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Human visitation rates to the Apostle Islands National Lakeshore and the introduction of the non-native species *Lymantria dispar* (L.)

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ABSTRACT

The introduction of non-native species has accelerated due to increasing levels of global trade and travel, threatening the composition and function of ecosystems. Upon arrival and successful establishment, biological invaders begin to spread and often do so with considerable assistance from humans. Recreational areas can be especially prone to the problem of accidental non-native species transport given the number of visitors that arrive from geographically diverse areas. In this paper, we examine camping permit data to the Apostle Islands National Lakeshore in northwestern Wisconsin, USA, from 1999 to 2007 relative to gypsy moth distribution, phenology and outbreak data. During this time, gypsy moth populations became established in this area ahead of the moving population front of the gypsy moth, suggesting anthropogenic introduction. The permit data revealed that the majority of visitors arrived from outside of the gypsy moth established area. However, there was a consistent yearly trend of visitors that arrived from areas of high gypsy moth populations and who arrived during the gypsy moth life stage (egg masses) most likely to be successfully introduced. Using available data on the gypsy moth and its relationship to camping permit data, we describe how recreational managers could optimize park strategies to mitigate unwanted introductions of the gypsy moth as well as develop analogous strategies for managing other biological invaders in recreational areas.

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1. Introduction

In an increasing global community, the unwanted movement of new species can occur with considerable frequency through trade and travel routes (Carlton, 1987; Reichard and White, 2001; Work et al., 2005; Brockerhoff et al., 2006; Liebhold et al., 2006; McCullough et al., 2006), resulting in decrease in biodiversity, natural resources and ecosystem services as well as increased management costs (Parker et al., 1999; Mack et al., 2000; Pimentel et al., 2005). Upon their arrival and successful establishment, a non-native species spreads to new areas, often through a process known as stratified dispersal in which local population growth and diffusive spread is coupled with long-range dispersal (Hengeveld, 1989; Andow et al., 1990; Shigesada and Kawasaki, 1997; Liebhold and Tobin, 2008). In particular, long-distance movement is an important mechanism of species dispersal to a new territory, and can be facilitated by anthropogenic, atmospheric and hydrological transport mechanisms (Shigesada and Kawasaki, 1997; Ruiz et al., 2000; Isard and Gage, 2001; Isard et al., 2005; Lockwood et al., 2007).

Humans tend to be a primary mover of biota, whether intentional or non-intentional, from the time our ancestors began to wander the planet (di Castri, 1989), explore the world in sailing ships (Crosby, 1986), or now through global trade and travel (Carlton, 1987; Reichard and White, 2001; Hulme et al., 2008). It comes as no surprise that many studies have attempted to quantify the risk of introduction based on the movement of humans and their goods using gravity models (Bossenbroek et al., 2001; Drake and Lodge, 2004; Leung et al., 2006). Other studies have examined the rate of non-native species arrival through foreign trade routes, or species that were intercepted at ports-of-entry (Work et al., 2005; Brockerhoff et al., 2006; McCullough et al., 2006; Liebhold et al., 2006). Because of the strong association between the movement of goods and the introduction of non-native species, state and federal governments often enact regulatory measures, such as quarantines and compliance agreements, to minimize the accidental transport of non-native species. Recreational areas can be especially prone to invasion given the quantity of visitors from potentially geographically diverse areas, as well the degree of

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habitat disturbance due to human impact that could facilitate successful invasions (Chaloupka and Domm, 1986; Bennett et al., 2003; Dickens et al., 2005; Britton-Simmons and Abbott, 2008; Morgan and Carnegie, 2009).

The gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), is no exception to the role humans play in importing non-native species. After being introduced to North America in 1869 by an amateur entomologist (Liebhold et al., 1989), the gypsy moth has spread throughout eastern North America and now is established from Nova Scotia to the eastern half of Wisconsin, and Ontario to Virginia (Tobin et al., 2007a). It continues to be transported anthropogenically to new areas in North America on various vectors such as vehicles, wood and wood products, and household goods (Doane and McManus, 1981; Liebhold and Tobin, 2006; Hajek and Tobin, 2009). Dispersal can also be accomplished through male moth flight, which is believed to be limited in scope unless atmospherically assisted, and early instar ballooning although larvae are usually deposited within a few hundred meters from their source (Doane and McManus, 1981). In North America, adult females do not fly and generally oviposit within 1–2 m from their site of emergence from pupae (Odell and Mastro, 1980). Males locate females for mating through a sex pheromone. The gypsy moth undergoes one generation per year. Larvae hatch from overwintering eggs in spring, and larval development occurs over approximately 6–8 weeks followed by 1–2 weeks for the pupal stage. Adults emerge in summer and mate, and females oviposit diapausing egg masses. Its estimated rate of spread based upon local growth and diffusion rates, but in the absence of long-distance dispersal (e.g., anthropogenic movement of life stages) is approximately 2.5 km yr^{-1} (Liebhold et al., 1992). However, the observed rate of gypsy moth spread along the leading edge ranges from 6 to 18 km yr^{-1} due to long-distance dispersal (Tobin et al., 2007a).

Egg masses tend to be the primary life stage transported by humans because they are sessile, remain in the stage for ≈8 months, and as the diapausing stage they are more likely to survive transport. Moreover, egg masses can each contain 250–450 eggs (Doane and McManus, 1981), and all eggs within a mass would be exposed to similar climatic conditions and hatch within the same time frame; hence, given the initial colony size associated with egg masses, establishment success would likely be higher than it would be for other life stages (Liebhold and Bascompte, 2003; Whitmire and Tobin, 2006; Tobin et al., 2007b, 2009). Gypsy moth larvae can attack over 300 deciduous and coniferous host tree species, particularly hosts within *Quercus*, *Populus*, *Salix*, *Betula* and *Larix* (Elkinton and Liebhold, 1990).

Under federal and state gypsy moth management programs, pheromone-baited traps that attract adult males are deployed to detect potential new colonies that arrive within a transition zone between infested and uninfested areas, and areas far from the established area (i.e., western North America), so that they can be targeted for management (USDA, 2004; Tobin and Blackburn, 2007). Traps have been deployed on the Apostle Islands National Lakeshore (AINL) since 1992, and the first male moths were detected from traps in 1997. Most initial male moth detections on the AINL failed to result in the successful detection of established reproducing populations as determined through alternate life stage surveys. However, beginning in 2005, egg masses were detected on Basswood and Stockton Islands of the AINL, and on Madeline Island.

There are 22 Apostle Islands in Lake Superior off the Bayfield Peninsula in northwestern Wisconsin of which the AINL consists of 21 islands (Fig. 1). The AINL was established in 1970, while the Gaylord Nelson Wilderness area was established in 2006 and includes 80% of the park. Recreational camping is or has been allowed on up to 19 of the Islands. Prior to 1970, many of the Islands were used extensively for agriculture, logging, and quarrying,

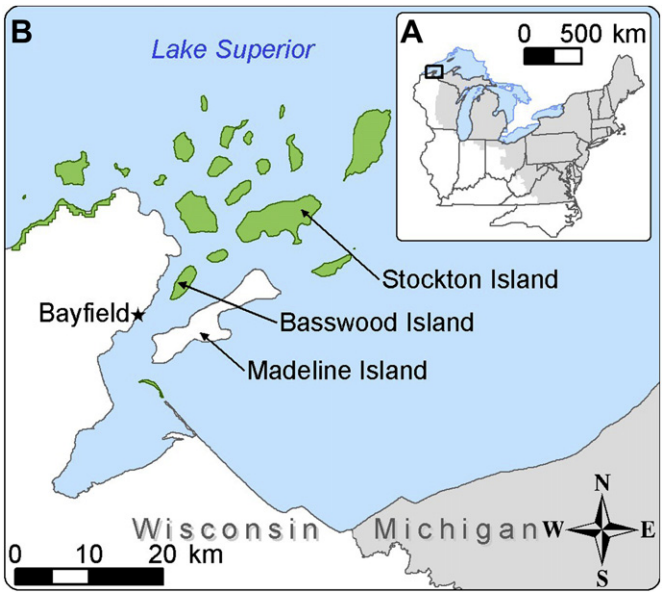

Fig. 1. Gypsy moth quarantined area (grey) in 2008 (A), and area of The Apostle Islands National Lakeshore (green) (B). The first gypsy moth egg masses were detected on Basswood, Stockton, and Madeline Islands in 2005. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mostly prior to the 1940s, and some supported year-round human populations up to at least 1960 (Beals and Cottam, 1960). Only one Island, Madeline, which is the lone island not part of the National Lakeshore, contains privately-owned lands and a year-round, permanent human population of 246 (U.S. Census, 2000). The forests of the Islands can be generally classified as hemlock-white pine-northern hardwoods (Beals and Cottam, 1960). Despite the presence of reproducing gypsy moth populations on many of the Islands now, populations on the AINL were spatially segregated from the leading edge of the established gypsy moth range when higher densities of male moths and established reproducing populations (in the form of egg masses, 2005) were first detected (Supplemental Material A). Because the AINL attracts visitors from throughout the United States, we used park visitation data (1999–2007), male moth trap catch data (1992–2007), and gypsy moth distribution and outbreak data (1999–2007) to assess the relationship between rates of human visitation and the establishment of gypsy moth populations on the AINL.

2. Methods

2.1. Visitation data

Recreational camping in the AINL is allowed with a valid permit from the National Park Service, U. S. Department of Interior. Camping permit data from 1999 to 2007 were used in this analysis, which included the dates of visit, the island and campsite number, the mode of transport to the Island, and the campers' zip code of origin.

2.2. Gypsy moth distribution data

County-level quarantine records for the gypsy moth are maintained by the United States Department of Agriculture, U.S. Code of Federal Regulations, Title 7, Chapter III, Section 301.45–3. Generally, an entire county is designated part of the quarantined area when established gypsy moth populations are first detected in the

county. These records are updated annually and exist from 1912 to the present. Depending on the year of visit, we determined – based upon the zip code of origin – whether a permit was issued to someone from within or outside of the gypsy moth quarantined area. We focused the bulk of our analysis on permits issued to campers that originated from within the quarantined area.

2.3. Gypsy moth phenology

For each year from 1999 to 2007, the dates of 5% egg hatch, 95% completion of 2nd instars, 5% pupation, 5% male moth flight, and 95% male moth flight were estimated for the gypsy moth quarantined area using the gypsy moth phenology model GMPHEN (Sheehan, 1992) implemented using BioSIM software (Régnière and Sharov, 1998). The timing of these phenological events was interpolated over a 1 × 1 km scale. These predicted phenological dates were then used to characterize the most likely gypsy moth life stage that could have been introduced anthropogenically depending on the zip code of origin of the campers and the date of their respective visit to the AINL (Supplemental Material B). This was done only for campers that originated from within the gypsy moth quarantine. The following life cycle categories were used: (1) early instars, bounded by the dates of 5% egg hatch and 95% completion of 2nd instars; (2) late instars, bounded by the dates of 95% completion of 2nd instars and 5% pupation; (3) pupae, bounded by the dates of 5% pupation and 5% male moth flight; (4) early male moth flight, bounded by the dates of 5% male moth flight and midpoint date between 5% and 95% male moth flight (i.e., 50% male moth flight); and (5) egg masses, bounded by the dates of 50% moth flight and 5% egg hatch of the following year.

2.4. Gypsy moth defoliation

For each permit zip code within the quarantined area, we measured the distance to the nearest gypsy moth outbreak based upon defoliation records (Supplemental Material B). Spatial data on gypsy moth defoliation were obtained from the National Aerial Survey Spatial Database (USDA Forest Service, 2009). Aerially-detected defoliation by the gypsy moth was collected by State agencies and the USDA Forest Service (on National Forest Land), and then compiled into the National Aerial Survey Spatial Database. From 1999 to 2007, a total of 3,295,732 ha were recorded as defoliated by the gypsy moth, and yearly amounts ranged from 70,816 ha (2004) to 802,481 ha (2001) (Gypsy Moth Digest, 2009). The proximity to areas defoliated by the gypsy moth could potentially provide a proxy for the likelihood that gypsy moth life stages could have been transported to the AINL on vehicles or equipment.

2.5. History of gypsy moth on the Apostle Islands

Gypsy moth population densities were determined through the deployment of pheromone-baited traps, which attract male moths. A limited number of traps (2) were placed on the Islands beginning in 1992, and increased to 32 traps in 1998 after the first male moth was trapped in 1997. No moths were recorded in 1998. Beginning in 2003 (14 traps set, 58 moths recorded), gypsy moth populations began to increase in each subsequent year (Fig. 2, Supplemental Material A), and the first signs of a reproducing population were recorded in 2005 through the detection of egg masses on Basswood, Stockton, and Madeline Islands. In 2007, 203 traps were set and >50,000 moths were recorded, and several traps individually recorded >1000 male moths.

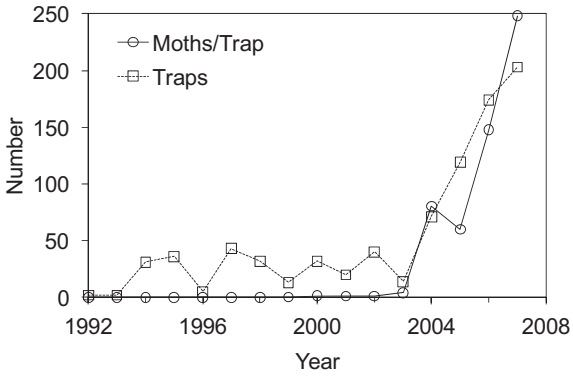

Fig. 2. Time series of trap intensity and male moth trap catch on the Apostle Islands National Lakeshore, 1992–2007.

3. Results

There were 34,150 permits issued from 1999 to 2007, ranging from 3519 to 4239 per year of which 1016–1488 were to visitors originating from the quarantined area at the time of their visit (Table 1). The majority of permits were issued to campers from the Great Lakes region (Fig. 3). In particular, roughly half of all permits were issued to visitors from one of five metropolitan areas: St. Paul/Minneapolis/Bloomington, Minnesota (23.1% of permits), Duluth, Minnesota/Superior, Wisconsin (9.5%), Chicago/Naperville/Joliet, Illinois (6.7%), Madison, Wisconsin (5.9%), and Milwaukee/Waukesha/West Allis, Wisconsin (4.2%). Most of the permits to visitors from the quarantined area were from eastern Wisconsin and Michigan (75.5% of 10,737 permits). Overall, 25, 50, and 90% of permits were issued to visitors that arrived within 122.8, 261.9, and 571.8 km, respectively, of the AINL. Nevertheless, visitors arrived from every US state except Nevada (Fig. 3), with a maximum distance of 6242.1 km.

As with many recreational areas, camping on the AINL is very seasonal: 68.1% of all permits were issued during July and August, and 92.1% were issued from June to September (Supplemental Material C). Most of the permits were issued for camping on Stockton (32.2%), Oak (16.7%), Sand (11.6%), Basswood (8.7%), York (6.8%), and Rocky Islands (5.7%), while the remaining Islands each had less than 900 total permits issued for camping across all years. The primary means of transport to the Islands were by way of canoe or kayak (54.7% of all permits), local transport services (i.e., water taxis, shuttle services; 22.5%), and power or sailboats (generally privately owned; 18.7%).

When considering the 10,737 permits that were issued to campers with zip codes that were within the gypsy moth

Table 1
Yearly summary of the number of permits and unique zip codes of visitors to the Apostle Islands National Lakeshore.

Year	Number of permits		Number of unique zip codes	
	Total	From within the quarantine (%)	Total	From within the quarantine (%)
1999	3667	1233 (33.6)	548	214 (39.1)
2000	3678	1281 (34.8)	573	235 (41.0)
2001	4195	1328 (31.7)	608	243 (40.0)
2002	4239	1488 (35.1)	613	238 (38.8)
2003	3752	1027 (27.4)	499	198 (39.7)
2004	3519	1032 (29.3)	482	193 (40.0)
2005	3772	1016 (26.9)	506	205 (40.5)
2006	3699	1222 (33.0)	514	207 (40.3)
2007	3629	1110 (30.6)	519	199 (38.3)
TOTAL	34,150	10,737 (31.4)	4862	1932 (39.7)

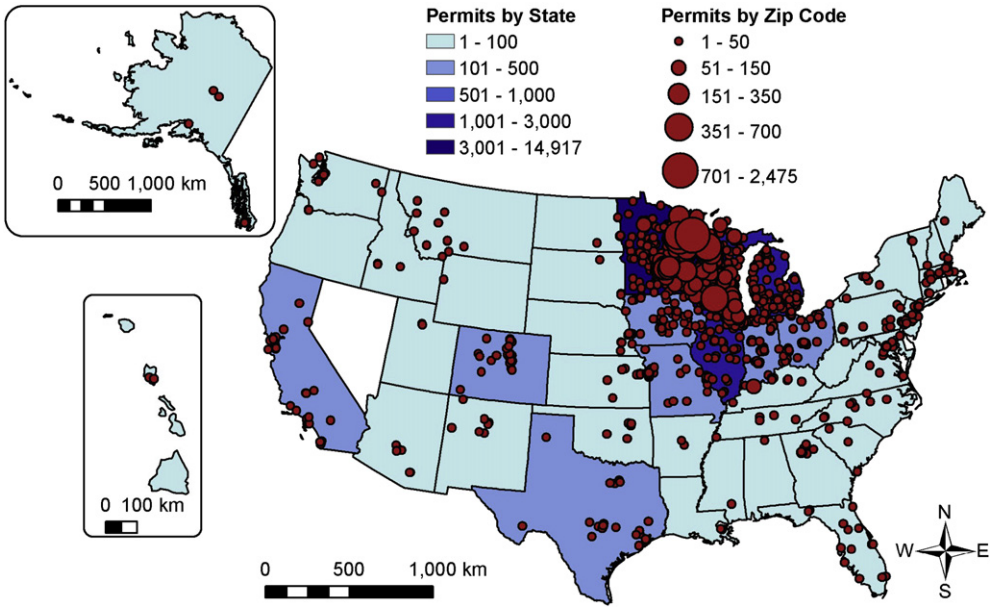

Fig. 3. Proportional bubble plot of the total number of permits issued for camping on the Apostle Islands National Lakeshore, 1999–2007 (34,150 permits).

quarantined area at the time of their respective visit (Table 1), most of these visits (6090; 56.7%) phenologically occurred when diapausing egg masses are most likely to be present in the originating zip code area (Fig. 4). Among these 6090 permits, the majority of visitors went to the Islands by way of kayak or canoe (57.2%), while 27.2 and 13.9% relied on local transport services, or powerboats and sailboats, respectively. Although the permit data do not permit a determination of boat ownership, the mode of transport does provide some insight into cargo load and the accessibility for females to oviposit on them. For example, the use of local transport services would likely have a lower probability of serving as a transport vector for the initial gypsy moth infestation given that they are generally locally maintained and cargo is limited to what a visitor can carry. Canoes and kayaks are often privately owned and do arise from within the quarantined area, but each has limited carrying capacity. Power or sailboats likely represent the most problematic vector for introducing gypsy moth because they can be privately owned, shuttled from areas within the quarantined area, maintained outside such that females could oviposit on the boat and trailer, and have a greater capacity for carrying cargo on which egg masses could be deposited.

When considering those permits that were issued when egg masses would most likely be present (6090 permits), the distances between the zip code of this subset and the nearest recorded areas of gypsy moth defoliation by year are presented in Fig. 5. For all years, the minimum distance was <8 km and in most years, over half of these permits were from zip codes that were >150 km away from the nearest area of defoliation. There were exceptions, most notably in 2002 in which half of the permits were issued to visitors that were <48 km away from an area of recorded defoliation.

4. Discussion

The introduction of any non-native species through recreational travel can be a stochastic event, especially for seasonal destinations in which visitors originate from nearly every US state (Fig. 3). The availability of data on gypsy moth distribution, a phenology model that can be used to predict the timing of gypsy moth life stages, management programs aimed at an initial detection through the

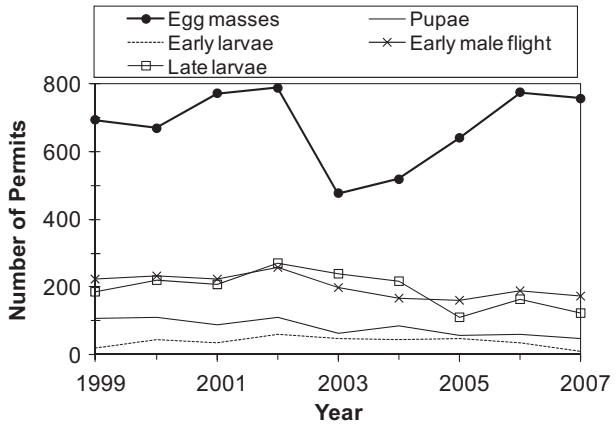

Fig. 4. The timing of visitors to the Apostle Islands National Lakeshore relative to the predicted gypsy moth phenological stage at the visitors' origin. Data shown include only visitors from within the gypsy moth quarantined area (10,737 permits).

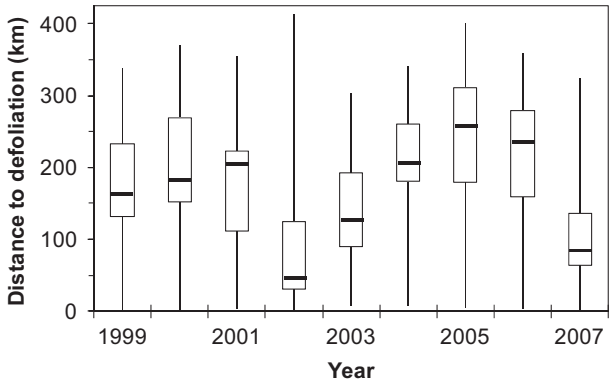

Fig. 5. Box-and-whisker plots of the distance between visitors' origin and the nearest area recording gypsy moth defoliation. Data shown include visitors from within the gypsy moth quarantined area that arrived to the Apostle Islands National Lakeshore during the egg mass stage (cf. Fig. 4; 6090 permits).

use of pheromone-baited traps, and aerial defoliation surveys that indicate the location of gypsy moth outbreaks allows for an assessment of possible gypsy moth introduction on the AINL. Although it is very challenging to definitely assign an introduction event, this analysis should underscore the considerable challenges in managing potential gypsy moth introduction events given the timing of visitation, largely coinciding with the presence of egg masses, and the extent of the gypsy moth infested area. In a general context, this analysis also highlights the importance of insect phenology in the movement of life stages (Isard et al., 2009). Insects have species-specific development and diapause strategies; consequently, certain life stages are more likely to be transported (e.g., due to the length of a particular life stage), survive transport (e.g., such as the diapausing stage that can survive cold temperature extremes), and successfully establish once introduced (e.g., such as egg masses that contain numerous individuals and hence represent a larger founder population).

It was of particular interest to observe that in each year we considered, at least some visitors were arriving from areas close to gypsy moth outbreak areas (Fig. 5), regardless of the yearly variation in outbreak intensity (Gypsy Moth Digest, 2009). For example, in 2002 when the median distance of visitors from an outbreak area was $<$48 km, $\approx$165,422 ha were defoliated while in 2001, the median distance was 206.1 km even though $\approx$802,481 ha were defoliated. Incidentally, in 2002 when the most visitors arrived from or nearby gypsy moth outbreak areas (Fig. 5), most of the visits phenologically corresponded to the availability of egg masses (789 permits; Fig. 4). Moreover, this would have been one year before male moth populations increased in the AINL (Fig. 2), and three years prior to the initial detection of gypsy moth egg masses. The detection of egg masses, in this case on Island trees (as opposed to being detected on vehicles or other transportable items) provides the most irrefutable evidence of established populations since gypsy moth females do not fly. This is also not an unreasonable time lag based upon prior empirical evidence on the lag time between gypsy moth introduction and subsequent detection (Liebhold and Tobin, 2006).

Despite the uncertainty, this exploratory analysis should be of value to managers who could modify regulatory programs aimed at minimizing gypsy moth introductions by considering the zip code of origin (i.e., whether visitors originate from within the quarantine), the timing of the visit (i.e., whether it coincides with the presence of egg masses), and the proximity to potential source populations (i.e., proximity to gypsy moth outbreaks). Although aerial detection of outbreaks is not always available during the current year, an examination of prior year's defoliation records could provide a reasonable spatial approximation of high-density gypsy moth populations. Using this information could help optimize the assessment of introduction risk based upon the origin of visitors. At the least, regulatory measures at this and other recreational areas could be enhanced during years following high intensity gypsy moth outbreaks and particularly those visits that occur when egg masses are most likely to be phenologically available.

In the broader context of managing biological invasions, particularly with regard to quarantine zones and other regulatory guidelines, these results highlight the challenges in minimizing the unwanted introductions of non-native species. The wealth of available information on the gypsy moth is rare among non-native species, and in most cases managers have limited information they can use to mitigate introduction events. For example, many states have a formal ban against the movement of firewood as a means of regulating the movement of the Emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) (EAB Info, 2009); however, the distribution of *A. planipennis*, and hence the source of new infestations, is mostly based upon the discovery of ash mortality as opposed to initial detection. Also, both basic biological information on *A. planipennis* and a sensitive monitoring tool for detecting incipient populations are lacking. Thus, it is not always feasible to optimize a management program aimed at recreational users without assuming a broader and costlier approach (i.e., limiting all firewood movement). However, as more information for this and other non-native species becomes available and accessible through online databases, it should be possible for recreational park managers to incorporate a more focused management strategy that targets recreational visitors from areas that pose the greatest risk of introduction. For example, visitors list their home address on the application permit to the AINL; thus, it should be possible to georeference the zip code with a database of the known established area of gypsy moth, as well as other non-native species, to identify potential risks.

5. Conclusion

There is considerable diversity in the spatial origin of visitors to the AINL, which poses a great challenge to managers and in their efforts to mitigate the introduction of non-native species. Gypsy moth data are robust and accessible (Alien Forest Pest Explorer, 2009; Decision-Support System for the Slow-the-Spread Project, 2009; Gypsy Moth Digest, 2009), and thus would allow for a more precise management strategy by selectively assessing visits of those that originate from within the quarantine, especially those originating from or nearby an outbreak area and visiting at a time when egg masses are most likely to be present. Management strategies could include follow-up questions and outreach efforts, such as during the permit application process, to educate campers on the importance of cargo inspection, especially to those arriving from within the quarantined area. Also, specific areas of the park that have been most frequented by campers that meet the above criteria could be intensively surveyed for gypsy moth life stages at the end of the camping season. Although many of the islands of the AINL now have well-established gypsy moth populations, managers of other recreational areas that are not yet infested by the gypsy moth could benefit from this assessment in their attempts to limit the introduction of gypsy moth and other non-native species.

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Appendix. Supplemental material

Supplemental material associated with this article can be found in the online version, at doi:10.1016/j.jenvman.2010.05.005.

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