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INTRODUCTION AND ESTABLISHMENT OF THREE PARASITOIDS OF THE LILY LEAF BEETLE, *Lilioceris lilii*, (COLEOPTERA: CHRYSOMELIDAE) IN NORTH AMERICA

BY

ELIZABETH A. TEWKSBURY

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

IN

ENVIRONMENTAL SCIENCE

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DOCTOR OF PHILOSOPHY DISSERTATION

OF

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ABSTRACT

Following three years of discovery and evaluation, three larval parasitoids were imported from Europe and introduced into North America to control Lilioceris lilii (Coleoptera: Chrysomelidae), an introduced herbivore of native and cultivated lilies. The first species, Tetrastichus setifer Thomson (Hymenoptera: Eulophidae), introduced in Massachusetts in 1999, was found to be established in 2002. We made additional releases of T. setifer, introduced the parasitic wasps, Lemophagus errabundus Szepligeti (Hymenoptea: Ichneumonidae) and Diaparsis jucunda (Holmgren) (Hymenoptera: Ichneumonidae), and evaluated the establishment and distribution of the three parasitoids through 2013. Tetrastichus setifer is now established in Massachusetts, Rhode Island, New Hampshire, Maine, Connecticut, and Ontario, Canada. Lemophagus errabundus is established in Massachusetts and Rhode Island, and D. jucunda is established in Massachusetts, Rhode Island, and Maine. All three parasitoids have spread a considerable distance from release sites. The establishment of these parasitoids is associated with substantial reductions of L. lilii populations in some locations. In time it is likely that the parasitoids will spread throughout the North American range of *L.lilii*, but it may be useful to redistribute the parasitoids to accelerate this process.

Key Words: Lilioceris lilii, Tetrastichus setifer, Lemophagus errabundus, Diaparsis jucunda, lily leaf beetle, parasitoid, biological control, establishment

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This research is a culmination of a program begun many years ago, and therefore I have benefited from the help, guidance, and support of many people. Heather Faubert stands out on that list as a source of encouragement, good ideas, and help whenever I asked. Sayles Livingston and Marion Gold came before me and paved the way for my contributions to this research project. There were also many undergraduate and graduate student employees in the biological control lab who made invaluable contributions to this work. I would like to thank each one individually, but there are too many! Their assistance is greatly appreciated.

I would also like to acknowledge the love and support of my family who made sacrifices, and believed in my abilities. This includes my parents, Ann and Bill Nyce, my mother and father-in-law Shirley and Hamilton Tewksbury, my daughters, Rachel, Alison, and Sara, and my husband, Thaxter Tewksbury. Thaxter has always provided me with constant love and support, and this has been even more critical to me during the completion of this dissertation.

DEDICATION

I would like to dedicate this dissertation to my mother, Ann Gallivan Nyce, and my father Jim Gallivan. My mother never really understood why I wanted to be a "bug girl", but was proud of me nevertheless, and my father must have known something because his nickname for me was "Lisa bug".

PREFACE

This dissertation is a culmination of fourteen years of evaluation of classical biological control releases, and documents the release and establishment of three species of parasitoids for lily leaf beetle management.

This dissertation has been prepared in manuscript format, contains one manuscript, and is being prepared for submission to Environmental Entomology.

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MANUSCRIPT FORMAT

To be submitted to Environmental Entomology

INTRODUCTION AND ESTABLISHMENT OF THREE PARASITOIDS OF THE LILY LEAF BEETLE, *Lilioceris lilii* (COLEOPTERA: CHRYSOMELIDAE), IN NORTH AMERICA

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INTRODUCTION

The lily leaf beetle, *Lilioceris lilii* Scopoli, was first found in North America near Montreal, Canada in 1943 (LeSage 1992). The first report of the beetle in the United States was in Cambridge, Massachusetts in 1992 (Livingston 1996) and the beetle now occurs in all of the New England states as well as New York, New Jersey, Pennsylvania, and Washington. In Canada it is widely distributed in the Maritimes as well as Quebec and Ontario and is also established in Manitoba and Alberta. (Figs. 1 & 2) (NAPIS Pest Tracker 2014, Lily Leaf Beetle Tracker 2014, Cappuccino 2013). The beetle is a serious pest of both native and cultivated lilies in the family Liliaceae (Livingston 1996, LeSage and Elliott 2003).

The lily leaf beetle is univoltine, overwinters as an adult, and after initiating feeding in the spring, lays rows of eggs on the undersides of leaves. The larvae carry a fecal shield, which is believed to provide some defense against predators (Jolivet & Verma 2002, Keefover-Ring 2013) but may also serve to attract parasitoids (Schaffner and Müller 2001). Larvae complete four instars before pupating in the soil or leaf litter (Livingston, 1996). *Lilioceris lilii* is present in Europe and Asia as far north as Siberia

and to Morocco in the south (Slate 1953, Labeyrie 1963), and in China (Yu et al., 2001, Lu et al. 1998). Based on the wide geographic and climatic range of the beetle's native distribution, it is likely to be able to establish itself across all of North America (Kenis et al. 2002).

Since its introduction into North America, *L. lilii* has been considered a serious pest of cultivated lilies in Canada (LeSage 1992) and the United States (Livingston 1996). Adult and larval feeding of *L. lilii* causes extensive defoliation of lily leaves, buds, and flowers (Ernst 2005). Even avid lily growers often give up growing lilies after repeat infestations of *L. lilii* (LeSage 1992). Infested lilies continue to send up new sprouts for a few years before they die, but in the meantime the plants and flowers are so damaged that they have lost their aesthetic value (Stocker 2002).

An additional concern is that the lily leaf beetle will also feed on native lilies. Northeastern USA is home to four species of native lilies: *Lilium superbum* L. (Turk's-cap lily), *L. canadense* L. (Canada lily), *L. philadelphicum* L. var. *philadelphicum* (wood-lily), and *L. michiganense* Farw. (Michigan lily) (Gould et al. 1998, Adams and Dress 1982, Skinner 2008, USDA plants database 2014). *Lilium superbum* is a facultative wetland plant that is common in Rhode Island, but is endangered in New Hampshire and New York. *Lilium canadense* is threatened in Rhode Island and New York. *Lilium philadelphicum* is rare or endangered in Rhode Island, New York, Maryland and Ohio, and *L. michiganense* is considered endangered in New York (USDA plants database). The dispersal of

Lilioceris lilii throughout North America is likely to have a negative impact on these and other rare native lilies (Ernst et al. 2007, Bouchard et al. 2008).

The genus *Lilioceris* Reiter is a large genus with the largest concentration of species found in China (Yu et al. 2001) and approximately six species found in Europe (Livingston 1996). *Lilioceris lilii* is now thought to be native to Asia and introduced into Europe about 400 years ago, possibly with ornamental lilies (Orlova-Bienkowskaja 2012). From its introduction into North America in 1943 until 2011, *L. lilii* was the only species in the genus *Lilioceris* known to be present in North America¹. Three insects from the same subfamily as *L. lilii* (Criocerinae) that were introduced into North America prior to *L. lilii* became serious agricultural pests: cereal leaf beetle, *Oulema melanopus* (L.); common asparagus beetle, *C. duodecimpunctata* (L.).

A complex of European larval parasitoids was introduced into North America to manage these pests. *Tetrastichus julis* (Walker) (Hymenoptera: Eulophidae), *Diaparsis temporalis* Horstman (Hymenoptera: Ichneumonidae), *Anaphes flavipes* Förster (Hymenoptera: Mymaridae), and *Lemophagus curtus* Townes (Hymenoptera: Ichneumonidae) were introduced against the cereal leaf beetle (Haynes and

¹ In 2011 and 2012, another *Lilioceris* species, *L. cheni* was introduced into Florida as a weed biological control agent for *Dioscorea bulbifera* (air potato) (Center et al. 2013).

Gage 1981). *Tetrastichus asparagi* Crawford (Eulophidae) and *Lemophagus crioceritor* Aubert (Hymenoptera: Ichneumonidae) were released against the common asparagus beetle, and *T. crioceridis* Graham (Hymenoptera: Eulophidae) and *Diaparsis truncatus* (Gravenhorst) (Ichneumonidae) were introduced to control the spotted asparagus beetle (Hendrickson et al. 1991). *Tetrastichus julis* and *T. asparagi* established in the areas of release, dispersed from the release sites, and are considered successful biological control agents of cereal leaf beetle and common asparagus beetle, respectively (Evans et al. 2006, Poll et al. 1998). These historically successful introductions of European parasitoids of other species in the Criocerinae increased our expectations of finding successful parasitoids for control of *L. lilii*.

Prior to 1996 there was very little in the literature about parasitoids of *L. lilii*. Examination of North American populations revealed no native parasitoids and no sign of predation (Livingston 1996). Early trials with the cereal leaf beetle egg parasitoid *Anaphes flavipes* showed that it could reproduce on *L.lilii* in Petri dishes but would not attack in larger cages and did not establish in field plots (Livingston 1996).

Lataste (1932) referred to a gregarious larval parasitoid in France, and *Lemophagus errabundus* was also reported from *Lilioceris merdigera* (L.) in France (Elliott and Morley, 1911). These reports led to exploration in France and nearby European countries (Gold et al. 2001), resulting in the discovery of a suite of seven European parasitoids: one egg parasitoid,

Anaphes sp. (Hymenoptera: Mymaridae), and six larval parasitoids; Meigenia simplex Tschorsnig & Harting (Diptera: Tachinidae), Meigenia uncinata Mesnil (Diptera: Tachinidae), Tetrastichus setifer Thomson (Hymenoptera: Eulophidae), Lemophagus errabundus Gravenhorst (Hymenoptera: Ichneumonidae), *Lemophagus pulcher* (Szepligeti) (Hymenoptera: Ichneumonidae), and Diaparsis jucunda Holmgren (Hymenoptera: Ichneumonidae) (Gold et al. 2001, Kenis et al., 2002, Haye and Kenis 2004). Parasitism is common in lilies growing in gardens, but populations found on native lilies are particularly heavily parasitized (Gold et al. 2001, Haye and Kenis 2004). The discovery of these parasitoids led to European studies on parasitoid distribution and biology (Kenis et al. 2002) and a series of experiments to reveal host specificity, including parasitism of sympatric field populations of native *Lilioceris* species (L. tibialis, L. martagon, and L. merdigera), host range testing with these congeneric species in Europe, laboratory tests of chemical ecology, and host range testing in quarantine, as summarized in Casagrande and Kenis 2004.

The egg parasitoid, *Anaphes sp.* and the two dipteran larval parasitoids, *Meigenia spp.* were rejected as potential biological control agents for *L. lilii* because they lacked sufficient host specificity. The remaining four were sent to the URI quarantine facility for host-specificity testing. *Lemophagus pulcher* was rejected as a biological control agent because, as initially indicated by European studies with sympatric

populations and chemical ecology, this species may lack adequate host specificity. In quarantine, the parasitoid attacked the North American native *Lema trilineata* and the asparagus beetle *Crioceris asparagi* (Gold 2003). The three remaining parasitoids, *T. setifer*, *L. errabundus*, and *D. jucunda* were found to be host specific to the level of the genus *Lilioceris*, and all were approved by USDA APHIS PPQ for field release (Casagrande and Kenis 2004).

If in the (distant) future it is determined that these three agents which were released against *L. lilii* are not providing adequate control, *L. pulcher* might warrant additional research. It has the advantage of being multivoltine and its ecological host range may be more limited than indicated by laboratory tests. For instance, if it were to attack asparagus beetles in nature, that would likely have been shown in the European research (Hendrickson et al.1991) that led to biocontrol releases against the asparagus beetles in the USA. Furthermore, *Lema trilineata* (three-lined potato beetle) is often a serious pest and could itself be a legitimate target of biological control. However, *L. pulcher* would require extensive host range testing, so we set it aside for now.

Tetrastichus setifer is a gregarious larval parasitoid, found very commonly in commercial lily fields in France and Switzerland. It was described in 1978 and is known from Czech Republic/Slovakia, France, Yugoslavia and Sweden (de V. Graham 1991). It is univoltine and overwinters as mature larvae in host cocoons in the soil (de V. Graham

1991). *Tetrastichus setifer* is the most widespread parasitoid of *L. lilii* in Europe, found in all regions investigated from Bulgaria to the UK and Northern Germany to Italy (Kenis et al. 2002). This parasitoid is found in a broad range of climatic conditions in Europe from the warmer maritime regions of northern Germany to the colder high altitudes of the Alps. Based on this European distribution, we expect *T. setifer* to survive in most of the presently invaded range of the lily leaf beetle.

Lemophagous errabundus (Elliott and Morley 1911) was reported to attack *Lilioceris merdigera*, in France. It is a solitary, univoltine larval parasitoid that kills *L. lilii* in the pre-pupal stage and overwinters as a teneral adult in the host cocoon (Haye and Kenis 2004). It is more prevalent in extreme northern Germany, Holland and western France with parasitism rates reaching over 70% among late instars in these areas with ocean-moderated climates (Kenis et al. 2002). It has recently been found in England (Salisbury 2003). Based upon the European distribution, we consider *L. errabundus* to be climatically suited for release in coastal southern New England.

Diaparsis jucunda was reported by Horstmann (1971) from Sweden, Finland, Denmark, Germany, and the Czech Republic. It is a solitary univoltine larval parasitoid which attacks all stages of *L. lilii*. It was very common in surveys conducted in native lilies in Switzerland (Kenis et al. 2002), and was the dominant parasitoid of *L. lilii* in central and southern Europe, which represent the colder range where *T. setifer* is

also found. Total parasitism in the last instar averaged about 60% in lily fields, 74% in gardens, and 90% on wild lilies (Kenis et al. 2002, Scarborough 2002). Based on USDA plant hardiness zones, New England releases of *Diaparsis jucunda* are most appropriate for release at inland and northern New England sites.

Surveys by Kenis et al. (2002) revealed that throughout Western Europe a complex of parasitoids was found attacking *L. lilii* with different parasitoids predominating in different regions, but more than one species was important at virtually all sites. We released all three host-specific parasitoids in New England, based on knowledge of their different climatic ranges in Europe (Kenis et al. 2002) to determine release sites (Haye and Kenis 2004). This document summarizes the parasitoid releases made over the past 14 years and includes results of surveys for establishment, distribution, and apparent impact on *L. lilii*.

MATERIALS AND METHODS

Source of parasitoids

Parasitoids of *L. lilii* were collected by colleagues from CABI Switzerland beginning in 1998 from France, Switzerland, Germany, Italy, Holland, Belgium, Bulgaria, and Ukraine (Table 1). Field-collected larvae were held in the laboratory at CABI at 25°C and fed lily leaves until pupation in vermiculite and emergence of adult *L. lilii*. The remaining parasitized pupae were held at 4° C in a growth chamber for a minimum of two months before being shipped to the University of Rhode Island in chilled insulated boxes. After a shipment arrived at the URI Insect Quarantine Laboratory, parasitoids were stored at 4° C, and then moved to 25° C as needed for adult emergence. Emerged adults were kept in 1.8 L plastic jars in growth chambers under fluorescent lights with a photoperiod of 16:8 (L:D) and a day: night temperature cycle of 20°C:15°C. Jars contained cotton wicks with honey water to provide water and food for the adult parasitoids. Males and females of the same species were placed within jars for mating for 3-4 days.

Parasitoid Release Plots

Following completion of host range and host preference tests, we received USDA APHIS PPQ and Rhode Island and Massachusetts state departments' approval to release *T. setifer* in 1998. From 1999 to 2001 release plots were established in Massachusetts (Wellesley, Waltham, and Cambridge) and Rhode Island (Cumberland), along with two control plots (Belmont, MA) (Fig. 3) and releases of *T. setifer* were made in these plots from 1999 to 2003 (Table 1) (Gold 2003). Prior to release, adult parasitoids were examined individually in the University of Rhode Island Quarantine Facility to confirm identity, then packaged in vials and moved to the field plots in coolers. Parasitoids were released on *L. lilii-*infested

foliage at several locations within field plots. Release plots measured 6m x 6m, and were planted with approximately 800 mixed Asiatic and Oriental lily bulbs.

In 2003 we received USDA and state approval to release *Lemophagus errabundus* and *Diaparsis jucunda*. We established three release plots for *L. errabundus* (Kingston, RI, Plainville, MA, and Falmouth, MA) along with one control plot (Barnstable, MA) (Table 2) (Fig. 3). We also established three release sites for *D. jucunda* (Kingston, RI, Cumberland, RI, Belmont, NH) with one control plot (Deerfield, NH) (Table 3) (Fig. 3). The Kingston, RI release sites were made in 6m x 6m plots, but the other release and control plots established in Massachusetts, New Hampshire, and Maine (Fig. 3) were approximately 2 m x 2 m., and were planted with 100 Asiatic lily bulbs. We released adult *L. errabundus* and *D. jucunda* as described above for T. setifer.

All larger plots in Kingston, RI, Wellesley, MA, Cumberland, RI, and Plainville, MA were monitored weekly from the end of May until the end of June or early July. This began on the year of establishment, and continued until approximately 2008 for most release and control plots. The other plots were monitored by cooperators on a weekly basis when possible. On each sample date we counted adults, eggs, and four larval instars of *L. lilii* on 40 haphazardly chosen lily stems in the larger plots, and 20 stems in the smaller plots, and we removed 20 fourth instar larvae from these plants (when available) for dissection to determine parasitism

by *T. setifer*. Control plots were sampled in the same manner as release plots (40 stems per plot) to establish baseline data for long-term evaluation of parasitoid releases. We used cages at release sites to allow release of additional parasitoids while sampling for establishment of parasitoids from releases made in the previous year.

Additional Release Sites

In conjunction with more formal release sites where we released one of the three *L. lilii* parasitoids and monitored the *L. lilii* population for parasitism, we also collected larvae from residential gardens for dissection and evaluation for parasitism. Once we had documented establishment of all three parasitoids in our release plots we also made additional releases in residential sites in Rhode Island, SE Massachusetts, Maine, and Connecticut (Table 4). In 2010, we shipped *T. setifer* parasitoids to Dr. N. Cappuccino who, with a Canadian permit, released them into a research plot near Ottawa, Ontario in Canada. Residential sites for both releases and recovery were identified through a variety of methods: proximity to initial release plots, collaboration with university or state department of agriculture personnel, and contacts through master gardener programs and local newspapers. Recovery sites are listed in Appendix A.

RESULTS

Tetrastichus setifer establishment and spread

The establishment and spread of *T. setifer* from the first release in 1999 until 2013 are represented here with all release sites and all positive recovery sites (Fig. 4). Gold (2003) reported on the 2002 establishment of *Tetrastichus setifer* in the Wellesley,MA release plot. Overwintered *T. setifer* were first recovered in the Cumberland, RI release plot in early June of 2003, two years post release. Parasitism reached 95% on June 23, 2003. We have measured high parasitism of *T. setifer* from *L. lilii* larvae collected in home gardens in Cumberland, RI every year since 2003 (Table 5). In spite of this, we still continue to find many home gardens with damaging *L. lilii* populations.

Additional *T. setifer* adults were released in other release plots in New England (Table 1) and in home gardens (Table 4). Overwintered parasitoids were first recovered near the Bridgton, ME release plot in 2004, in the Hudson, NH release plot in 2005, and in the release plot near Ottawa, Ontario in 2011 – the year after release (Cappuccino et al. 2013). Releases of *T. setifer* in Cambridge, MA and Waltham, MA never resulted in establishment within the plot, and both release sites were abandoned, Cambridge in 2002 and Waltham in 2004.

The rate of spread of *T. setifer* is graphed in Fig. 7 using the date of first recovery for each of the recovery sites in Fig. 4. A linear regression equation fit to these data results in a slope of 0.88, indicating an average

spread of a bit less than 1 km per year with all points indicating spread less than 2 km per year.

T. setifer effectiveness

Tetrastichus setifer was first released in the Wellesley, MA plot from 1999 to 2001. Parasitism at the Wellesley site peaked at 100% on June 12 in 2003 and total number of L. lilii larvae declined from 6.75 per stem in 2001 to less than 0.5 per stem in 2008 (Fig. 10). After 2008 we stopped monitoring the Wellesley plot because there were so few larvae, and the land was required for other uses. Between 2001 and 2008, densities in the Belmont, MA control plot started at roughly 10.6 larvae per stem and declined to about 5.9 larvae per stem, always causing significant defoliation and never revealing any parasitism during this period. To evaluate the effectiveness of T. setifer in reducing L. lilii density we calculated percent control using a modification of Abbott's formula (Henderson and Tilton 1955) using the Wellesley, MA treatment data and the Belmont, MA control data (Fig. 11). These results show that percent control increases over time, and were significant when analyzed with a one-sample t-test (SAS Institute 2012).

The graph of percent control shows that percent control increased through time at this site.

Residents of areas infested with *L. lilii* were very interested in this biological control program and were very enthusiastic about participating in it. In 2007 we enlisted the help of residents of Cumberland, RI to collect

larvae and send them to us for dissection. Residents of other states participated as well, after responding to Master Gardener training sessions, local newspapers, web sites, or email requests. From 2007 to 2013 we received over 2,000 larvae from more than 240 home gardens in RI, MA, NH, ME, CT, and NY. These samples presented additional evidence of the establishment and distribution of *T. setifer* (Table 5).

Several gardeners have corresponded with us over the past decade on the status of their *L. lilii* populations. Through this source, there is some anecdotal evidence of a decline in *L. lilii* in the vicinity of the first *T. setifer* release in Wellesley, MA. In 2009 twelve emails from Massachusetts residents indicated that their previously large and destructive population of *L. lilii* were either gone or much reduced. These gardeners were from 12 towns in Massachusetts all located within 40 km of the original *T. setifer* releases in Wellesley, MA (1999-2001). Two were from towns that are also near the Rhode Island border and are less than 24 km from the Cumberland, RI *T. setifer* release site.

Lemophagus errabundus establishment and spread

Releases of *L. errabundus* adults were made from 2003 to 2007 at three release plots (Table 2). The establishment and spread of *L. errabundus* from the first release in 1999 until 2013 are represented here with all release sites and all positive recovery sites (Fig. 5). We did not detect overwintering *L. errabundus* parasitoids from any of the three release plots in Kingston, RI, Plainville or Falmouth, MA. The Falmouth, MA site was abandoned in 2004 because it was at a fairground where extensive damage to the lilies was deemed intolerable. The other two sites were monitored until 2008. The Kingston, RI site did not maintain a sufficient *L. lilii* population to support the development of parasitoids (perhaps because of prior pesticide use in this orchard site), and the high population of *L. lilii* in the Plainville, MA site decimated all of the lilies.

The first evidence of establishment was found in 2005 in a home garden 1.2 km from the Plainville, MA release site (Table 6). Subsequently, it was found in a home garden 2.9 km from the release site in 2006 (Table 6). One home garden recovery site (4 km from the Plainville release site) had steadily increasing parasitism, from a peak of 9 % in 2009, to 50% in 2010, 78% in 2011, and 94% in 2012 (Table 6). In 2013 we visited the site when we should have found peak parasitism, but could not find any larvae to evaluate for parasitism.

The rate of spread of *L. errabundus* is graphed in Fig. 8 using the date of first recovery for each of the recovery sites in Fig. 5. A linear regression line fit to these data results had a slope of 0.79 km/yr, with all points indicating spread less than 2 km per year.

Diaparsis jucunda establishment and spread

Diaparsis jucunda adults were released in five plots from 2003 to 2007 (Table 3) and in a number of smaller garden sites (Table 4). The establishment and spread of *D. jucunda* from the first release in 1999 until 2013 are represented here with all release sites and all positive recovery

sites (Fig. 6). Overwintered *parasitoids* were recovered for the first time in a home garden near the Cumberland, RI release site in 2007, four years after the first release at this site. In 2007 *D. jucunda* was recovered from four home garden sites in Maine in 2007, one year after being released in two Maine sites: Orono and Stillwater. In the last three years of monitoring (2011-2013), there has been a significant increase in the number of recoveries of *D. jucunda* parasitized by *L. lilii* (Table 7).

The rate of spread of *D. jucunda* is graphed in Fig. 9 using the date of first recovery for each of the recovery sites in Fig. 6. Linear regression showed a non-significant relationship between years and distance spread. It is noteworthy that years 4-6 indicate that this parasitoid is capable of moving as much as 4-5 km per year. There are a number of recoveries of *D. jucunda* in Massachusetts and Maine which indicate that this parasitoid has been found approximately 15-20 km from a release site.

Control plots

No parasitism was found in any of the control plots until *T. setifer* and *D. jucunda* were found in the Belmont, MA plot in 2011 (Tables 5 and 7). Control plots in Maine and in Falmouth, Massachusetts were abandoned due to the extensive lily damage caused by the lily leaf beetle. Also because of high beetle populations, other control plots, such as the Deerfield, NH plot were converted from a *T. setifer* control plot into a release site for *D. jucunda*.

DISCUSSION

Since the introduction of *L. lilii* into North America in 1943, it has experienced a familiar pattern of long-range redistribution with potted plants or bulbs and then a localized spread throughout the new area. In 1992 the beetle showed up in several disjunct sites, including Boston, apparently as a result movement of plants or plant parts (Lesage and Elliott 2003). It was only several years later that the population spread throughout the northern New England states, now making a continuous distribution with the Canadian population (Fig 2). The beetle's arrival in Manitoba, Canada was attributed to plant movement (Lesage and Elliott 2003) and the populations in Alberta, Canada (Cappuccino et al. 2013) and the state of Washington were likely established in the same manner.

In 2002 Kenis et al. predicted that the beetle's distribution would eventually encompass suitable habitats throughout all of North America, and it now appears that this prediction may come true. If this is the case, then the successful application of a classical biological control program early in the invasion of this introduced species could be an important tool in reducing the severity of the invasion as it reaches new areas. It is also apparent that a complex of parasitoids will be important for managing this pest in different climatic zones.

Tetrastichus setifer was the first parasitoid evaluated, and the first to be released in North America. In European surveys, T. setifer was found in a wide range of climatic conditions (Kenis et al. 2002), and appeared to have the best chance of establishing throughout North America. In Sweden T. setifer and L. errabundus are the most abundant L. lilii parasitoids (Ramert et al. 2009). In the UK T. setifer has been found everywhere that L. lilii is found (Salisbury 2008). Our program has now resulted in establishment of *T. setifer* in every state and province where we have released it (Massachusetts, Rhode Island, New Hampshire, Maine, Connecticut, and Ontario, Canada). It has spread at least 32 km from release sites, and is associated with reductions in L. lilii populations and damage to lilies. Tetrastichus setifer was found one season after release in both Connecticut and Maine, and established in most locations in 2-3 years. In the Wellesley site that received the first releases of T. setifer, densities of L. lilii larvae declined from roughly 7/stem to 0.5/stem in the 7 years following parasitoid release, a decline that was statistically significant compared to a control plot 17 km distant.

Lemophagus errabundus is most prevalent in Europe in areas with ocean-moderated climates (Kenis et al. 2002). This knowledge led us to make our releases in similar locations in New England: Plainville, MA, Falmouth, MA, and Kingston, RI. We confirmed establishment of *L*. *errabundus* in Plainville, MA. Newly established in North America, *L*. *errabundus* may have a greater impact on *L. lilii* than it does in Europe, because it was introduced without its hyperparasitoid, *Mesochorus lilioceriphilus*, which is very common in the UK, Sweden, and most of Europe (Salisbury 2008; Ramert et al. 2009; Kenis et al. 2002).

Diaparsis jucunda is the dominant parasitoid found in native lilies in mountainous sites in Switzerland and in colder areas of central and southern Europe (Kenis et al. 2002). For this reason we wanted to release *D. jucunda* in more northern or inland sites of New England, specifically five locations in Maine and New Hampshire. In more southern releases of *D. jucunda* we did not detect parasitism until four years after release, but in our northern Maine releases we found successfully overwintered parasitoids the year following release. *Diaparsis jucunda* is now established in Massachusetts, Rhode Island, New Hampshire, and Maine.

It is clear from Figs. 4-6 that all 3 parasitoids are established and spreading from a number of release sites. It is important to determine how they can best be used in a management program for *L. lilii*. The movement of the parasitoids is fairly slow, which may in part be due to the patchy distribution of lilies. Most home gardeners have small numbers of lilies, and then it may be a distance to the next garden. Native lilies have a similar patchy distribution. This distribution is not unlike that of Europe where we found parasitoids to be widely distributed in gardens – including finding *T. setifer* in a third-floor balcony in central Angers in France. Thus, in time it is likely that the parasitoids we have released in North

America will spread throughout the range of *L. lilii*, but how long might this take?

Monitoring the rate of spread is difficult because of the highly discontinuous distribution of lilies and the fact that many of our recoveries are from samples collected by homeowners and sent to us for dissection. In a little over a decade, parasitoids have become well established in the area between southern Rhode Island and Boston and show good potential for providing control of *L. lilii*. However this area is a tiny portion of the current distribution of L. lilii and this pest is spreading rapidly. This raises the question of how rapidly the parasitoids can spread on their own and to what extent their spread will need to be supplemented by additional releases. Figures 7-9 give an indication of spread potential by showing distance from release site for each new positive recovery. The results for T. setifer and L. errabundus are quite similar, with an average spread of 0.8 to 0.9 km per year. The maximum values for both of these parasitoids are on the order of 1.5 to 2 km per year. The results for *D. jucunda* are much more variable, possibly because of the greater N-S gradient of release sites, but also more encouraging because they show a potential for spread on the order of 4-5 km per year.

It is possible that as parasitoids further increase their distribution and abundance that their rate of spread will increase, but at present it appears that if homeowners are expecting to see positive results in less than a decade, releases may be on the order of 20 km distant. Releases made at

16 sites spread throughout Connecticut in the past two seasons should add considerably to our knowledge of parasitoid spread and also to the optimal numbers of parasitoids to release per site. Based upon our experience to date, it appears that releases of 50-100 *T. setifer* should result in establishment and ichneumonid releases should be roughly 25 to 50 per plot of 20 lilies with a high infestation of *L. lilii*.

The success of a classical biological control program depends on the successful establishment and dispersal of the introduced predators or parasitoids. The habitat fragmentation (or patchiness) of lilies, as previously mentioned, will affect the future dispersal of both the beetle and its parasitoids, although predators and parasitoids are often more strongly affected by habitat fragmentation than the abundance and diversity of herbivorous hosts (Zabel and Tscharntke 1998). Specialists such as the lily leaf beetle parasitoids may be better dispersers than generalist predators and parasitoids because they are more susceptible to the patchy distribution of available hosts, whereas generalists may find alternate hosts available (Zabel and Tscharntke 1998). Larger parasitoids (*Lemophagus* and *Diaparsis*) could be expected to be better fliers and disperse more easily to new locations with hosts, but smaller ones, such as the eulophid T. setifer, may be more easily dispersed by wind. Small gregarious specialist parasitoids, like *Tetrastichus setifer* tend to be good dispersers, reported to travel at least 2 km within a season (Elzinga et al. 2007). The issue of parasitoid dispersal may be more important in a classical biological control

program in a landscape setting, such as this one, than in an agricultural setting.

To date, rearing and release of agent has been done through URI at a fairly small scale. As the beetle spreads into more states and provinces there may be interest in a larger program of collecting and redistributing, or rearing of all three parasitoids. The cereal leaf beetle biological control program of the 1970's provides precedence for distribution of close relatives of the three Oulema melanopus (cereal leaf beetle) parasitoids (T. julis, D. temporalis, and L. curtus). This program used large field plots to produce cereal leaf beetle larvae and county agents were brought in for field days to successfully redistribute parasitized larvae throughout the state (Haynes and Gage 1981). This program also benefited from a USDA parasitoid rearing laboratory in Niles, MI which distributed parasitoids throughout the infested states (Haynes and Gage 1981). The cereal leaf beetle was considered a major threat to US agriculture and the biological control program was a well funded priority of the USDA. With limited funding for lily leaf beetle, no major parasitoid redistribution programs have been initiated. The cost and shortage of organic lily bulbs is an important issue: at \$0.50 per bulb it costs over \$2.00 per square foot to establish a rearing plot vs. pennies to grow oats in the cereal leaf beetle

program. We have worked out procedures for laboratory rearing, but it is also quite expensive.

The popular practice of mulching lilies in the garden may not support the development of parasitoid populations. Unlike lily leaf beetle adults which can fly to suitable overwintering habitats, all three parasitoids overwinter as immature larvae or pupae directly under their host plants. Mulch may not provide adequate protection from cold, desiccation, and predation. Gold (2003) suggested that our initial establishment efforts with *T. setifer* benefited from the removal of mulch from the plot. This may also be one explanation for the continued prevalence of persistent *L. lilii* populations in many home gardens in Cumberland, RI, in spite of ten years of high *T. setifer* parasitism. All three parasitoids we have released are also present in Sweden, but *L. lilii* still causes significant damage to lilies. It has been suggested that cultivation practices, use of mulch, and the practice of fall digging and spring replanting of bulbs may negatively impact parasitoid success in Sweden (Ramert et al. 2009, Kroon 2009).

Another complication in biological control of *L. lilii* is the fact that most lily bulbs purchased by gardeners have been treated with the insecticide imidacloprid for protection against aphids. From our rearing experience, we know that this systemic insecticide kills *L. lilii* feeding on treated plants for at least one season. During that time the lilies will not support *L. lilii* populations, and therefore will not support development of *L. lilii* parasitoids. We have used organically-produced lily bulbs in our

rearing program for over a decade and gardeners wishing to encourage parasite establishment should consider this as well. Experiments on the impact of mulching on parasitoid populations would also be useful in developing management recommendations to enhance biological control.

We have established in North America the three host-specific parasitoids that are most commonly found attacking lily leaf beetle populations in Europe. Based upon research conducted to date, we believe they have potential to manage this pest in North America and we encourage further work on parasitoid redistribution and subsequent management. As the parasitoids spread throughout North America, there will also be an opportunity to compare the distribution of these three species to the distributions found in Europe using a predictive model such as CLIMEX. Documentation of this program as a successful biological control program will be improved with an understanding of the factors that contributed to the success of the parasitoids in different areas.


Fig. 1. Distribution of *Lilioceris lilii* in northeastern USA; NAPIS Pest Tracker, 3/30/14 (All Data from 2005-2013).



Fig. 2. Distribution Map for *Lilioceris lilii* in North America. (Lily Leaf Beetle Tracker, 3/30/14).



Fig. 3: Lily leaf beetle parasitoid release plots in New England 1999-2003.



Fig. 4. All *T. setifer* release sites from 1999-2013 and positive recovery sites as of 2013.



Fig. 5. All *L. errabundus* release sites from 2003-2007 and positive recovery sites as of 2013.



Fig. 6. All *D. jucunda* release sites from 2003 to 2012 and all positive recovery sites as of 2013.



Fig. 7. Plot of positive recovery of *T. setifer*. Distance from closest release site (km) by year of first recovery after first year of release.



Fig. 8. Plot of positive recovery of *L. errabundus*. Distance from closest release site (km) by year of recovery after first year of release.



Fig. 9. Plot of positive recovery of *D. jucunda*. Distance from closest release site (km) by year of recovery after first year of release.



Fig. 10. Total *L. lilii* larvae per 40 stem sample Wellesley, MA *T. setifer* release site and Belmont, MA control site with standard error bars.



Fig. 11. Percent control over time for Wellesley release site and Belmont Control site (Henderson and Tilton 1955).

Table 1. Tetrastichus setifer release plots: Date of release (number released) Parasitoid source:
a. Angers, France; b. various sites in Switzerland; c. lab rearing from Angers, France and Switzerland; d. N. Germany
(Heiligenhafen), N. Germany, (S. Holstein), Switzerland, N. Italy/S. Switzerland and Central Holland; e. N. Germany
(S. Holstein) and Eastern France (Franche-Comte); f. N. Germany (Heiligenhafen);

	Wellesley,	Waltham, MA	Cambridge,	Cumberland,	Kingston, RI	Cotuit, MA	Hudson, NH	Concord, NH	Bridgton, MF
1999	$\frac{6}{4}(100)$ a			M				1111	
2000	$\frac{6}{12(100)}$	5/30(100)c	6/12(152)						
2000	6/19(100)b	6/5(322)c	0/12(152)						
2001	6/11(510)d	6/6(300)d	6/11(704)	6/14(584)					
2001	6/20(100)a	6/20(100)a	0/11(704)	7/6(400)					
	6/26(100)e	6/20(100)e		//0(400)					
	6/26(200)d	6/26(200)e							
		7/4(400)e							
2002		6/26(719)f		6/21(660)f					
				7/2(1000)f					
2003		7/2(300)			6/27(100)b,f	6/27(140)b,f	6/27(310)b,f		7/16(237)b,f
		7/8(200)			7/7(300)b,f	7/3(375)b,f	7/8(200)b,f		
2004					6/11(185)b	6/4(200)b	6/4(300)b		
					6/18(60)b,	6/16(150)b	6/14(200)b		
					6/23(122)b	. ,	. ,		
					6/29(27)b				
2005					6/23(150)	6/1(130)	6/6(150)		
						6/7(150)			
2006					6/8(200)	. ,		6/8(288)	6/12(200)
					6/20(78)				

	Kingston,	Plainville,	Falmouth,
	RI	MA	MA
2003	6/17(26)	6/25(72)	6/27(33)
	6/27(23)	7/1(25)	7/3(55)
	7/8(24)		
2004	6/15(10)	6/11(32)	
	6/18(4)		
	6/23(7)		
	6/29(4)		
2005	6/10(40)	6/6(64)	
	6/14(20)	6/14(16)	
	6/16(16)		
	6/24(15)		
2006	6/8(41)	5/31(27)	
	6/15(50)	6/5(33)	
	6/20(35)	6/8(39)	
	6/29(24)	6/19(60)	
2007	6/5(14)	6/6(8)	

Table 2. Lemophagus errabundus release plots:Date of release (number released)

	Kingston,	Cumberland,	Belmont,	Deerfield,	Wells,
	RI	RI	NH	NH	ME
2003	6/17(31)	6/25(79)	6/27(37)		
	6/20(59)	7/7(39)	7/8(66)		
	7/7(31)				
2004	6/11(33)	6/7(30)	6/9(32)		6/26(36)
	6/18(9)	6/11(38)	6/14(30)		7/14(33)
	6/23(20)	6/17(9)			
	6/29(26)	6/23(12)			
	7/2(29)				
2005	6/24(42)	7/5(40)			7/5(37)
	7/2(37)				
2006	6/12(18)	5/31(39)	6/27(56)	6/8(54)	
	6/14(39)	6/5(70)	7/7(57)	6/27(52)	
	6/20(16)	6/8(39)		7/7(53)	
	6/29(56)	6/22(41)			
	7/3(36)	7/3(35)			
	7/6(35)				
2007		6/1(15)	6/7(21)	6/7(20)	
			6/18(18)	6/11(20)	
				6/18(18)	

Table 3. Diaparsis jucunda release plots

Table 4. Residential releases for <i>L</i> .	lilii parasitoids,	2003-2013:
Date (Number released), Location		

	T. setifer	L. errabundus	D. jucunda
2003	7/4(50) S. Kingstown, RI		
2004	6/16(50)Nottingham, NH	6/23(37)Middleboro, MA	
2006	6/14(195) Orono, ME 6/14(150) Hampden, ME		6/14(35) Stillwater, ME 6/19(38) Orono, ME
	6/19(186) Orono, ME 6/19(129) Hampden, ME		6/19(18) Stillwater, ME 6/27(49) Orono, ME
			6/27(56) Stillwater, ME 6/30(35) Orono, ME
			6/30(35) Stillwater, ME 7/12(42) Orono, ME 7/12(40) Stillwater, ME
2007	6/7(100) Hampden ME		$\frac{1}{12(40)}$ Sullwater, ME
2007	6/11(100) Hampden ME		6/7(20) Stillwater ME
	6/18(100) Hampden, ME		6/8(7) Kingston RI
	0/10(100) Humpden, ME		6/11(7) Stillwater, ME
			6/13(14) Warwick, RI
			6/18(18) Stillwater. ME
2010	6/7(100) Boothbay, ME		
	6/9(50) Brimfield, MA		
	6/10(81) Ottawa, ON,		
	CA		
	6/10(50) Pittsfield, MA		
	6/11(50) Charlestown,		
	RI		
2011	6/30(532) Boothbay, ME		
	7/6(137) Hope Valley,		
	RI		
2012	6/15(120) Hampton, CT		7/3(33)New London, CT
	6/20(50) Kensington, CT		
	6/20(50) Rocky Hill, CT		
	6/2/(1/)Forestville, CI		
	6/2/(36)Plantsville, CT		
	6/2/(29) Waterbury, C1		
	6/2/(33) Windsor, CI		
	0/28(07) Morris, C1 7/2(22) Kansington CT		
	//3(33)Kensington, C1		
2013	6/13(47)Stafford		
	Springs, CT		
	6/13(55)Watertown, CT		
	6/13(52)Windsor, CT		
	6/26(85)Bethel, CT		
	6/26(35)Nortolk, CT		
	6/26(83)Stonington, CT		
	6/26(90) waterford, CT		

Town, State	Date	Peak %	Distance to	Nearest Release
		Parasitism	Nearest	Site
			Release Site (km)	
Cumberland, RI	6/17/04	100	1.6	Cumberland, RI
Cumberland, RI	6/6/05	39	1	Cumberland, RI
Cumberland, RI	6/14/05	67	1	Cumberland, RI
Cumberland, RI	6/21/05	50	8	Cumberland, RI
Cumberland, RI	6/16/06	80	1.1	Cumberland, RI
Cumberland, RI	6/19/06	23	4.3	Cumberland, RI
Cumberland, RI	6/23/06	91	3.2	Cumberland, RI
Cumberland, RI	6/14/07	93	0.9	Cumberland, RI
South Attleboro, MA	6/9/08	100	5	Cumberland, RI
Cumberland, RI	6/3/09	90	1.2	Cumberland, RI
Cumberland RI	6/8/09	64	11.3	Cumberland, RI
Cumberland, RI	6/8/09	95	6.2	Cumberland, RI
Cumberland, RI	5/28/10	82	5.6	Cumberland, RI
Cumberland, RI	5/28/10	100	1.2	Cumberland, RI
Belmont, MA	6/2/11	57	14.5	Wellesley, MA
Cumberland, RI	6/7/11	100	1.2	Cumberland, RI
Cumberland, RI	6/8/11	71	4.4	Cumberland, RI
Cumberland, RI	6/10/11	100	0.9	Cumberland, RI
Lincoln, RI	6/10/11	8	3.9	Cumberland, RI
Cambridge, MA	6/4/11	29	3	Cambridge, MA
Cumberland, RI	5/31/12	81	1.1	Cumberland, RI
Cumberland, RI	6/5/12	42	11.4	Cumberland, RI
Lexington, MA	6/12/12	9	28.6	Wellesley, MA
Lincoln, RI	6/15/12	15	2.2	Cumberland, RI
West Kingston, RI	5/31/12	4	4	Kingston, RI
Cumberland, RI	6/4/13	50	4.2	Cumberland, RI
Cumberland, RI	6/4/13	21	9.8	Cumberland, RI
Cumberland, RI	6/4/13	67	11.3	Cumberland, RI
Brighton, MA	6/4/13	36	15.8	Wellesley, MA
Waterbury, CT	5/31/13	17	0	Waterbury, CT

Table 5. *T. setifer* peak parasitism at recovery sites, and distance to nearest release site.

Town, State	Date	Peak % Parasitism	Distance to Nearest	Nearest Release Site
			Release Site (km)	
Cumberland, RI	6/6/05	20	4	Plainville, MA
Cumberland, RI	6/14/05	38	3	Plainville, MA
Cumberland, RI	6/8/06	71	8.2	Plainville, MA
Cumberland, RI	6/19/06	57	3.2	Plainville, MA
Kingston, RI	5/30/07	50	0	Kingston, RI
Cumberland, RI	5/30/07	4	9.4	Plainville, MA
Cumberland, RI	6/16/09	9	4	Plainville, MA
Cumberland, RI	5/28/10	50	4	Plainville, MA
Cumberland, RI	6/3/11	78	4	Plainville, MA
Cumberland, RI	6/7/11	7	10	Plainville, MA
Cumberland, RI	6/8/11	67	5.4	Plainville, MA
Charlestown, RI	6/1/12	44	17.2	Kingston, RI
Cumberland, RI	6/6/12	94	4	Plainville, MA
Cumberland, RI	6/7/12	50	10	Plainville, MA
Exeter, RI	6/14/12	10	3.7	Kingston, RI

Table 6. *L. errabundus* peak parasitism at recovery sites, and distance to nearest release site

Town, State	Date	Peak %	Distance to Nearest	Nearest Release
		Parasitism	Release Site (km)	Site
Cumberland, RI	6/26/07	7	6.8	Cumberland, RI
Belmont, MA	6/2/11	32	14.5	Wellesley, MA
Cumberland, RI	6/3/11	28	3.9	Cumberland, RI
Cumberland, RI	6/7/11	5	9.4	Cumberland, RI
Cumberland, RI	6/7/11	4	8.3	Cumberland, RI
Cumberland, RI	6/10/11	6	6.9	Cumberland, RI
Cambridge, MA	5/24/12	17	19.8	Wellesley, MA
West Kingston, RI	5/31/12	67	4.4	Kingston, RI
Cumberland, RI	6/5/12	35	7.3	Cumberland, RI
Cumberland, RI	6/5/12	55	5	Cumberland, RI
Cumberland, RI	6/6/12	33	8	Cumberland, RI
Cumberland, RI	6/6/12	33	7.5	Cumberland, RI
Cumberland, RI	6/7/12	25	8.5	Cumberland, RI
Exeter, RI	6/14/12	7	14.6	Kingston, RI
Wakefield, RI	6/14/12	25	10.6	Kingston, RI
Cambridge, MA	5/27/13	4	19.8	Wellesley, MA
Cumberland, RI	6/4/13	22	6.8	Cumberland, RI
Cumberland, RI	6/4/13	63	6.8	Cumberland, RI
Brighton, MA	6/4/13	27	12.6	Wellesley, MA
Charlestown, RI	6/10/13	40	4	Kingston, RI
East Greenwich, RI	6/12/13	100	19.6	Kingston, RI
Wakefield, RI	6/12/13	100	10.7	Kingston, RI
North Kingstown, RI	6/12/13	60	16	Warwick, RI
Warwick, RI	6/12/13	22	0	Warwick, RI

Table 7. *D. jucunda* peak parasitism at recovery sites, and distance to nearest release site

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Town	Date	Ν	% Para	Dist (km)	Release Site	UTM coordinates
Nottingham, NH	6/23/2004	3	33	0	Nottingham, NH	329166, 4775673
Wellesley, MA	6/1/2004	6	50	0	Wellesley, MA	311033, 4685276
Kingston,RI	6/23/2004	7	57	0	Kingston, RI	288644, 4595847
Cumberland, RI	6/17/2004	28	100	0.9	Cumberland, RI	301103, 4645150
Wellesley, MA	5/28/2004	5	100	0	Wellesley, MA	311033, 4685276
Cotuit, MA	6/28/2004	12	33	0	Cotuit, MA	379851, 4612406
Hudson, NH	7/004	19	90	0	Hudson, NH	300373, 4737581
Bridgton, ME	7/1/2004	18	6	0	Bridgton, ME	362798, 4879386
Cumberland, RI	6/6/2005	18	39	0.9	Cumberland, RI	301103, 4645150
Cumberland, RI	6/14/2005	23	100	0	Cumberland, RI	301121, 4645120
Cumberland, RI	6/14/2005	14	93	0.9	Cumberland, RI	301103, 4645150
Hudson, NH	6/17/2005	20	90	0	Hudson, NH	300373, 4737581
Cotuit, MA	6/17/2005	21	71	0	Cotuit, MA	379851, 4612406
Cumberland, RI	6/27/2005	21	62	1.1	Cumberland, RI	301599, 4646070
Cumberland, RI	6/21/2005	2	50	6.5	Cumberland, RI	299640, 4652603
Cumberland, RI	6/14/2005	6	67	1	Cumberland, RI	300994, 464078
Wellesley, MA	5/30/2006	12	33	0	Wellesley, MA	311033, 4685276
Kingston, RI	6/12/2006	12	58	0	Kingston, RI	288644, 4595847
Cumberland, RI	6/12/2006	14	100	0	Cumberland, RI	301121, 4645120
Cumberland, RI	6/16/2006	4	100	3.3	Cumberland, RI	299844, 4642780
Cumberland, RI	6/16/2006	5	80	1.1	Cumberland, RI	301474, 4645403
Cumberland, RI	6/19/2006	13	23	2.4	Cumberland, RI	302180, 4646914

APPENDIX Tetrastichus setifer Recovery Data

Town	Date	N	% Para	Dist (km)	Release Site	UTM coordinates
Kingston, RI	6/20/2006	8	80	0	Kingston, RI	288644, 4595847
Bridgton, ME	6/20/2006	6	17	0	Bridgton, ME	362798, 4879386
Cumberland, RI	6/21/2006	8	88	1.7	Cumberland, RI	301599, 464070
Cumberland, RI	6/23/2006	5	40	1.9	Cumberland, RI	301366, 4644788
Cumberland, RI	6/23/2006	11	91	2.7	Cumberland, RI	301560, 4648091
Cumberland, RI	6/23/2006	20	5	3.6	Cumberland, RI	301548, 4649151
Cumberland, RI	6/23/2006	14	7	6.0	Cumberland, RI	294885, 4650342
Cumberland, RI	6/23/2006	2	50	6.1	Cumberland, RI	300165, 4651278
Cumberland, RI	6/23/2006	6	100	7.4	Cumberland, RI	301151,4645892
Cumberland, RI	6/23/2006	2	100	1.2	Cumberland, RI	300684, 4643961
Orono, ME	6/27/2006	30	23	0	Orono, ME	525533, 4973007
Hampden, ME	6/28/2006	20	30	0	Hampden, ME	505051, 494618
Orono, ME	7/6/2006	14	57	0	Orono, ME	525533, 4973007
Hampden, ME	7/6/2006	19	16	0	Hampden, ME	505051, 494618
Cumberland, RI	5/30/2007	13	38	0	Cumberland, RI	301121, 4645120
Cumberland, RI	5/30/2007	24	8	4.1	Cumberland, RI	302236, 4648362
Wellesley, MA	5/31/2007	5	80	0	Wellesley, MA	311033, 4685276
Cambridge, MA	6/4/2007	20	15	1.8	Cambridge, MA	324500, 4694625
Plainville, MA	6/12/2007	3	33	5.9	Cumberland, RI	303220, 4650939
Cumberland, RI	6/17/2010	22	23	0	Cumberland, RI	301121, 4645120
Cumberland, RI	5/26/2010	17	100	2.6	Cumberland, RI	296916, 4649754
Cumberland, RI	5/26/2010	19	74	2.7	Cumberland, RI	300852, 4643492
Cumberland, RI	5/26/2010	32	94	1.1	Cumberland, RI	301474, 4645403
Cumberland, RI	5/28/2010	22	100	1.9	Cumberland, RI	301366, 4644788
Cumberland, RI	5/28/2010	20	100	1.7	Cumberland, RI	301599, 464070
Cumberland, RI	6/4/2010	20	35	4.1	Cumberland, RI	300369, 4650148

Town	Date	N	% Para	Dist (km)	Release Site	UTM coordinates
Cumberland, RI	6/4/2010	16	94	11.3	Cumberland, RI	292407, 4653038
Lincoln, RI	6/4/2010	12	8	3.8	Cumberland, RI	299557,4642267
Lincoln, RI	6/4/2010	14	29	2.7	Cumberland, RI	299152, 4643561
Cumberland, RI	6/11/2010	3	100	2.4	Cumberland, RI	301058, 4643904
Hampden, ME	7/5/2010	3	33	0	Hampden, ME	505051, 494618
Cumberland, RI	5/26/2011	19	79	0	Cumberland, RI	301121, 4645120
Belmont, MA	6/2/2011	14	57	17.1	Wellesley, MA	320773, 469002
Cumberland, RI	6/2/2011	25	88	0	Cumberland, RI	301121, 4645120
Cumberland, RI	6/2/2011	23	9	6.9	Cumberland, RI	299605, 4652882
Cumberland, RI	6/3/2011	49	4	5.1	Cumberland, RI	302719, 4650361
Cambridge, MA	6/4/2011	45	44	3.7	Cambridge, MA	326921, 4692594
Cumberland, RI	6/7/2011	6	83	2.4	Cumberland, RI	300638,4643784
Cumberland, RI	6/7/2011	19	100	1.2	Cumberland, RI	300831, 4644085
Cumberland, RI	6/7/2011	9	89	2.6	Cumberland, RI	296916, 4649754
Cumberland, RI	6/7/2011	19	100	1.1	Cumberland, RI	301474, 4645403
Cumberland, RI	6/7/2011	21	81	2.4	Cumberland, RI	301058, 4643904
Cumberland, RI	6/7/2011	17	94	0	Cumberland, RI	301121, 4645120
Cumberland, RI	6/7/2011	20	85	1.7	Cumberland, RI	301599, 464070
Cumberland, RI	6/7/2011	44	52	1.9	Cumberland, RI	301366, 4644788
Cumberland, RI	6/8/2011	16	44	2.7	Cumberland, RI	301560, 4648091
Cumberland, RI	6/8/2011	14	71	3.4	Cumberland, RI	302285, 4648519
Cumberland, RI	6/8/2011	18	6	6.9	Cumberland, RI	299605, 4652882
Cumberland, RI	6/8/2011	2	100	4.1	Cumberland, RI	302203, 4649392
Cumberland, RI	6/8/2011	15	73	4.1	Cumberland, RI	302236, 4649362
Cumberland, RI	6/8/2011	19	47	3.6	Cumberland, RI	301548, 4649151
Boothbay, ME	6/8/2011	31	39	0	Boothbay, ME	447054, 4858323

Town	Date	N	% Para	Dist (km)	Release Site	UTM coordinates
Cumberland, RI	6/10/2011	37	32	4.2	Cumberland, RI	299932, 4650283
Cumberland, RI	6/10/2011	4	100	0.9	Cumberland, RI	301103, 4645150
Lincoln, RI	6/10/2011	44	2	4.0	Cumberland, RI	297999, 4642525
Belmont, MA	6/15/2011	25	88	17.1	Wellesley, MA	320773, 469002
Cumberland, RI	6/15/2011	29	10	0	Cumberland, RI	301121, 4645120
Orono, ME	6/20/2011	43	9	2.5	Orono, ME	525573, 4970560
Old Town, ME	7/6/2012	76	4	8.8	Orono, ME	523992, 4981672
Old Town, ME	7/6/2012	31	29	3.8	Orono, ME	527288, 4976316
Waterbury, CT	5/31/2013	6	17	0	Waterbury, CT	662485, 4602553
Cumberland, RI	6/4/2013	10	50	2.4	Cumberland, RI	302180, 4646914
Cumberland, RI	6/4/2013	9	67	11.3	Cumberland, RI	292407, 4653038
Cumberland, RI	6/4/2013	19	21	2.3	Cumberland, RI	292402, 4653045
Brighton, MA	6/4/2013	11	36	15.9	Wellesley, MA	323265, 4691559
Boothbay, ME	7/1/2013	21	33	0	Boothbay, ME	447054, 4858323

Town	Date	N	% Para	Dist (km)	Release Site	UTM coordinates
Kingston, RI	6/17/03	1	100	0	Kingston, RI	289984, 4594269
Kingston, RI	7/7/03	5	40	0	Kingston, RI	289984, 4594269
Kingston, RI	714/03	10	10	0	Kingston, RI	289984, 4594269
Plainville, MA	6/23/04	16	6	0	Plainville, MA	303220, 4650939
Plainville, MA	6/12/07	18	28	0	Plainville, MA	303220, 4650939
Kingston, RI	6/23/05	19	47	0	Kingston, RI	289984, 4594269
Kingston, RI	6/30/05	10	10	0	Kingston, RI	289984, 4594269
Kingston, RI	6/9/06	7	57	0	Kingston, RI	289984, 4594269
Kingston, RI	6/12/06	20	55	0	Kingston, RI	289984, 4594269
Kingston, RI	6/20/06	13	85	0	Kingston, RI	289984, 4594269
Kingston, RI	6/27/06	22	50	0	Kingston, RI	289984, 4594269
Kingston, RI	7/3/06	10	50	0	Kingston, RI	289984, 4594269
Kingston, RI	7/10/06	8	50	0	Kingston, RI	289984, 4594269
Kingston, RI	5/30/07	2	50	0	Kingston, RI	289984, 4594269
Cumberland, RI	5/30/07	51	4	5.2	Plainville, MA	298394, 4648917
Plainville, MA	6/12/07	16	63	0	Plainville, MA	303220, 4650939
Kingston, RI	6/14/07	8	13	0	Kingston, RI	289984, 4594269
Kingston, RI	6/18/07	6	50	0	Kingston, RI	289984, 4594269
Kingston, RI	6/25/07	11	18	0	Kingston, RI	289984, 4594269
Kingston, RI	6/5/08	13	15	0	Kingston, RI	289984, 4594269
Kingston, RI	6/13/08	38	3	0	Kingston, RI	289984, 4594269
Cumberland, RI	6/6/05	20	20	0.8	Plainville, MA	302719, 4650361
Cumberland, RI	6/14/05	19	5	0.8	Plainville, MA	302719, 4650361
Cumberland, RI	6/8/06	48	71	4.1	Plainville, MA	302143, 4649360
Cumberland, RI	6/19/06	7	57	3.2	Plainville, MA	299832, 4651080

Lemophagus errabundus Recovery Data

Town	Date	Ν	% Para	Dist (km)	Release Site	Address
Cumberland, RI	6/16/09	32	9	0.8	Plainville, MA	302719, 4650361
Cumberland, RI	5/28/10	70	81	0.8	Plainville, MA	302719, 4650361
Cumberland, RI	6/3/11	49	78	0.8	Plainville, MA	302719, 4650361
W. Kingston, RI	6/5/11	18	78	3.2	Kingston, RI	286733, 4593618
Cumberland, RI	6/7/11	44	5	6.4	Plainville, MA	301366, 4644788
W. Kingston, RI	6/9/11	7	29	2.7	Kingston, RI	289594, 4593976
Cumberland, RI	5/31/12	44	34	6.9	Plainville, MA	299605, 4652882
Charlestown, RI	6/1/12	9	44	11.6	Kingston, RI	286260, 4597872
Cumberland, RI	6/6/12	17	18	6.9	Plainville, MA	299605, 4652882
Cumberland, RI	6/7/12	4	50	6.4	Plainville, MA	301366, 4644788
Exeter, RI	7/10/12	30	10	8.4	Kingston, RI	286203, 4604240