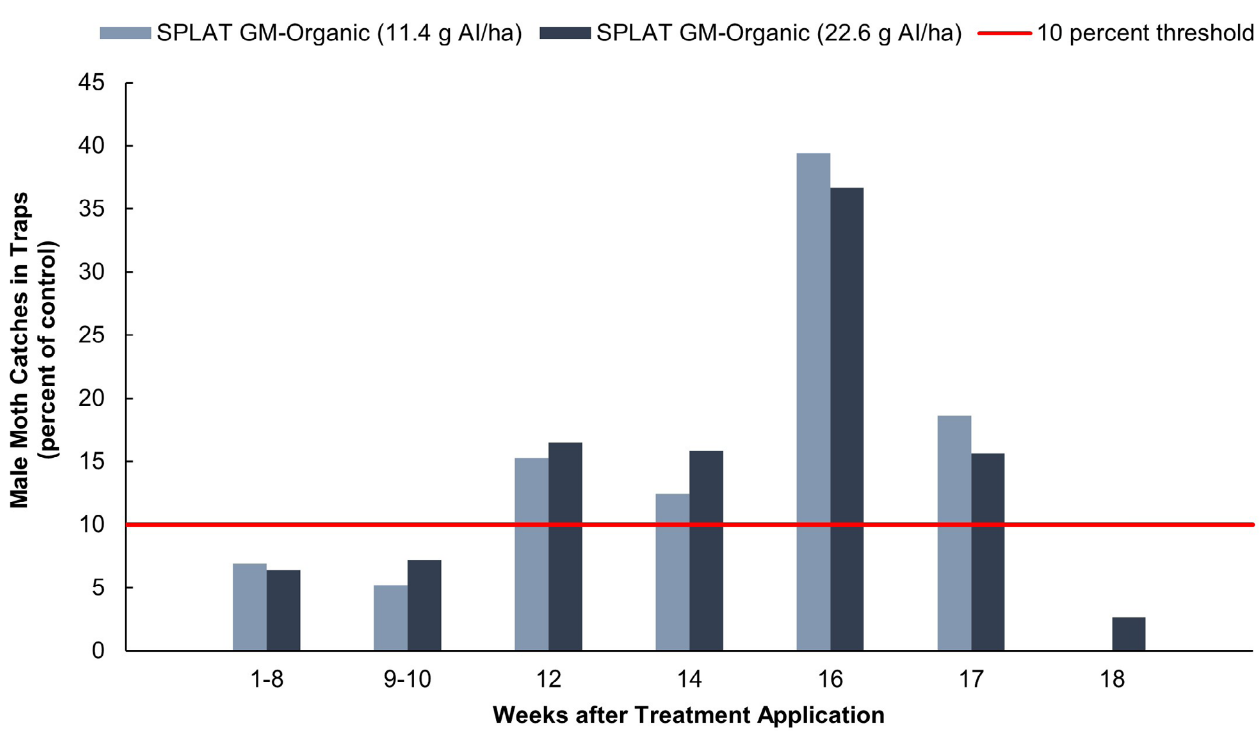

Figure 8.—Weekly *Lymantria dispar* trap catches in plots treated with SPLAT GM and SPLAT GM-Organic in 2010 in Goshen Wildlife Management Area, VA. To satisfy the National Slow the Spread Program criteria, bars should be below the red line. Missing bar for week 18 represents 100 percent trap catch reduction compared to untreated control.

Based on these results, SPLAT GM formulations were approved for operational use and were not evaluated again in the study plots until 2017, when SPLAT GM-Organic transitioned to being the sole product for treating STS operational plots. In 2018, in an attempt to reduce the cost of operational aerial treatments, we tested lower dosages (7.4 and 11 g AI/ha) of pheromone formulated as SPLAT GM-Organic and compared their efficacies to the efficacy of the operational dosage (15 g AI/ha). All tested dosages of SPLAT GM-Organic, including the operational dosage of 15 g AI/ha, failed to reduce trap catches to the levels acceptable in the STS Program (Fig. 9). These results were inconsistent with the results of the previous studies conducted using this formulation, in which this product successfully reduced mating success and trap catches.

To understand the reason for SPLAT GM-Organic failure, we evaluated the distribution of droplet sizes and compared it to the distribution of droplet sizes evaluated in 2009.[3] A slight change in product formulation could alter droplet sizes and subsequently cause a change in efficacy. In both years, SPLAT GM-Organic was evaluated at Al's Aerial Spraying (Ovid, MI) and applied to paper cards using the same equipment and application parameters as in operational treatment applications. Droplets were measured using Bausch and Lomb (Laval, Quebec, Canada) measuring magnifier and were categorized according to sizes.

The droplet analysis indicated that aerial applications of SPLAT GM-Organic used in 2018 produced lower number of large droplets compared to the SPLAT GM formulation tested in 2009 (Fig. 10) due to lower viscosity. Reduced viscosity explains the failure of SPLAT GM-Organic to reduce trap catches in study plots to the required levels for eight weeks. Since droplets are spheres, when the droplet diameter is doubled, its surface area is squared and its volume is cubed. Therefore, the larger the droplet, the smaller the surface area to volume ratio, and thus larger droplets release pheromone more slowly than the small ones. For SPLAT GM formulation to be effective, droplets of various sizes need to be present in sufficient quantities: small droplets release pheromone quickly and build the initial pheromone cloud in the treated area, while larger droplets release pheromone at a slower rate and are essential for maintaining the pheromone cloud for the duration of the *L. dispar* flight season.

In 2019, a modified, thicker formulation of SPLAT GM-Organic was tested at both an operational dosage of 15 g AI/ha and a reduced dosage of 11 g AI/ha; however, the modified formulation still did not meet the program's criteria (Fig. 9). In 2020, SPLAT GM-Organic was modified to further increase viscosity, which restored its efficacy to match the efficacy observed in 2006 through 2017 (Fig. 11). Analysis of the droplet size distribution of SPLAT GM-Organic evaluated in 2020 indicated that this formulation produced 7.3 percent and 14.5 percent more large droplets compared to the formulations evaluated in 2009 and 2018, respectively (Fig. 10). The data collectively suggest that for successful mating disruption, the distribution of large droplets (≥ 1500 μ) of SPLAT GM formulations need to range from 16 to 24 percent.

This highlights the importance of quality control and the need for periodic testing of each operational formulation to ensure adequate efficacy.

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[3] Unpublished data on file with John F. Kyhl, USDA Forest Service, 1992 Folwell Ave., St. Paul, MN 55108, john.f.kyhl@usda.gov, (651)366-7706.

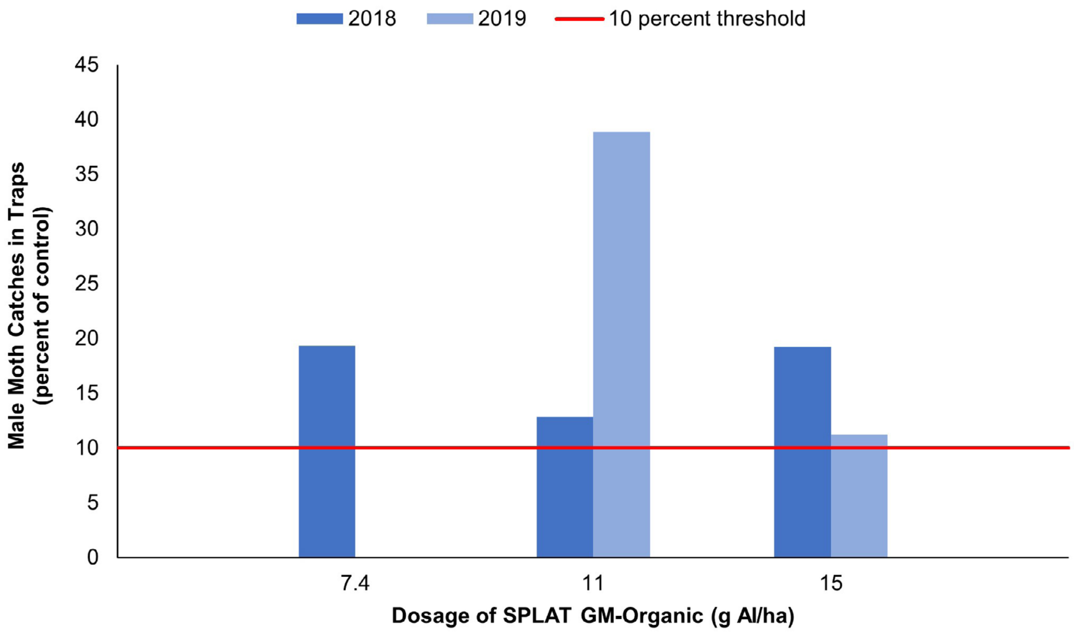

Figure 9.—*Lymantria dispar* males captured in plots treated in 2018 and 2019 with various dosages of pheromone formulated as SPLAT GM-Organic in Goshen Wildlife Management Area, VA. To satisfy the National Slow the Spread Program criteria, bars should be below the red line.

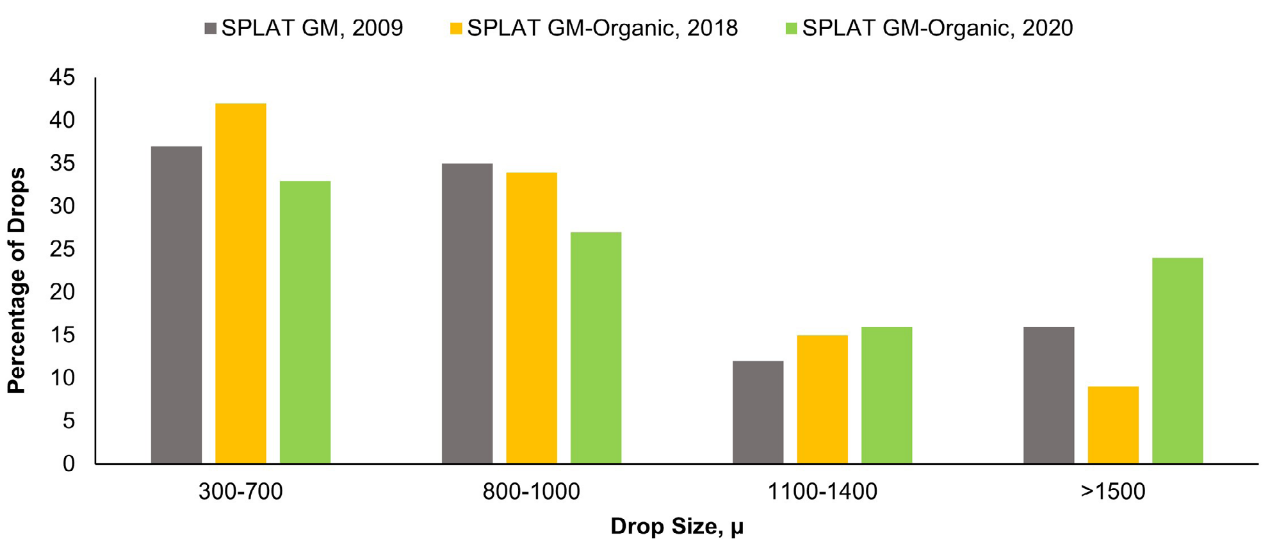

Figure 10.—Frequency distribution of drop sizes of aerially applied SPLAT GM in 2009 and SPLAT GM-Organic in 2018 and 2020.

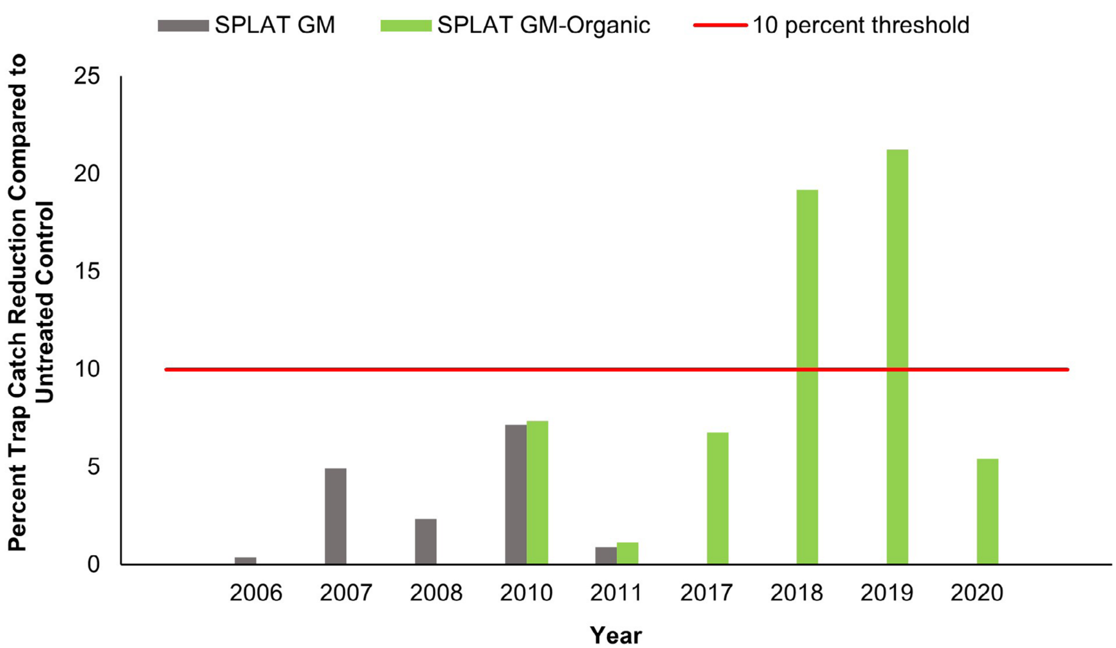

Figure 11.—Summary of *Lymantria dispar* males trap catches in experimental plots treated and monitored from 2006 through 2020 with SPLAT GM and SPLAT GM-Organic at 15 g AI/ha in Goshen Wildlife Management Area, VA. To satisfy the National Slow the Spread Program criteria, bars should be below the red line.

Flake Formulations

The Hercon® Disrupt® II formulation consists of plastic flakes composed of polyvinyl chloride (PVC) outer layers and an inner polymer layer containing 17.9 percent racemic disparlure. The flakes are mixed with diatomaceous earth (3 percent weight/weight) to reduce clogging and aerially applied using a fixed-wing aircraft (Air Tractor) equipped with specialized application pods (Schweitzer Aircraft, Elmira, NY). Within the pods, the flakes are mixed with a multipolymer emulsion glue (Gelva 2333, Solutia, Springfield, MA) and dispensed through a spinner (Thorpe et al. 2006). Flakes release between 30 and 50 percent of their disparlure content over the six-week period of male moth flight (Leonhardt et al. 1992, Thorpe et al. 2006).

In response to the increasing concern regarding microplastics accumulation in the environment and its adverse effects on living organisms (Andrady 2011, Barnes 2002, Moore 2008), Hercon Environmental developed two new biodegradable formulations: BioFlakes (small and regular size) a and BioGM+ (Fig. 12). We evaluated the efficacies of these new formulations applied at 15 g AI/ha with the efficacy of the same dosage of the operational Hercon® Disrupt® II formulation.

Efficacy of Hercon BioFlakes (2008–2009, 2015)

In each experiment, the male moth catches in the pheromone-baited traps were reduced by all treatments to the levels acceptable in the STS Program (Fig. 13). As a result of this test, the BioFlake formulation was approved for operational use and applied to 1,214 ha in 2015 and 4,128 ha in 2016.

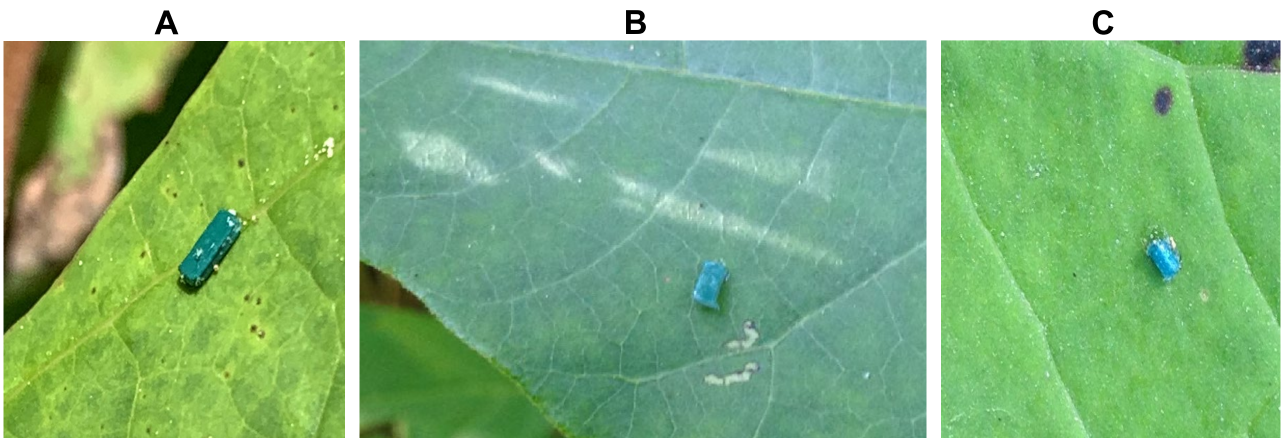

Figure 12.—Hercon® Disrupt® II plastic flake (A), BioFlake (B) and BioGM+ flake (C) pictured on leaves in study plots.

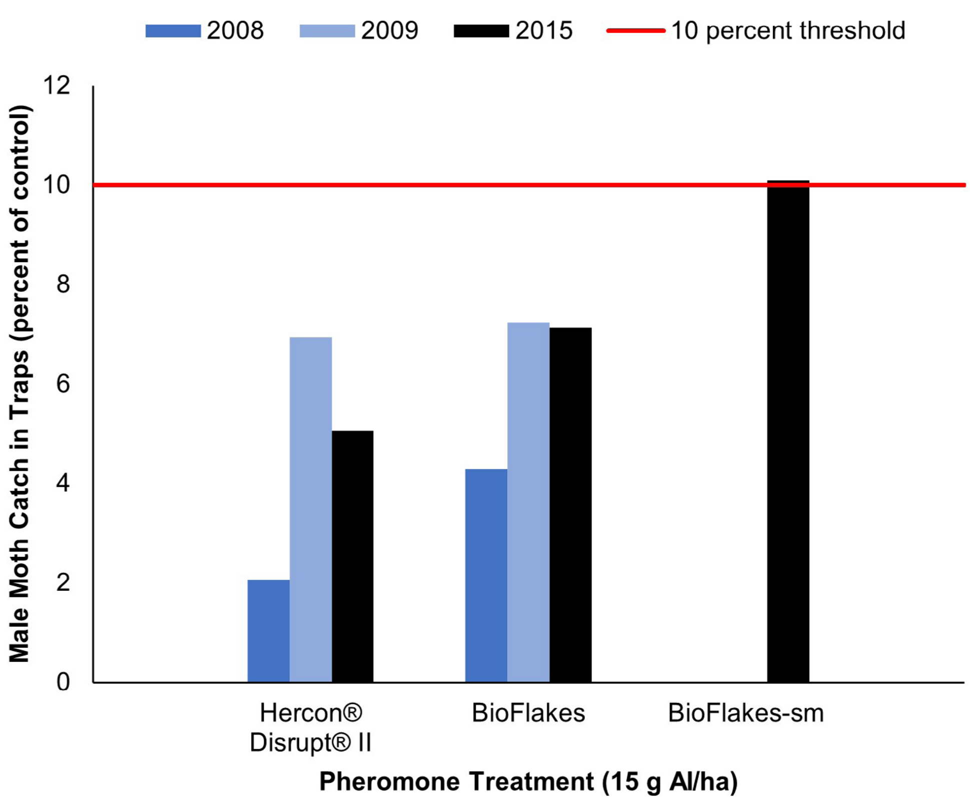

Figure 13.—Male moths collected in pheromone-baited traps in plots treated with various formulations of Hercon flakes compared to untreated controls. To satisfy the National Slow the Spread Program criteria, bars should be below the red line.

Efficacy of BioGM+ (2016–2017)

In 2016 and 2017, we evaluated the efficacy of BioGM+ and compared it to the efficacies of Hercon® Disrupt® II and BioFlakes. In 2016, both BioFlakes and BioGM+ failed to reduce the trap catches to the levels acceptable in the STS Program during the entire period of data collection; however, in 2017 the efficacy of BioGM+ was comparable to the efficacy of Hercon® Disrupt® II (Fig. 14). Despite the positive results, additional tests were not conducted, and BioGM+ did not become an operational formulation due to costs of production and change of personnel at Hercon Environmental.

PHEROMONE PERSISTENCE IN THE ENVIRONMENT

Synthetic pheromone applied for mating disruption can sometimes continue to reduce trap catches one year after application, producing a so-called "persistent effect." Persistent effect of aerial *L. dispar* pheromone treatments was first observed in 2004 (Thorpe et al. 2007b), but the reason for significant reduction of trap catches one year after the pheromone application remained unknown. Pheromones are known to be adsorbed onto solid surfaces, such as bark, foliage, and leaf litter, and released back into the environment (Gut et al. 2004, Karg et al. 1994, Suckling et al. 1996, Wall et al. 1981). Thus, trap catches could be reduced by the residual disparlure emitted by the natural surfaces or by the old plastic flakes left in the plots.

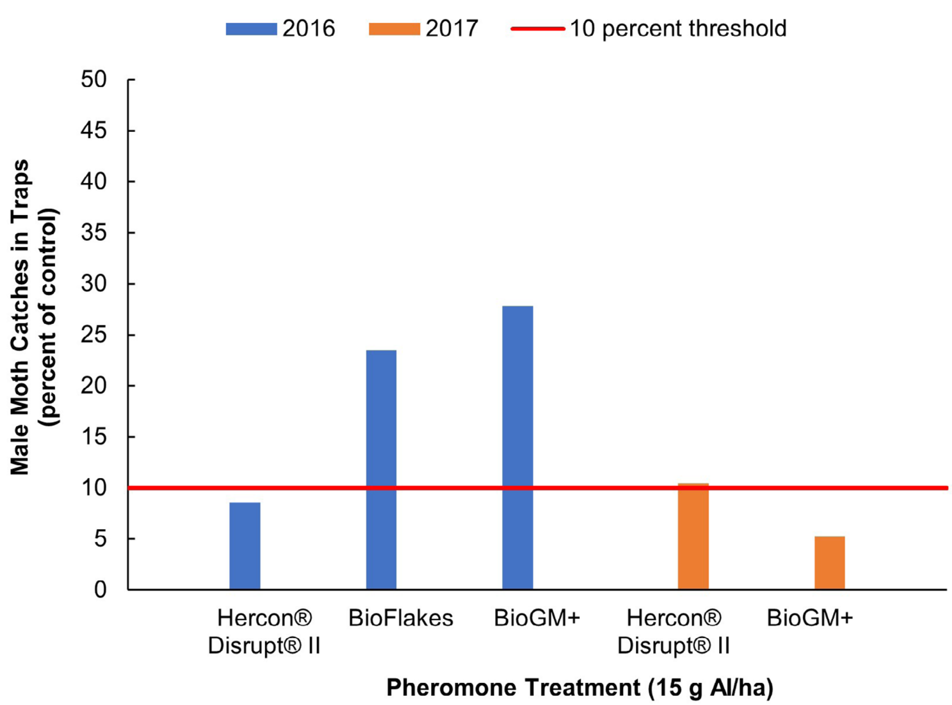

Figure 14.—Male moths collected in pheromone-baited traps in plots treated with various formulations of Hercon flakes compared to untreated controls. To satisfy the National Slow the Spread Program criteria, bars should be below the red line.

Hercon® Luretape® GM Experiment (2006–2007)

To study the source of pheromone one year after the treatment application, we treated study plots with ground applications of 90 cm-long strips of Hercon® Luretape® GM at a density of 40 point sources/ha for an overall dosage of 75 g active ingredient (AI)/ha and evaluated for short-term (one week after Hercon® Luretape® GM removal) and long-term (one year after Hercon® Luretape® GM removal) persistent effects of disparlure (Onufrieva et al. 2013). Monitoring of study plots after the removal of Hercon® Luretape® GM allowed us to evaluate persistent effect of pheromone produced by natural surfaces alone. Similar to the aerially applied formulation of disparlure, Hercon® Disrupt® II, Hercon® Luretape® GM is a three-layered plastic laminated dispenser. It is 3.8 cm wide, has two PVC outer layers, and contains racemic disparlure at a concentration of 12.9 mg/cm^2 (Kolodny-Hirsch et al. 1990). This controlled-release formulation is a standard for use in ground applications against *L. dispar* populations. The Hercon® Luretape® GM treatment reduced female mating success to 4.8 percent of that in control plots, which meets the STS Program requirement for successful treatment. During the week following the removal of the Hercon® Luretape® GM dispensers from the short-term plots, mating success increased gradually relative to untreated controls (Fig. 15). In long-term plots, Hercon® Luretape® GM was removed at the end of the flight season. During the following year, mating in these long-term plots was not different from the untreated control plots. These results suggest that a strong persistent effect one year after an aerial application of disparlure reported in previous studies (Thorpe et al. 2007b) is produced by the effects of residual pheromone in the dispensers.

Since the discovery of the persistent effect of pheromone treatments, monitoring of treated plots one year after the treatment application became a part of the standard procedure for each new pheromone formulation evaluation.

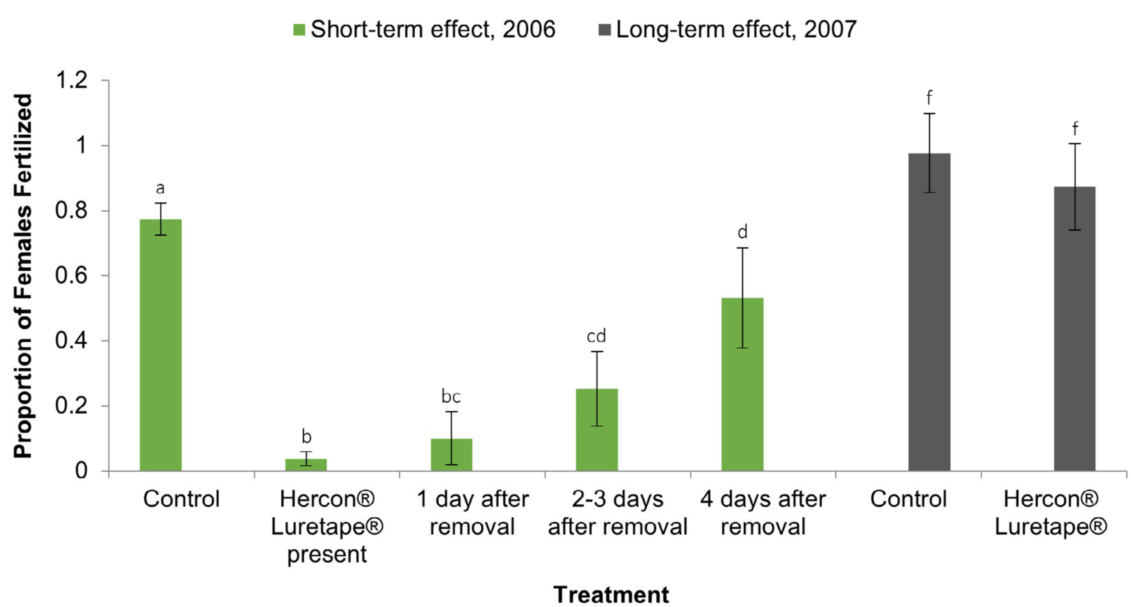

Figure 15.—Proportion of females fertilized (± SE) in plots treated in 2006 with Hercon® Luretape® GM in Goshen Wildlife Management Area, VA. Bars within each year with the same letter are not significantly different.

Persistence of Various Formulations in the Environment

Second-Year Effects of SPLAT GM and SPLAT GM-Organic (2008–2009, 2012)

We evaluated effects of SPLAT GM and SPLAT GM-Organic on trap catches one year after the application and compared them to the second-year effect of Hercon® Disrupt® II (Fig. 16). It appeared that in plots treated with SPLAT GM formulations, trap catches were reduced by 29 to 60 percent compared to untreated plots; however, the differences were not significant. In contrast, application of Hercon® Disrupt® II formulation significantly reduced trap catches compared to untreated control plots, and trap catch reductions ranged between 53 and 70 percent.

Second-Year Effects of BioFlake and BioGM+ (2009, 2010, 2018)

We compared effects of Hercon® Disrupt® II, Hercon BioFlakes, and Hercon BioGM+ on trap catches one year after the treatment applications. The results demonstrated that trap catches were significantly reduced by Hercon® Disrupt® II and Hercon BioFlakes compared to untreated control plots. We observed trap catch reductions by 50 to 70 percent in plots treated with Hercon® Disrupt® II and approximately 75 percent in plots treated with Hercon BioFlakes (Fig. 17). Trap catches in plots treated with BioGM+ were reduced by 50 percent compared to untreated control plots, but the difference was not significant, suggesting that BioGM+ formulation does not degrade faster than Hercon® Disrupt® II plastic flake formulation.

Despite extensive research conducted to understand the mechanisms of persistence effect and estimate its strength for various pheromone formulations, the effect of pheromone persistence in the environment on assessment of treatment success in management programs remains unclear.

COMPARISON OF MATING DISRUPTION IN VARIOUS CLIMATE ZONES

Previous studies have shown that the rate of disparlure release is temperature-dependent (Leonhardt et al. 1992, Leonhardt et al. 1990, Nation et al. 1993, Tobin et al. 2011), which prompted us to determine the persistent effect of synthetic racemic disparlure when applied in two climate extremes within the current STS Program action area, Virginia and Wisconsin. These two states represent transition areas of the program, which is where the majority of trapping and treatments occur (Tobin et al. 2011). Average temperatures at the time of data collection were 24.4 °C in Virginia and 20.2 °C in Wisconsin. In both Virginia and Wisconsin, male moth trap catch was significantly suppressed by all pheromone treatments relative to untreated control plots in the year of treatment. Trap catches in treated plots relative to untreated control plots were suppressed to >90 percent in both Virginia and Wisconsin (Fig. 18). Therefore, all tested formulations appear to release pheromone at adequate rates over a range of temperatures, which allows them to be used throughout the current range of *L. dispar* in the United States (Onufrieva et al. 2013).

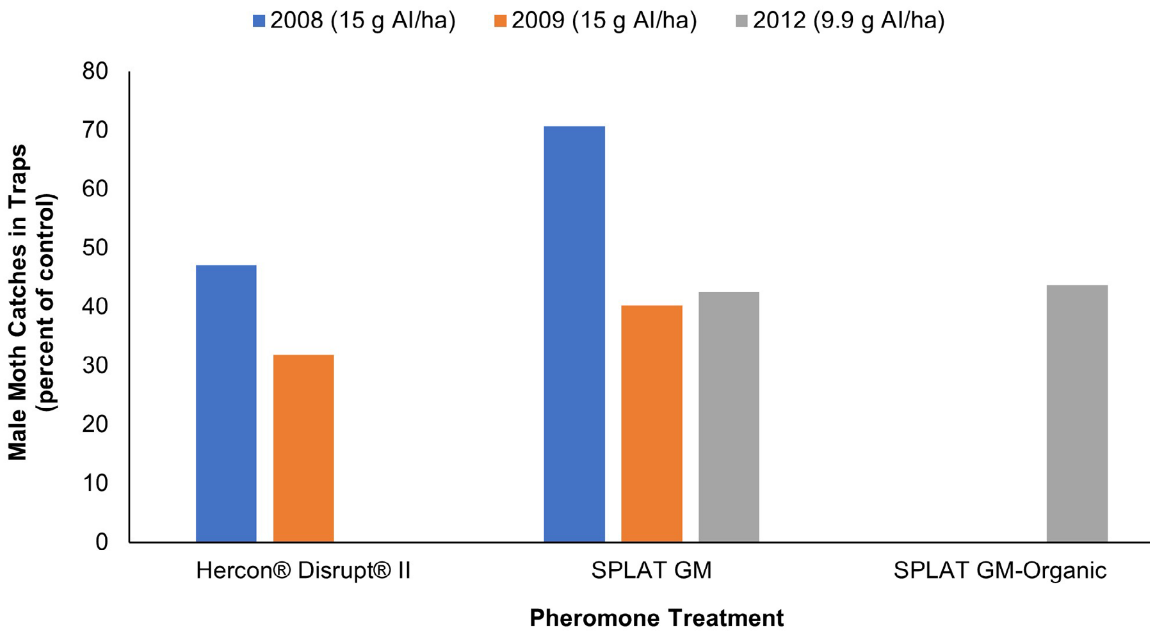

Figure 16.—Male moths captured in pheromone-baited traps one year after pheromone application from 2008, 2009, and 2012 in Goshen Wildlife Management Area, VA.

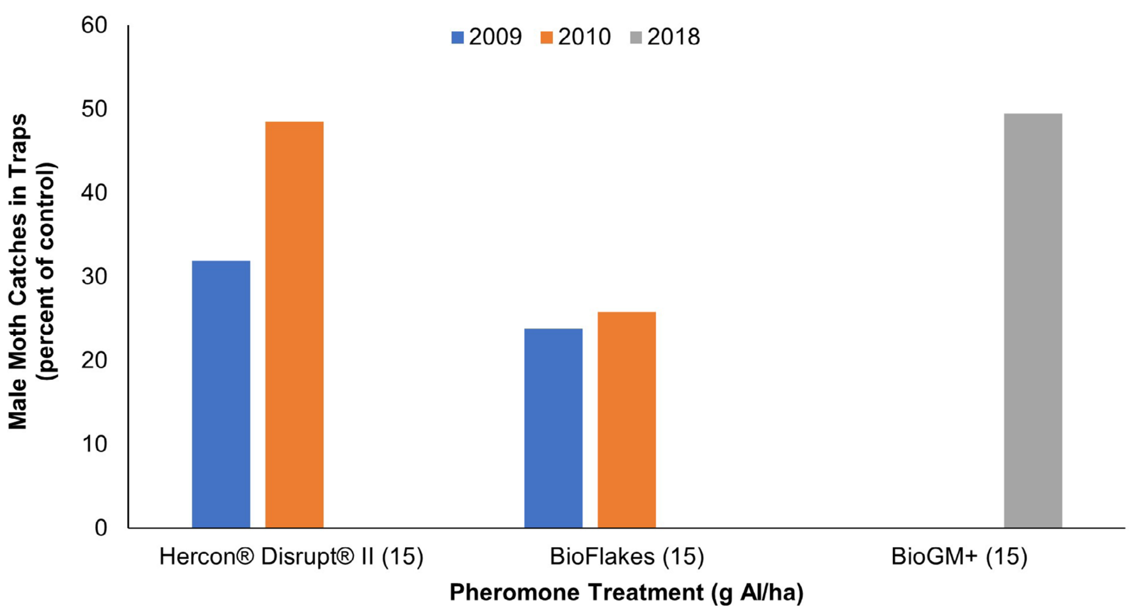

Figure 17.—Male moths captured in pheromone-baited traps one year after application of pheromone formulated as flakes in 2009, 2010, and 2018 in Goshen Wildlife Management Area, VA.

One year after treatment application, trap catches in treated plots in Wisconsin were still significantly suppressed by all treatments compared to control plots (Fig. 19). The trap catches in plots treated with Hercon® Disrupt® II, SPLAT GM, and SPLAT GM-Organic were suppressed by 70, 44, and 30 percent, respectively, compared to untreated control plots. In Virginia, the same applications of Hercon® Disrupt® II reduced trap catches by 53 percent compared to untreated control plots, while SPLAT GM reduced trap catches by 29 percent compared to control plots (Onufrieva et al. 2015). In both states, one year after the application, the liquid formulation SPLAT GM produced a weaker second-year effect than the plastic flake formulation Hercon® Disrupt® II (Onufrieva et al. 2013). Since SPLAT GM is a liquid formulation, it is applied as a mixture of droplets of different sizes. The smaller droplets degrade and release pheromone faster than the larger ones, and the number of point sources is constantly reduced. This may explain the difference in the second-year effects of aerial SPLAT GM applications between Virginia and Wisconsin. In Virginia, SPLAT GM may have been degrading faster than in Wisconsin due to higher temperatures and increased exposure to UV radiation. Both of these factors are known to affect mating disruption (Gut et al. 2004).

METHODS DEVELOPMENT

Alternative Methods of Pheromone Application

Skipped Swath Tests with Hercon® Disrupt® II and SPLAT GM (2008)

The current method for applying pheromone is in nonoverlapping swaths (30.5 m) in the same manner as conventional pesticides. Although the spray from aircraft is calibrated to deliver the correct amount of flakes in each swath, the flakes within a swath are not deposited uniformly, presumably because of lower rates of application under the fuselage and wing tips (Trent and Thistle 1999). Previous studies have indicated that aerial applications of *L. dispar* pheromone Hercon® Disrupt® II at 37.5 g AI/ha using 30 m gaps between treated swaths reduce mating disruption to the same extent as conventional uniform applications (Tcheslavskaia et al. 2005a). The skipped-swath application method allows for reduction of costs associated with fuel and flight time. We evaluated the skipped-swath method of application using Hercon® Disrupt® II and SPLAT GM at 15 g AI/ha. The results indicate that the male moth catches in pheromone-baited traps were significantly reduced by both treatments. There were no significant differences between trap catches in treated and untreated swaths for both formulations. The trap catches inside the treated plots were significantly lower than the trap catches within the 150 m area outside the plots and in the control area established about 1 km away from both of the treated plots. The trap catches in plots treated with Hercon® Disrupt® II were reduced by 95 and 88 percent in treated and untreated swaths, respectively. In plots treated with SPLAT GM, trap catches were reduced by <85 percent in both treated and untreated swaths (Fig. 20). Since both treatments failed to satisfy criteria for a successful treatment (at least 90 percent trap catch reduction), the skipped-swath method of treatment application is not suitable for the low dosage (15 g AI/ha) treatments.

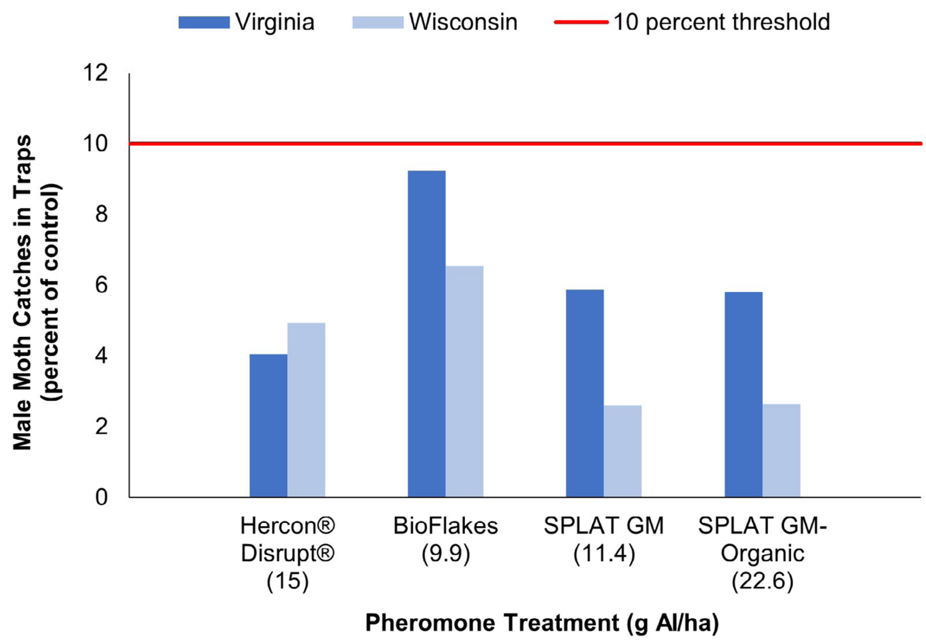

Figure 18.—Male moths collected in pheromone-baited traps in 2010 in Virginia and Wisconsin. To satisfy the National Slow the Spread Program criteria, bars should be below the red line.

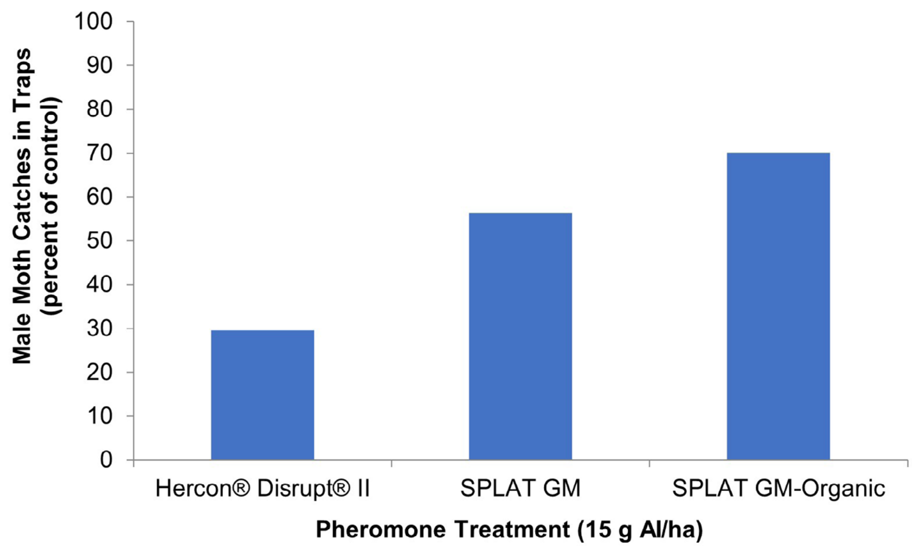

Figure 19.—Male moths collected in pheromone-baited traps one year after pheromone application in the Northern Highland American Legion State Forest, WI.

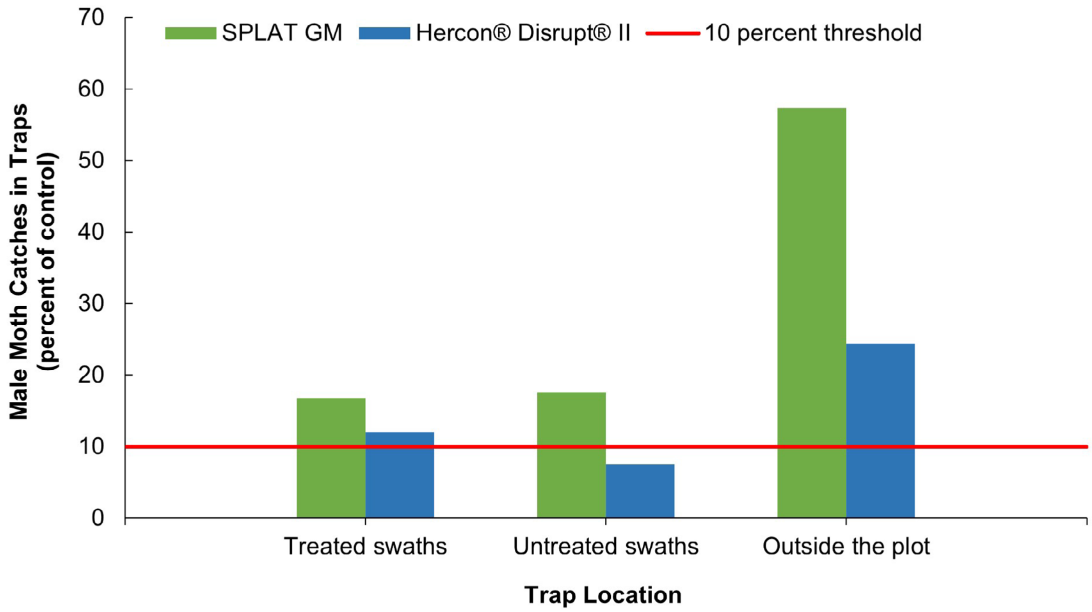

Figure 20.—Male moths captured in pheromone-baited traps located relative to the treated areas of the experimental plots. To satisfy the National Slow the Spread Program criteria, bars should be below the red line.

Method of Ground Application of SPLAT GM (2012–2014)

In the STS Program, mating disruption treatments are applied aerially to operational treatment blocks, which works well in large treatment areas such as contiguous forests or natural areas (Thorpe et al. 2006). However, aerial treatments are not always effective in small or fragmented areas (Onufrieva et al. 2019a) because they are often prohibited near ecologically sensitive areas, sensitive military installations, and bodies of water. These areas may require buffer zones to prevent drift and contamination (US EPA 1999).

Ground-based treatments are a feasible method of deploying mating disruption tactics in areas unsuitable for aerial applications. We evaluated ground applications of operational SPLAT GM formulation for their abilities to reduce mating success in low-density *L. dispar* populations (Onufrieva et al. 2019a). SPLAT GM designed for ground application (Fig. 3B) comes in plastic tubes that fit a caulking gun. We used a calibrated caulking gun for SPLAT products provided by ISCA (Riverside, CA). The results indicated that dosages of 49.4 and 123.6 g AI/ha applied using a caulking gun to tree trunks in an 11 by 11 m grid (every 11 m, 121 total release points/ha) reduced overall trap catches by >90 percent; however, the trap catches during the first week after the pheromone application were significantly higher than during the rest of the season (Fig. 21). We hypothesize that it takes SPLAT GM one week for a sufficient amount of pheromone to be emitted from ground-based treatments for adequate control. Consequently, SPLAT GM ground application should be made at least one week prior to anticipated start of *L. dispar* flight. Applications that are a week prior to flight should not present a problem because SPLAT GM applied at 49.4 and 123.6 g AI/ha sufficiently reduced trap catch for over 10 weeks (Fig. 21), which exceeds the approximate six-week flight period of adult males. Although ground treatments using SPLAT GM were proven effective against *L. dispar*, this method is not suitable for larger blocks because the application method is time-intensive and labor-consuming and because higher dosages are required to achieve efficacy similar to achieved by aerially applied SPLAT GM.

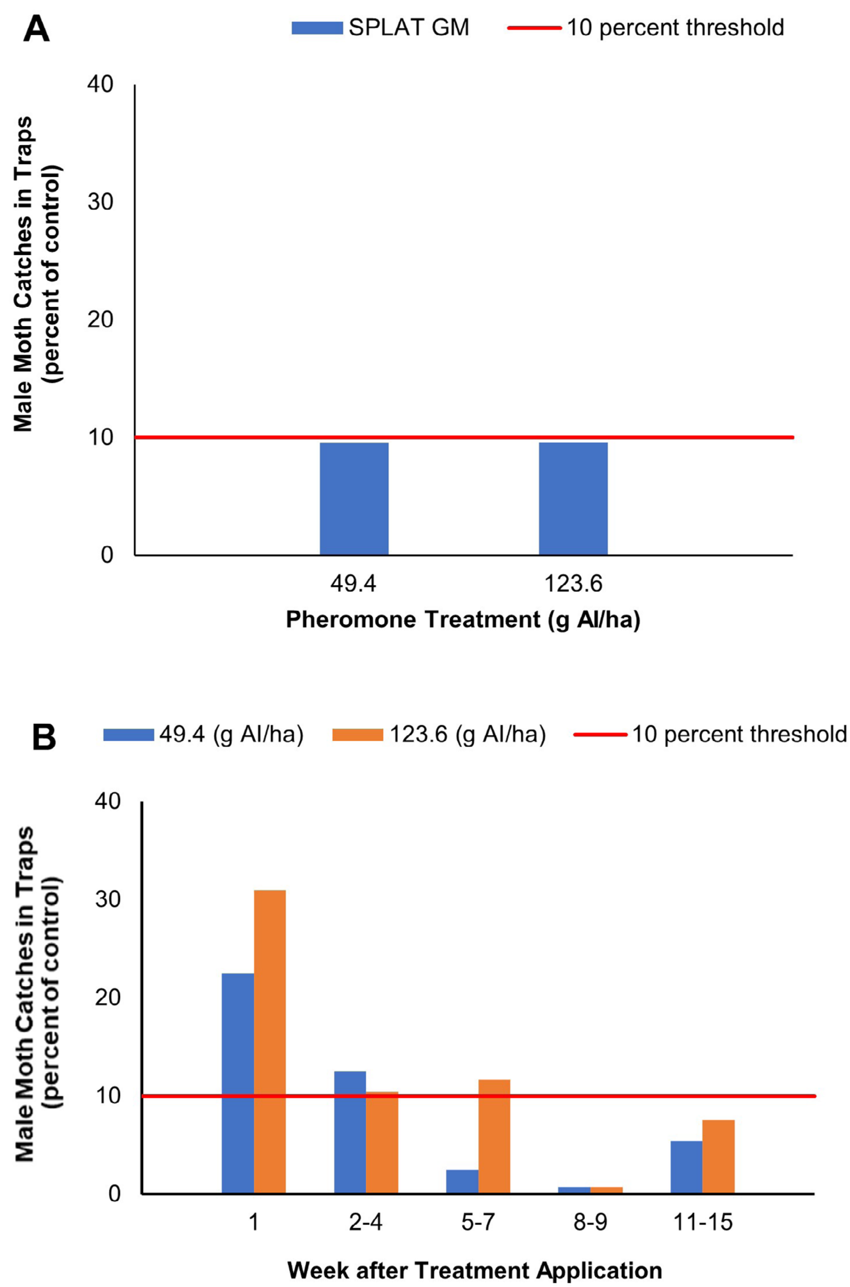

Figure 21.—Overall (A) and weekly (B) male moths captured in pheromone-baited traps in ground treated plots compared with untreated control plots, 2013. To satisfy the National Slow the Spread Program criteria, bars should be below the red line.

Method Development to Relate Daily to Season-Long Trap Catches (2015–2017)

To ensure equal population densities among experimental plots, we release laboratory-reared insects instead of relying on feral populations of *L. dispar.* Resulting trap catches can therefore be viewed as daily trap catches, but combined they do not amount to the season-long trap catches. To relate results of our field trials to the operational STS Program, in which decisions are based on season-long trap catches (Thorpe et al. 2006), we verified the assumption of Gaussian distribution of *L. dispar* trap captures as a function of time (Fig. 22) and established a predictive linear relationship between trap catches during the week of peak abundance, length of flight season, and season-long cumulative catch (Onufrieva and Onufriev 2018):

$$A \approx 0.41 M_{pw} F \tag{1}$$

where M_{pw} is catch during the week of peak abundance and F is length of flight season in weeks.

A wealth of data collected on *L. dispar* phenology over 16 years allowed us to conduct a comprehensive analysis and relate season-long and weekly trap catches and flight duration to the daily trap catches. Unlike weekly trap catches, daily values fluctuate significantly around the predicted Gaussian peak (Fig. 23). Flight duration also varies significantly from year to year, which leads to significant variability in peak trap catches in populations with the same density. To account for this variability, the model provides a range for a daily peak value (Eq. 2). Currently, we use this model to estimate the population density for which the treatment efficacy is assessed to better interpret research results and to appropriately apply them in the STS management program. This model can also be utilized to allow researchers and managers to estimate best- and worst-case scenarios, predict efficacy of control tactics, and make decisions to ensure optimal results, and to predict mating success of *L. dispar* females and likelihood of persistence of isolated low-density populations.

$$0.95 MpdF < \mathrm{A} < 1.9 MpdF \tag{2}$$

where M_{pd} is maximum daily catch during peak flight and F is length of flight season in weeks.

Method Development to Estimate Bounds on Absolute Population Density (2015–2020)

The STS Program relies on pheromone-baited trap catches to detect *L. dispar* populations, estimate moth abundance, and evaluate success of applied treatments because the trap catches are easier and less costly to obtain than counts of other life stages, especially if the population density is low, and because they have been shown to be well correlated with egg mass and pupal counts (Brown et al. 1981, Carter et al. 1994, Thorpe et al. 1993). However, interpretation of trap catches continues to be difficult, especially in low-density populations, where a high probability of false-negative trap catches has been demonstrated (Bau and Cardé 2016). The availability of statistically reliable estimates of the absolute population density would allow us to optimize efforts based on the goal, available resources, and the efficacy of the previous efforts. In our research program, such estimates would significantly improve the interpretation of results and facilitate optimization of existing tactics and development of new ones.

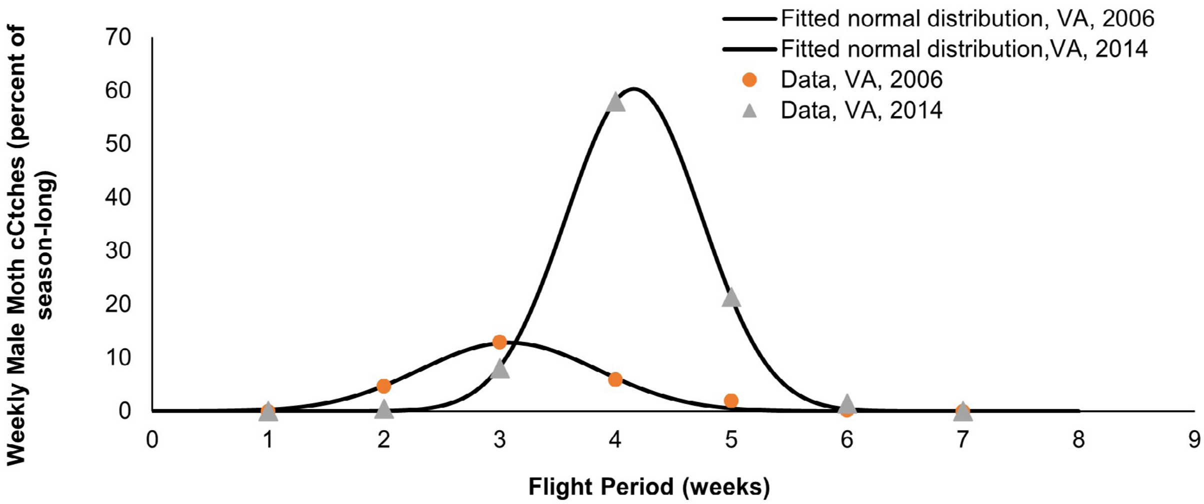

Figure 22.—Weekly male moths catches in pheromone-baited traps.

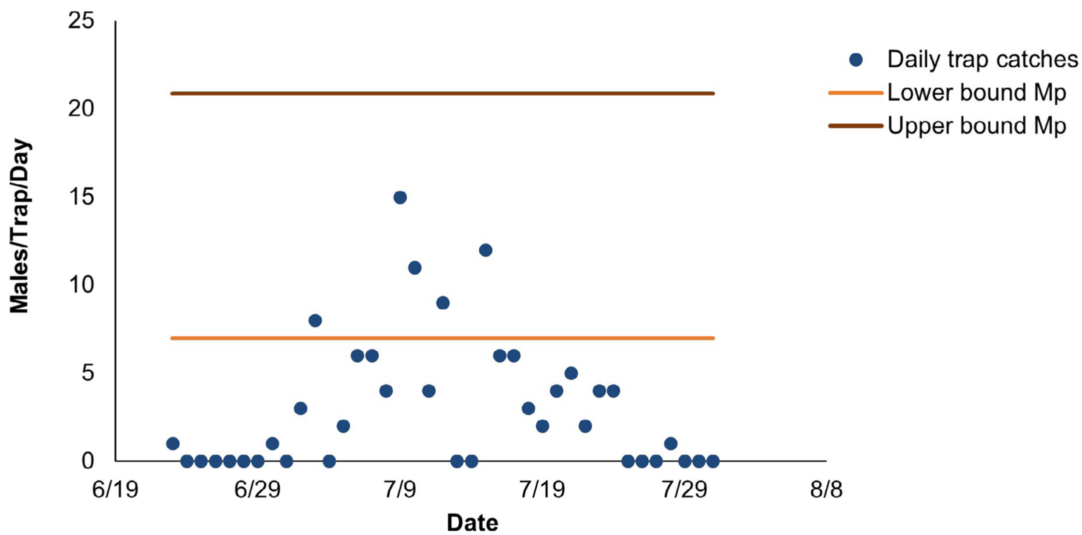

Figure 23.—Daily male moth catches in 2016 in a pheromone-baited trap in Blacksburg, VA.

To relate trap catches to the absolute population density of *L. dispar,* we analyzed catches in traps placed at various distances (0, 15, 25, 30, 45, 50, 60, 75, 80, 100, 150, 200, 250, 300, 500, 600, 900, 1000, 1200, and 1500 m) from the *L. dispar* male release points. Releases ranged from 50 to 500 males per release point at each time of release. We used 3- to 7-day intervals between male moth releases to allow males adequate time to find traps and to achieve converged catch (Robinet et al. 2008). The catch is assumed to be converged when it stops increasing with increased trapping time. We derived a simple mathematical relationship between catch probability and distance to a USDA milk carton pheromone-baited trap that faithfully approximates the experimental data (Fig. 24) (Onufrieva et al. 2020):

$$spT_{fer}(r) = \begin{cases} \frac{0.37}{1+\left(\frac{r}{25.6}\right)^2}, & r \leq 1600\ meters \\ 0, & r > 1600\ meters \end{cases} \tag{3}$$

where $spT_{fer}(r)$ is a probability to catch a male located at a given distance (r) from a pheromone-baited trap (Miller et al. 2010), 0.37 is the probability to catch a *L. dispar* male located in the immediate proximity to the USDA milk carton pheromone-baited trap ($spT_{fer}(0)$), 25.6 is the distance (D_{50}) at which a probability to catch a *L. dispar* male drops to ½ of $spT_{fer}(0)$, and 1600 m is the maximum dispersal distance for *L. dispar* (Elkinton and Cardé 1980).

This relationship, in turn, allows us to estimate the most likely population density $\overline{\rho_{mp}}$ along with its statistical upper and lower bounds from a single catch using quantile functions of chi-square distribution (see appendix, Onufrieva and Onufriev 2021).

However, the estimated most probable absolute population density and its bounds cannot be directly applied to season-long trap catches because the population density changes over time according to Gaussian distribution. Instead, season-long trap catches should be used to first estimate abundance during peak activity (Eq. 2), after which bounds on the absolute population density and the most probable density during peak flight can be estimated using the proposed procedure.

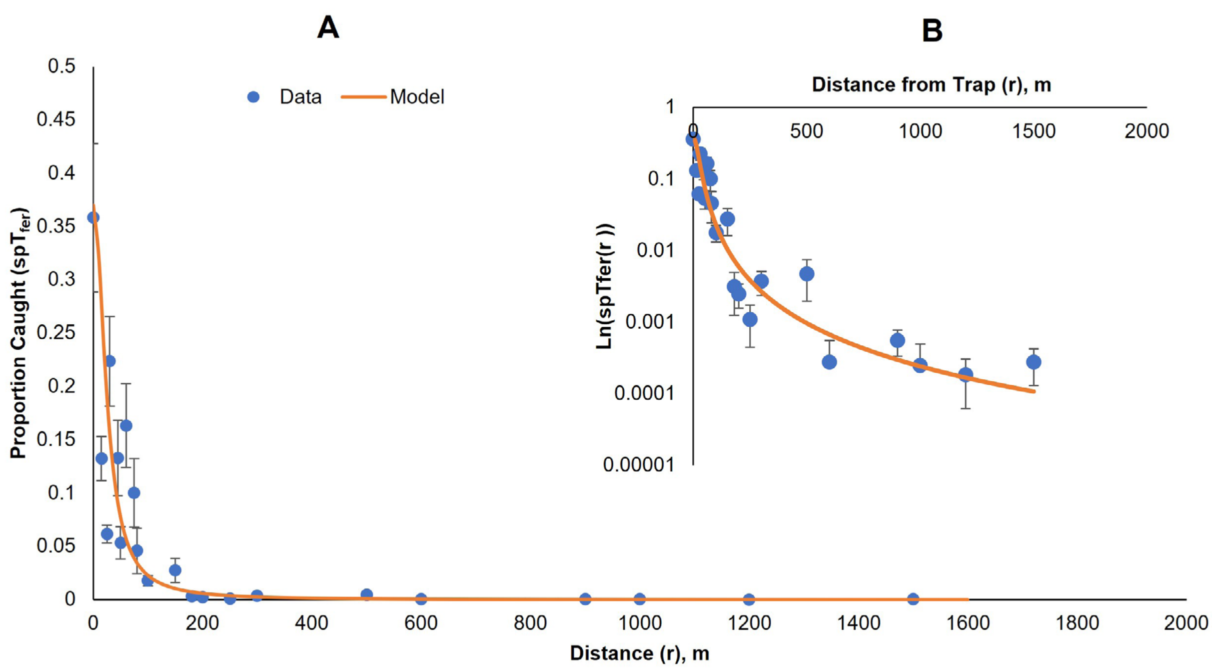

Figure 24.—Proportion of insects caught in pheromone-baited traps placed at various distances from the release point (±SEM). Error bar is not shown when smaller than the symbol size. Blue dots represent experimental data. The solid orange line represents the model described by Eq. 3. Overall fit (A) and fit at the large distances from the trap (ln(spTfer(0)) vs r), where trap catches are very low (B), are shown.

Automated Traps

Automated Pheromone-Baited Trap (2004–2008)

Automated pheromone-baited traps (Fig. 25) were developed and initially tested by the USDA APHIS (Buzzards Bay, MA). The automated trap is a modified USDA milk carton pheromone-baited trap containing a piezoelectric counter interfaced with an event data logger (Onset Computer, Bourne, MA) to record the unique date-time stamp of males as they enter the trap (Tobin et al. 2009).

A total of 352 automated traps were deployed under field conditions across several U.S. states over a 5-year period. Although there was a tendency for overcounting, and very few traps recorded the number of events equal to the number of males caught in traps, the number of recorded events generally correlated with male moth catches. The time stamp for recorded events provided valuable information on *L. dispar* behavior and phenology (Tobin et al. 2009). The timing of catches corroborated previous reports of crepuscular *L. dispar* male flight behavior (O'Dell and Mastro 1980) with a larger peak between 12 and 17 hours and a smaller peak between 20 and 22 hours. The duration of male flight was similar across latitude and averaged 24 days or 288 degree days (Tobin et al. 2009). However, a maximum flight period of 93 days was observed, which suggested an introduction of life stages that developed under different climatic conditions. This work demonstrates benefits of automated traps with sensors and data loggers to integrated pest management and research programs by improving the understanding of flight behavior and phenology.

Plurasense Moth TrapMonitor (2020)

The Plurasense Moth TrapMonitor (Plurasense Inc., Lake Oswego, OR) (Fig. 26) is a remote monitoring device baited with pheromone lures that holds a sticky insert like a wing trap and that gathers and uploads images of the insert for display on web-connected devices using a wireless network. The Moth TrapMonitor allows users to measure moth activity without visiting the field (Fig. 27). The efficiency of the Moth TrapMonitor was compared with the efficiencies of pheromone-baited USDA milk carton and delta traps (Scentry Biologicals, Inc., Billings, MT) used in *L. dispar* management programs (Fig. 26).

We estimated a D_{50} (the distance at which the probability to catch a *L. dispar* male drops to ½ of probability to catch a male located in the immediate proximity to the trap; see below), evaluated the sensitivities of Moth TrapMonitors and delta traps, and compared those parameters to the same parameters of USDA milk carton traps that were previously estimated. Results indicated that D_{50} of Moth TrapMonitor is larger (D_{50} = 68 ± 11.5 m), compared to both delta (D_{50} = 30 ± 7.6 m) and milk carton (D_{50} = 26 ± 3 m) pheromone-baited traps. This difference in D_{50} could be due to the differences in trap design: Moth TrapMonitor has significantly larger openings compared to delta and milk carton traps. These results also confirmed that delta and milk carton traps have similar trapping efficiencies; therefore, low-level catches from these two types of traps can be used interchangeably.

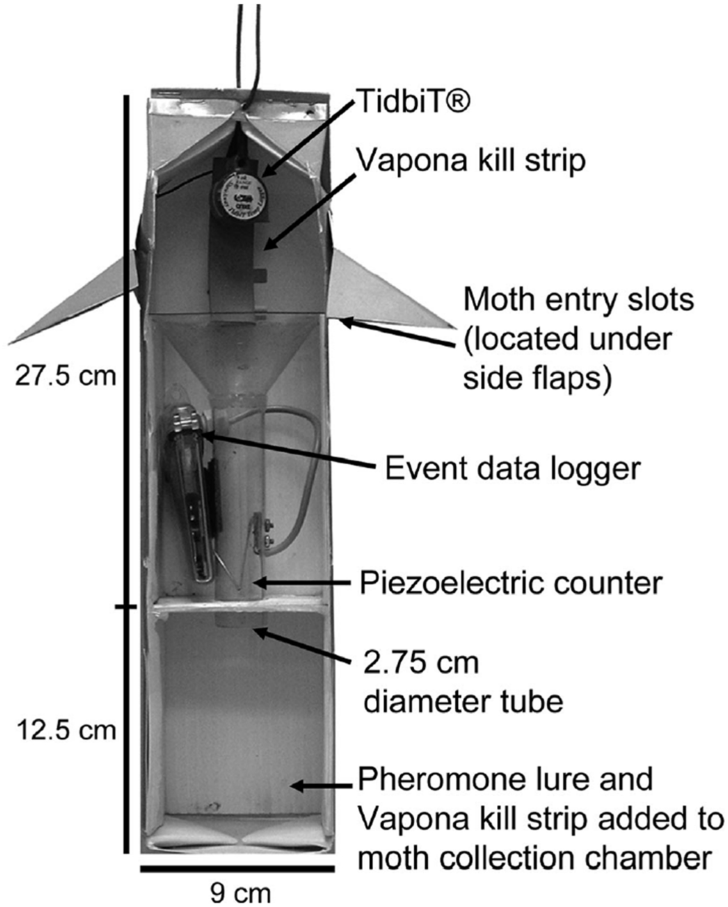

Figure 25.—Design of the automated pheromone-baited traps. Male moths displace the piezoelectric counter when they pass through the tube toward the pheromone source in the collection chamber, and a date-time stamp is recorded by an event-data logger (Tobin et al. 2009).

A **B** **C**

Figure 26.—*Lymantria dispar* pheromone-baited traps: (A) Moth TrapMonitor (photograph courtesy of Charles Oppenheimer), (B) USDA milk carton trap, (C) delta trap.

Figure 27.—*Lymantria dispar* trap catches in pheromone-baited Plurasense Moth TrapMonitor displayed on the web portal.

POPULATION THRESHOLD CONTROLLED BY LOW DOSAGE MATING DISRUPTION

Under current operational standards in the STS Program, mating disruption is generally used against populations in which the maximum male moth density does not exceed 30 males/trap/season (Thorpe et al. 2006). For populations above this threshold or when life stages (e.g., egg masses, pupal cases, and larvae) are observed, the biopesticide *Bacillus thuringensis* var. *kurstaki (Btk)* is generally used (Tobin et al. 2007). However, in cases of financial constraints (the cost for *Btk* per hectare is approximately 4 times greater than the cost for mating disruption) or in cases of nontarget concerns (unlike mating disruption treatments, *Btk* can affect nontarget Lepidoptera) (USDA FS and APHIS 2012), the STS Program has used mating disruption against high population densities without fully understanding its effectiveness at these higher densities.

Historical analysis of the STS Program mating disruption treatment success data suggested a tendency for more frequent treatment failure in smaller blocks, perhaps due to difficulties in ensuring adequate pheromone coverage, and in hillier terrain, perhaps due to potential *L. dispar* reproductive asynchrony in hillier terrain (Onufrieva et al. 2019b, Walter et al. 2015). The results also indicated the highest probability of success at approximately 30 moths. However, treatment successes were noted at maximum densities as high as 392 moths/trap, which motivated our field studies (Onufrieva et al. 2019b).

From 2013 through 2015, we evaluated the efficacy of operational 15 g AI/ha mating disruption treatments against artificially created *L. dispar* populations of various densities. Based on the results of the field tests, we recommended 20 males/trap/day in the year of treatment application to be an upper limit above which mating disruption fails (Fig. 28) (Onufrieva et al. 2019b). According to the model (Eq. 2, Onufrieva and Onufriev 2018), at this maximum daily trap catch during peak flight, the season-long trap catch would range from 115 to 344 males/trap. Assuming the unrestricted spread rate of 20.78 km/yr (Sharov and Liebhold 1998), the maximum season-long trap catch, at which mating disruption would be expected to be successful, is estimated as 62 males/trap/season, which is more than double the current operational standard of 30 males/trap/season. We note that these estimates are based upon work primarily conducted along the southern front of the *L. dispar* expanding range.

Daily pheromone release rates from the lures used in *L. dispar* traps differ significantly between Minnesota and North Carolina, which represent the climatic extremes of the STS Program action area and may yield significantly different trap catches despite similar population densities. This difference agrees with the result of our study on the relationship of mate-finding failure to population density in newly establishing populations in northern Wisconsin in 2003 and 2008 (Contarini et al. 2009): at low population densities (<5 males/trap), mating success of females in northern Wisconsin was higher than in Virginia and West Virginia and was sometimes observed even when no males were recorded from traps. Given this information, it may be prudent to be more conservative with mating disruption at the northern extent of *L. dispar.*

The results of this study indicate that mating disruption can potentially be used against higher population densities than previously thought. We tested the low dosage (15 g AI/ha) of mating disruptant, but based on these results, we hypothesize that the high dosage of 37.5 g AI/ha may be able to replace some of the *Btk* treatments currently used in the STS Program. Recent research conducted to evaluate any potential negative effects of operational *Btk* treatments in the STS Program on the monarch butterfly, *Danaus plexippus* L. (Lepidoptera: Nymphalidae), larvae concluded that spatial and temporal overlap between larvae and *Btk* treatments is marginal (Nunez-Mir et al. 2021). Therefore, *L. dispar* management in the STS Program is unlikely to negatively affect monarch butterfly populations, but it still could potentially adversely affect other threatened and endangered species. Replacing some of the *Btk* treatments with mating disruption would reduce both cost and any unknown nontarget effects of *L. dispar* management.

FACTORS AFFECTING MATING SUCCESS IN *LYMANTRIA DISPAR* POPULATIONS

Relationship Between Male Moth Density and Mating Success (2011–2013)

The initial size of a founder population is an important factor that affects the probability of establishment of nonnative species in new areas (Liebhold and Tobin 2008). Small founder populations comprised of fewer individuals tend to be subject to stochastic forces and Allee effects, which often prevent small founder populations from establishing in a new area. In an effort to develop a comprehensive understanding of the relationship between the season-long trap catch and the percentage of mated females, we analyzed data on the probability of female mating success related to background male moth densities published between 1974 and 2010 (Beroza et al. 1975, Beroza et al. 1974, Contarini et al. 2009, Granett and Doane 1975, Kolodny-Hirsch and Webb 1993, Kolodny-Hirsch et al. 1990, Onufrieva et al. 2010, Schwalbe et al. 1983, Sharov et al. 1995, Tcheslavskaia et al. 2002, Thorpe et al. 2006, Webb et al. 1990, Webb et al. 1988).

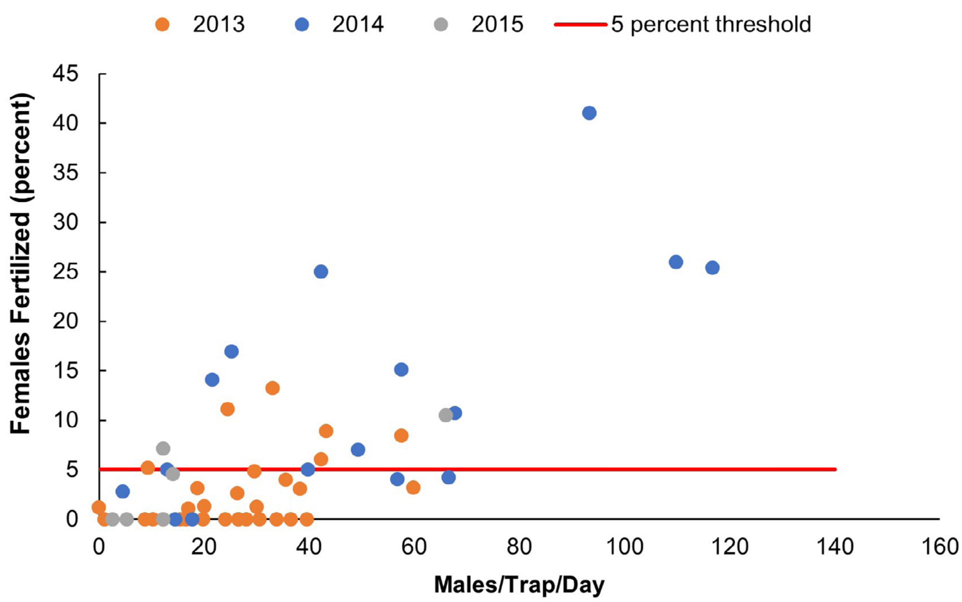

Figure 28.—Mating success of *Lymantria dispar* females at various male moth catches in USDA milk carton pheromone-baited traps observed in experimental plots with artificially-created populations of various densities from 2013 through 2015 in Virginia.

The predicted estimates from multiple quantiles highlight different measures of risk (Fig. 29) and can be used in management decisions to assign treatments based on the goals and available resources. The 50th quantile predicted that half of the females were successfully mated at a season-long trap catch of 207.1, whereas the least conservative (10th) and most conservative (99th) quantiles predicted that half of the females were successfully mated at a season-long trap catch of 727.4 and 6.7, respectively. The most conservative 99th quantile that can be used to determine the absolute minimum season-long male trap catch that resulted in successful female mating, predicted that 10, 25, 75, 90, and 99 percent of females would be mated at season-long trap catches of 1.4, 2.7, 18.3, 33.4, and 51.2, respectively (Tobin et al. 2013).

Age Effect on Mating Success and Mating Disruption (2012–2014)

Although mating disruption treatments do not always completely prevent mating, they reduce population growth by increasing the amount of time that males spend locating calling females and thus delaying mating (Mori and Evenden 2013). Delayed mating could result in lower fertilization success due to an increase in the age of one or both mates. We analyzed field data on mating success of females collected from 2001 through 2007 and in 2009 at study sites in the Appomattox-Buckingham and Cumberland State Forests and the Goshen Wildlife Management Area in Virginia. These data were collected as part of studies designed to evaluate mating disruption treatments against *L. dispar* (Onufrieva et al. 2008, Onufrieva et al. 2010, Tcheslavskaia et al. 2005b, Thorpe et al. 2007b). We also examined the effect of male and female age and multiple male matings in a controlled laboratory experiment and observed that increases in male and female age reduce the rate of female fertilization. The female fertilization rate was furthermore reduced when males mated multiple times (Tobin et al. 2014a). This work highlights the importance of both female and male age at the time of mating and contributes to better understanding of mechanisms of mating disruption tactics.

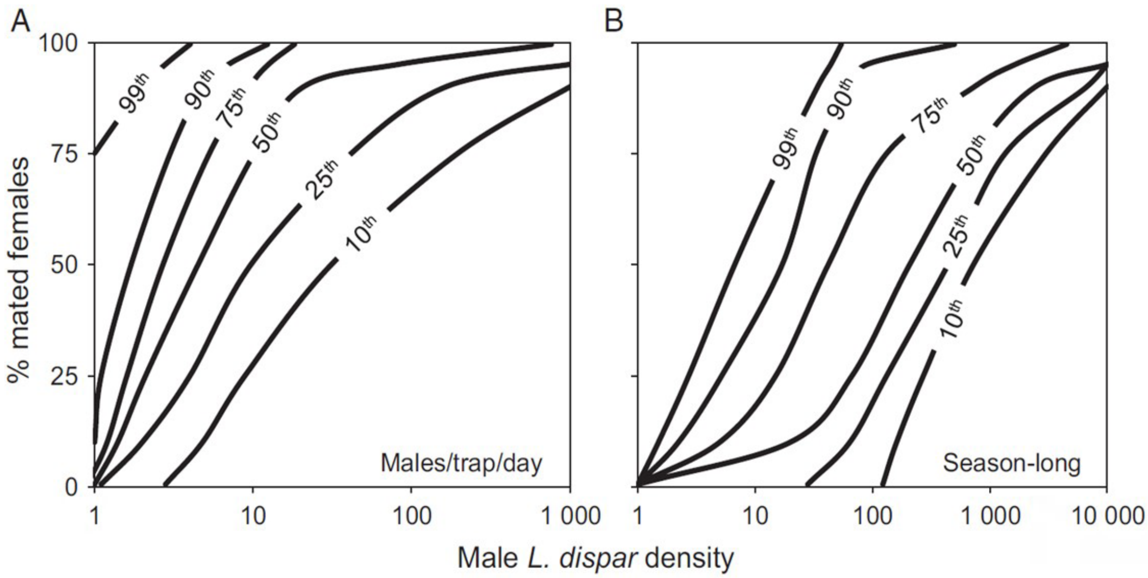

Figure 29.—Mating success of females relative to trap catch per trap per day (A), and the maximum percent of successful mating across the season-long trap catch (B). The fits from quantile regression represent different measures of uncertainty by highlighting the minimum male moth density required to result in various percentages of successful mating in a given percentage of observations (Tobin et al. 2013).

CONCLUSIONS

The technical committee is an integral part of the science-based STS Program with an ultimate goal to inform, optimize, and improve *L. dispar* management through field and analytical research. Research conducted over the past 14 years has resulted in (1) adding a second and effective operational formulation (SPLAT GM-Organic) to the STS Program and developing criteria for successful SPLAT GM-Organic formulation; (2) improved confidence in mating disruption treatments in various climate zones; (3) better understanding of persistence effects of pheromone treatments; (4) development of a method for ground SPLAT GM-Organic pheromone formulation application for use in areas not suitable for aerial treatments; (5) improved interpretation of field studies results and their application to the operational STS Program; (6) estimates of threshold *L. dispar* population density, beyond which low-dosage (15 g AI/ha) mating disruption treatments are no longer effective; (7) improved interpretation of male moth catches in pheromone-baited traps and relating them to the absolute population density of *L. dispar;* (8) improved understanding of factors affecting mating success and mating disruption; (9) improved understanding of *L. dispar* local spread and long-range dispersal; and (10) determination of factors affecting success of aerially applied treatments against *L. dispar* (Fig. 30).

The main challenge identified by the committee was decreased efficacy of SPLAT GM-Organic from 2017 through 2019. As *L. dispar* continues to spread across the United States, further research is needed to continue to optimize the STS Program. Although we confirmed similar effects of mating disruption treatments in the regions with relatively cold and warm climates, we showed that the pheromone release from the lures in pheromone-baited traps differs significantly and may affect our estimates of the population

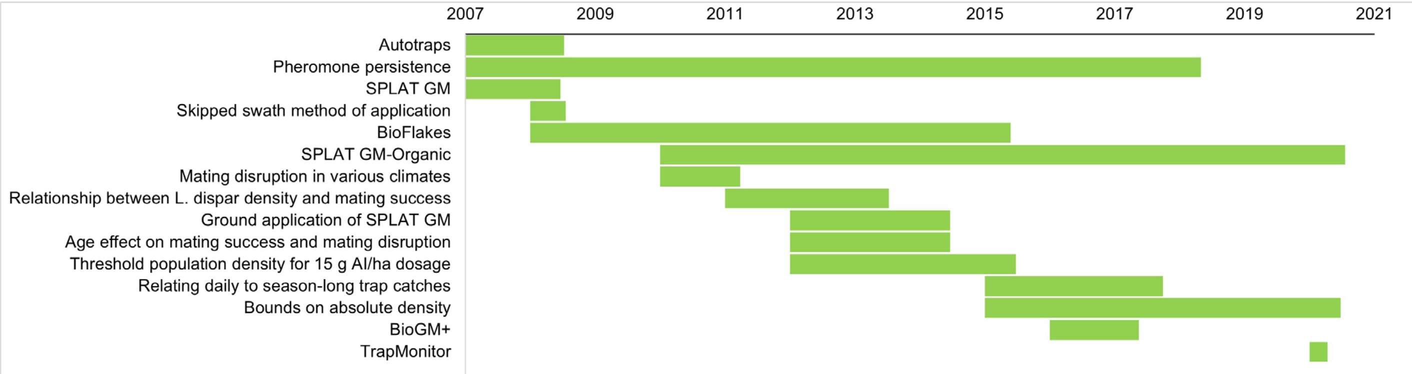

Figure 30.—Technical committee timeline.

density and subsequent management decisions. Therefore, further studies are needed to better interpret trap catches in the northern region of the STS Program. Other needs include estimating thresholds for *L. dispar* population densities that can be successfully controlled by high-dosage (37 g AI/ha) mating disruption treatments, development of pheromone application methods for areas not suitable for treatments using unmanned aerial vehicles (UAVs), better understanding of the effect of pheromone persistence in the environment on assessment of treatment success, and development of methods for field detection of *L. dispar* pheromone, disparlure, to improve monitoring and treatment evaluation.

Although research sponsored and conducted by the STS Program is specific to *L. dispar,* mating disruption is a tactic used against several other species, especially Lepidoptera (Louis and Schirra 2001, Pfeiffer et al. 1993, Stelinski et al. 2005, Stelinski et al. 2010, Stelinski et al. 2007, Witzgall et al. 2010, Witzgall et al. 2008, Witzgall et al. 2005). Therefore, this work also contributes to a framework for development and improvement of detection, monitoring, and mating disruption treatments to use against other existing and future agricultural and forest pests.

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APPENDIX

Overview

The following supplementary files and programs are available for download from https://doi.org/10.7294/BE34-ZS61 (accessed October 20, 2021):

TrappingData.xls (Microsoft Office 2019) contains two sheets: "Data table" (for entering experimental trap catch data) and "Absolute density" (for calculating most probable absolute density and its bounds associated with various trap catches).

Script Tfer0.jsl (JMP® Pro 16, SAS Institute, 2020) is used to estimate trap catch in the immediate proximity to a trap *($spT_{fer}(0)$)* by fitting the model to the available trap data points at larger distances from the trap; however, we strongly encourage empirical measurement of this important parameter.

Script AbsoluteDensity.jsl (JMP® Pro 16, SAS Institute, 2020) is used to calculate D_{50} from the experimental trapping data.

To run the scripts, all three files (TrappingData.xls, Tfer0.jsl, and AbsoluteDensity.jsl) need to be located in the same folder. Two likely usage scenarios are described below.

The units are as follows:

D_{50} and R_{max} in meters

absolute population density in number of insects per hectare

Step-by-Step Instructions for Calculating Most Probable Absolute Population Density and its 95 Percent Confidence Bounds

Scenario 1: Insect-Trap System with Known Parameters $spT_{fer}(0)$, D_{50} and R_{max}.

1. When the parameters of the insect-trap system are known, only TrappingData.xls is needed. See the above link.

   As an example, we will use the parameters obtained for *L. dispar* in Virginia using USDA milk carton pheromone-baited traps:

   $spT_{fer}(0) = 0.37$

   $D_{50} = 26$

   $R_{max} = 1600$

2. Plug these parameters in the corresponding cells in sheet "Absolute density" replacing values currently there. This will automatically update values of μ, lower and upper bounds, and most probable catches. The graph will also automatically update to reflect these changes (Fig. 31).

3. This graph (Fig. 31) can now be used to analyze future field data. Suppose one insect was caught in a trap over the converged catch period for this insect. The

graph and the table can be used to estimate absolute population density for the given insect; in this case one insect means that absolute population density ranges from 0.04 to 8.6 insects/ha, most probably 1.5 insects/ha.

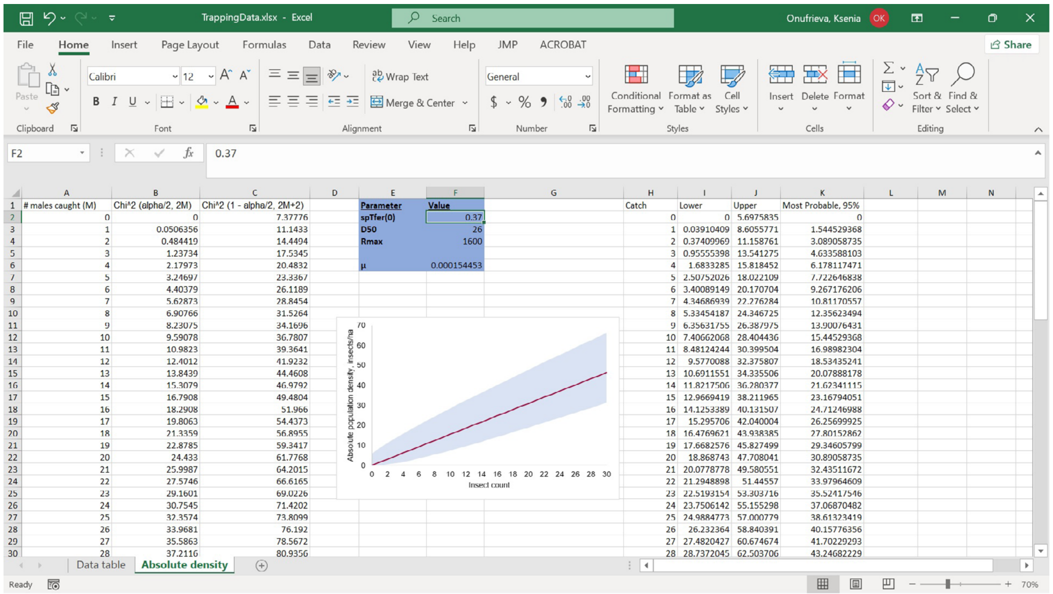

Figure 31.—Screen shot illustrating step 2.

Scenario 2: Insect-Trap Systems with Unknown Parameters $spT_{fer}(0)$ and/or D_{50}

1. Conduct release-recapture experiments to estimate recapture rates at ≥ 5 distances, including 0 m (in the immediate proximity to the trap, which is $spT_{fer}(0)$) and large distances to approximate R_{max} (smallest distance at which trap catch is 0). Catch should correspond to converged catch (minimum number of days N after which trap catch stops increasing). The same N needs to be used in the field experiments designed to sample wild populations.

2. Download TrappingData.xls and two JMP scripts, Tfer0.jsl and AbsoluteDensity.jsl, which are needed to perform a fit to estimate parameters ($spT_{fer}(0)$ and D_{50}) from experimental data.

3. Enter trap catch data in the “Data table” spreadsheet, replacing the data that are already there, but not changing the column headers.

4. If $spT_{fer}(0)$ is missing and cannot be obtained empirically, it can be estimated using Tfer0.jsl script (JMP® Pro 15, SAS Institute, 2019), but doing so is not recommended.

5. To conduct the analysis, ensure that all files are located in the same folder. As an example, we will use data that is already entered in the spreadsheet “Data table.”

6. If the $spT_{fer}(0)$ data is missing, users can estimate it using the script T_{fer}0.jsl. However, we do recommend collecting this data empirically. Follow these steps to estimate $spT_{fer}(0)$ using the script:

a. Double-click the script T_{fer}0.jsl, which will open the window shown in Figure 32.

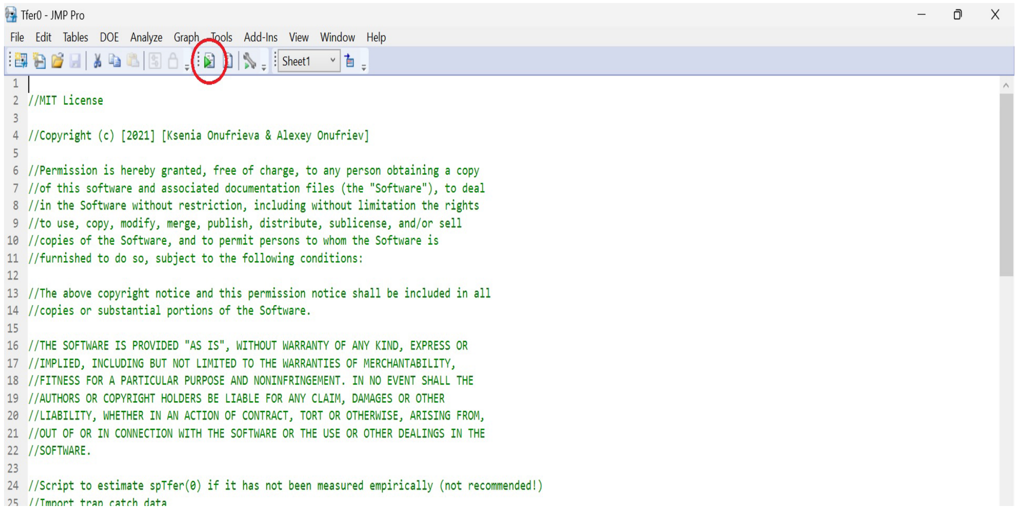

Figure 32.—Screen shot illustrating step 6a.

b. Click Run Script (Fig. 32, circled in red), which will calculate $spT_{fer}(0)$. The result will be reported as shown in the table (Fig. 33, circled in red).

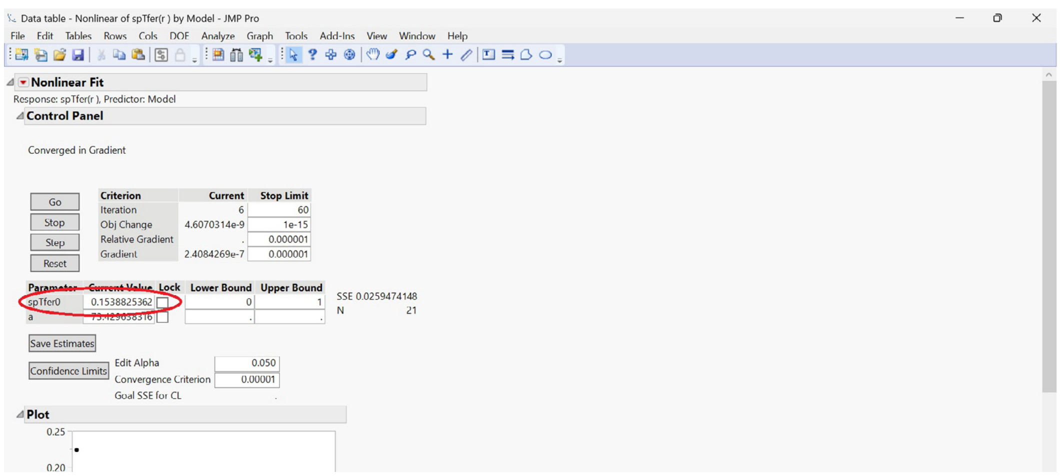

Figure 33.—Screen shot illustrating step 6b.

c. Add the value of $spT_{fer}(0)$ to the corresponding cell in the "Data table" sheet of the TrappingData.xls file. Now the data table is ready to use for estimating D_{50} from the data.

7. To estimate D_{50} by fitting Equation 3 to the log-transformed experimental data points:

a. Double-click the script AbsoluteDensity.jsl, which will open a window (Fig. 34).

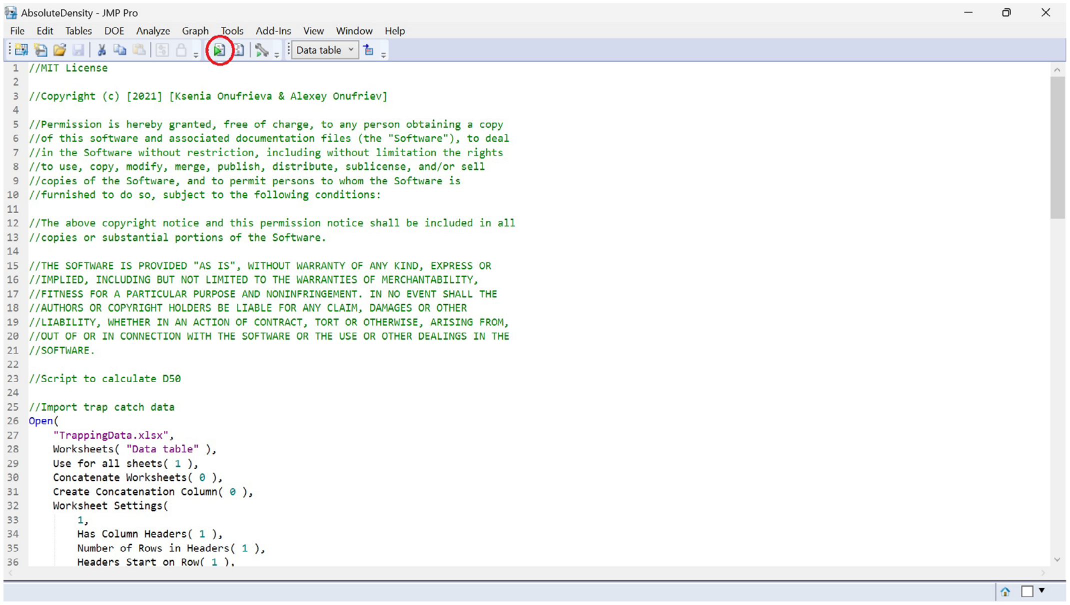

Figure 34.—Screen shot illustrating step 7a.

b. Click Run Script (circled in red in the screenshot above), which will calculate D_{50} (Fig. 35, circled in red).

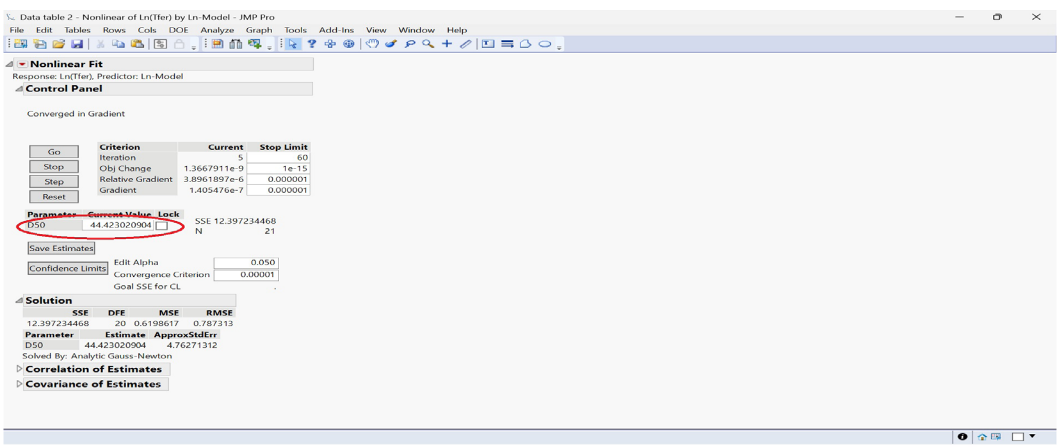

Figure 35.—Screen shot illustrating step 7b.

c. Plug both parameters, $spT_{fer}(0)$ and D_{50}, in the corresponding cells in the spreadsheet "Absolute density," replacing values that are currently there. Doing so will automatically update values of μ, lower and upper bounds, and most probable catches. The graph will also automatically update to reflect these changes (Fig. 36).

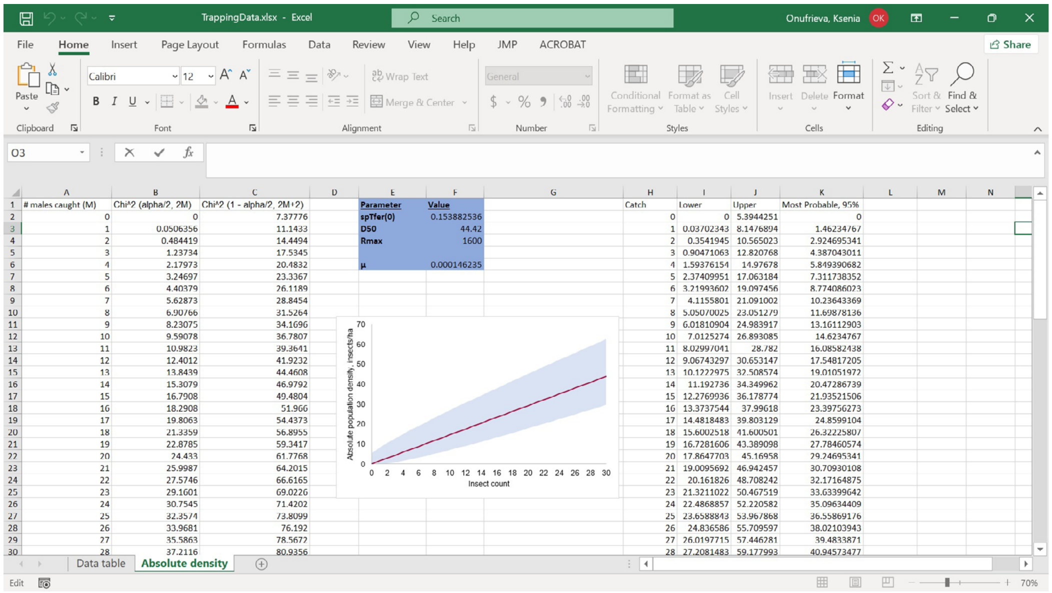

Figure 36.—Screen shot illustrating step 7c.

d. The graph is now ready to be used to interpret field data. Suppose one insect was caught in a trap over the converged catch period for this insect. The graph and the table can be used to estimate absolute population density for the given insect; in this case, one insect means that absolute population density ranges from 0.037 to 8.15 insects/ha, most probably 1.5 insects/ha.

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