Asian Longhorned Beetle (Coleoptera: Cerambycidae), an Introduced Pest of Maple and Other Hardwood Trees in North America and Europe

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ABSTRACT. The Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky), threatens urban and forest hardwood trees both where introduced and in parts of its native range. Native to Asia, this beetle has hitchhiked several times in infested wood packaging used in international trade, and has established breeding populations in five U.S. states, Canada, and at least 11 countries in Europe. It has a broad host range for a cerambycid that attacks living trees, but in the introduced ranges it prefers maples. Identification, classification, and life history of this insect are reviewed here. Eradication is the goal where it has been introduced, which requires detection of infested trees using several approaches, including ground and tree-climbing surveys. Several agencies and researchers in the United States and Europe are evaluating the use of pheromone- and kairomone-baited traps. Control options beyond cutting down infested trees are limited. To date, the parasitoids and predators of this beetle have broad host ranges and are unlikely to be approved in the United States or Europe. An effective delivery system under development for entomopathogenic fungi appears promising. Systemic insecticides have been widely used in the United States, but the ability of these chemicals to reach lethal doses in the crown of large trees is disputed by some scientists, and the potential nontarget effects, especially on pollinators, raise concerns. The most practical approach for eradicating Asian longhorned beetle is to optimize trapping methods using semiochemicals for early detection to eliminate the insect before it spreads over large areas.

Key Words: *Anoplophora glabripennis*, maple, *Acer* spp., invasive species

The Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae) (Fig. 1), is an invasive, polyphagous wood-boring insect that is capable of destroying 30.3% of the urban trees in the United States at an economic loss of US$669 billion (Nowak et al. 2001). The beetle's ability to attack multiple genera of apparently healthy hardwood trees could dramatically alter urban and forest ecosystems. Early, accurate detection of this nonnative pest is crucial for discovering infestations before they become unmanageable.

Taxonomy

A. glabripennis is a member of the family Cerambycidae, which are commonly known as the longhorned beetles (Lingafelter and Hoebeke 2002). These beetles are characterized by having long antennae, which are approximately 1.5–2 times the length of the insect's body. The subfamily, Lamiinae, is commonly referred to as flat-faced longhorns, which are exclusively xylophagous as larvae and phytophagous as adults and play an important role in nutrient cycling (Özdikmen and Hasbenli 2004). The genus *Anoplophora* contains 36 species native to Asia (Lingafelter and Hoebeke 2002).

Common names for Asian longhorned beetle in Asia include the starry sky beetle, basicosta white-spotted longicorn beetle, and smooth shoulder-star longicorn (Commonwealth Agricultural Bureaux International [CABI] 2014). In France and Germany, the beetles are known as longicorne asiatique and Asiatischer Laubholzkäfer, respectively. In the United States, the common name was derived from one of its most notable features, the uniquely long antennae, and its geographic origin. Even though this fairly generic common name is not the most desirable, it became widely used in North America and so has been maintained to prevent any public confusion that would arise by changing it now.

Description of Life Stages

Adults. Asian longhorned beetle adults are large, 17–39 mm in length, and although females tend to be larger than males, there is considerable variation in size both within and between the sexes (Figs. 1 and 2A and B, Lingafelter and Hoebeke 2002). Both sexes have 11-segmented antennae with an alternating white and black banding pattern. The tarsi may have a faint iridescent blue color. The pronotum has two large spines, while the elytra are shiny black and bear white or yellowish tan spots in variable patterns. Older females may have fewer or faded spots following prolonged mating and mate guarding, as the males will chew off the white hairs that create the spots. The decorative setae that create these spots closely resemble setae found on the antennae and other parts of its body.

The sexes can be distinguished as follows: females are generally larger and have shorter antennae than the males, and there are some abdominal tip differences as well. When the antennae are pulled back over the body, five antennomeres (segments) of the male and only one to two antennomeres of the female extend past the apex of the elytra (Lingafelter and Hoebeke 2002). From one-third to one-half of the upper side of each antennomere in both male and female antennae is covered with white hairs, but because male antennae are longer, the black sections appear longer in the male than the female, and this difference is even more pronounced on the underside where the white sections on the males may be almost absent (Wang et al. 2004). The terminal ventral segment on the female has a strong notch in the middle and is densely fringed with hairs, while the terminal ventral segment on the male has a flatter margin, with almost no notch and short hairs (Lingafelter and Hoebeke 2002).

Eggs. Oviposition often begins on branches or the main trunk of the lower crown of a tree. Females chew an oviposition pit through the bark and lay a single egg just under the bark in the cambium (Haack et al. 2006, Fig. 3). Under the bark, the egg ultimately sits in the middle of a localized necrotic tissue zone, either caused by a compound the female deposits or by the process of raising the bark during oviposition (Fig. 3A). In most cases, this prevents the egg from being crushed by the formation of callus tissue as the tree attempts to heal the wound.

Fig. 1. Asian longhorned beetle female on *Acer* twigs, showing the typical black and white body coloration and faint blue iridescence on the legs.

Eggs resemble a large grain of rice ∼5–7 mm in length (Haack et al. 2010, Fig. 3A). Often sap will ooze from oviposition pits and can stain the bark. Fresh oviposition pits are initially red to light brown (Fig. 3B) but darken as they weather (Fig. 3C). The shape of oviposition pits varies from a narrow slit (>1 mm in height) to an irregular oval pit up to 15 mm in diameter, depending on the bark thickness (Smith et al. 2002, Ric et al. 2007). Eggs require less time to hatch at higher temperatures (Keena 2006). See Table 1 for minimum temperature development thresholds and degree-days required for each life stage.

Larvae. The basic morphology of the Asian longhorned beetle is similar to that of other cerambycids in the Lamiinae, with a cylindrical body and no legs (Fig. 4A). Larvae are segmented, elongate, and light yellow or white. The head has a large pair of heavily sclerotized, black mandibles. The pronotum contains a heavily sclerotized, raised plate with shallow pits on the dorsal side (Cavey et al. 1998, Fig. 4A). Asian longhorned beetle larvae have a reported maximum body length and head capsule width of 50 and 5 mm, respectively (Cavey et al. 1998), but head capsule widths up to 5.38 mm have been seen in the laboratory (Keena and Moore 2010). Young larvae create galleries just under the bark, whereas larger larvae tunnel deep into the heartwood of a tree (Fig. 4B). Active larvae excrete a sawdust-like frass and wood shavings that are extruded from larval galleries in infested trees.

Pupae. Asian longhorned beetle pupae can be found in pupal chambers in the sapwood about 1 cm below the bark in the spring (M.K. unpublished data). Larvae pack wood shavings and frass behind themselves to block the larval tunnel and the partially excavated exit hole in front of them (Fig. 5A). Pupae are the same color as larvae but have some traits that resemble those of the adults (Figs. 2, 4A, and 5B). Sclerotized adult structures begin to darken as pupae approach eclosion (Fig. 5B). During metamorphosis, the mandibles and eyes darken first, followed by the legs and antennae (Fig. 5B).

Distinguishing Asian Longhorned Beetles From Other Insects. *Anoplophora chinensis* (Föster), the citrus longhorned beetle, is a closely related beetle that has also gained notoriety as an invasive species (Haack et al. 2010, Fig. 6A). Asian longhorned beetles can be differentiated from *A. chinensis* by the black scutellum and smooth elytra of the former (Fig. 7A vs. B). In the United States, pine sawyers (*Monochamus* spp.) can be easily mistaken for the Asian longhorned beetle. *Monochamus* spp. bear no or only faint markings on their elytra, tend to be smaller, and usually emerge before the Asian longhorned beetle (Fig. 6B and C). Another cerambycid native to the United States, the cottonwood borer (*Plectrodera scalator* F.), can also be mistaken for the Asian longhorned beetle, but can be distinguished by its black spots against a yellowish-white body (Fig. 6D).

Sequence-characterized amplified genes from random amplified polymorphic DNA (RAPD) fragments collected from a wing, leg, antennae, or frass can be used to differentiate the Asian longhorned beetle from other native and exotic cerambycid species, including *A. chinensis*, *Monochamus scutellatus* Say (white-spotted sawyer), *P. scalator*, *Saperda tridentata* Oliver (elm borer), and *Graphisurus fasciatus* (Degeer) (Kethidi et al. 2003). Additional RAPD markers have been found to be useful in intraspecific differentiation of Asian longhorned beetle populations (Gao et al. 2007). Seven mitochondrial DNA regions of the Asian longhorned beetle and three congenerics found in China have been evaluated and appear to be useful for identifying this species (An et al. 2004a,b).

Asian longhorned beetle larvae are not easily distinguished from other species of cerambycid larvae. Their throat ridge on the underside of the head near the mouthparts does not have distinct lateral margins (Lingafelter and Hoebeke 2002). The dorsal abdominal ambulatory ampullae (raised bumps) form two distinct rings around a central lobe that has no bumps, while larvae of *Monochamus* spp. and *P. scalator* have indistinct rings. A key "with good color figures" to distinguish Asian longhorned beetle larvae from closely related beetle species found in Europe is available (Pennacchio et al. 2012). Accuracy of larval stage identification can be greatly enhanced with the aforementioned genetic tools.

Mitochondrial DNA sequences have been used to evaluate the genetic diversity of Asian longhorned beetle introductions in the United States to determine if introductions were independent or expansions of previous infestations. Compared with Asian longhorned beetle populations in China, beetles introduced to the United States have limited genetic diversity as a result of bottlenecking, few separate introductions, or both (Carter et al. 2009a). This limited genetic diversity may also result from prior bottlenecking events in China where the Asian longhorned beetle has moved into man-made treed landscapes. Genetic analysis of Asian longhorned beetles from Ontario, Canada, found mitochondrial DNA haplotypes not present in U.S. populations, indicating that both of these introductions occurred independently (Carter et al. 2009b). Hardy–Weinberg equilibrium was not satisfied in the Canadian beetle populations, indicating nonrandom mating. Using RAPD analysis, Asian longhorned beetle introductions in Illinois and New York have also been determined to be independent (An et al. 2004a,b). Further work to refine the ability to determine the origin of each introduction is needed.

Biology

Distribution. The Asian longhorned beetle was first discovered in the United States in Brooklyn, New York, during August 1996 (Haack et al. 1997, Cavey et al. 1998). Following this initial discovery, it was also found in the greater New York City area, New Jersey, Massachusetts, Illinois, and Ohio (Poland et al. 1998, Haack 2006, Haack et al. 2006, Dodds and Orwig 2011, U.S. Department of Agriculture, Animal and Plant Health Inspection Service [USDA-APHIS] 2013a), and most recently in Babylon Township, New York (USDA-APHIS 2013b). The Asian longhorned beetle has been declared eradicated from Islip, Manhattan, and Staten Island, New York; Jersey City, New Jersey; Chicago, Illinois; Boston, Massachusetts; and Toronto, Ontario, although the Asian longhorned beetle was recently discovered in Toronto in late 2013 (Canadian Food Inspection Agency [CFIA] 2013). Infestations have been found in other countries where eradication has also been the goal, including Austria, Belgium, England, France, Germany, Italy, Switzerland, and
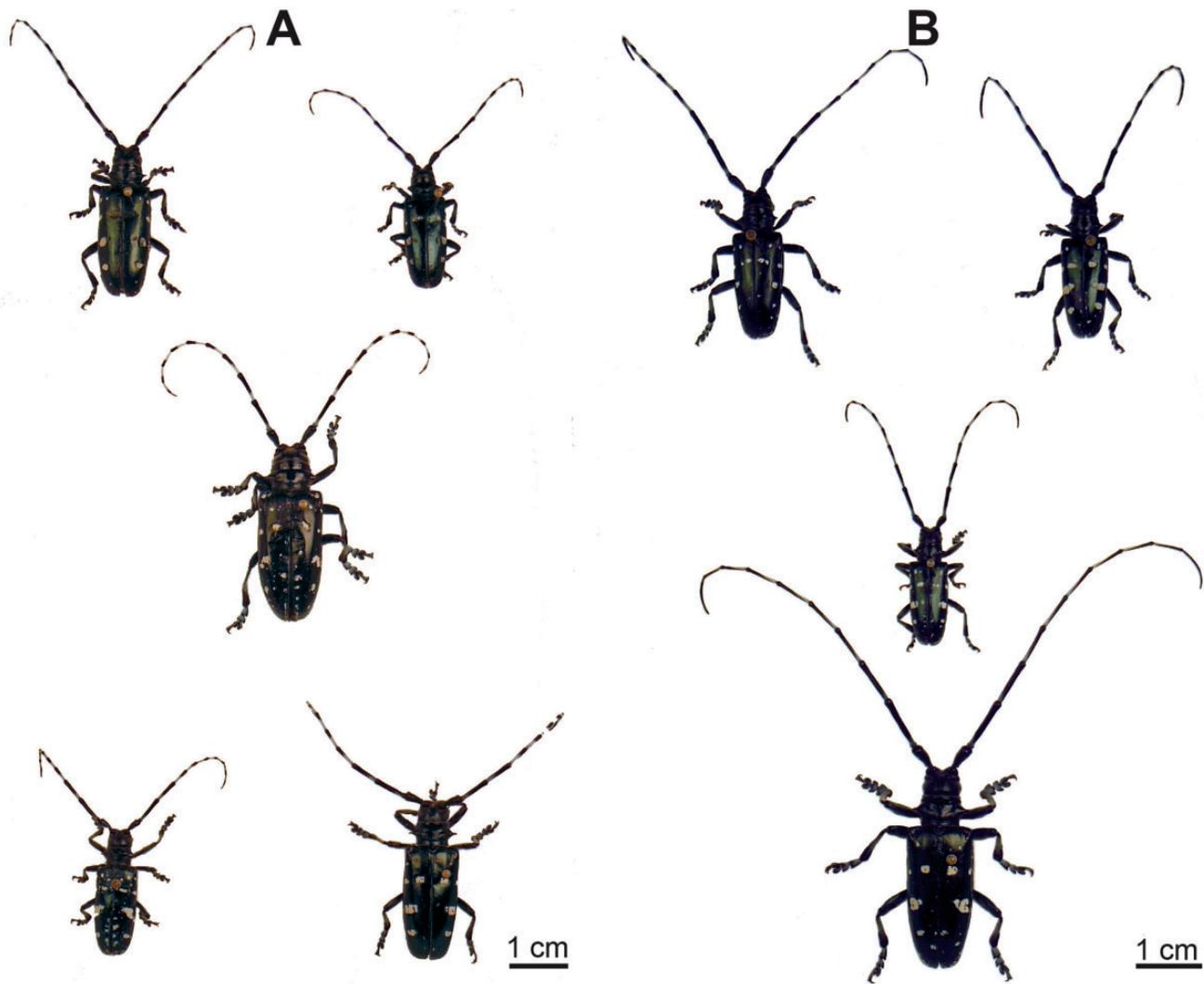
Fig. 2. Adult Asian longhorned beetles are large, have two sharp tubercles (spines) on the pronotum, and a distinct black-white banding pattern on the antennae. The legs and feet are pubescent with a white or blue iridescence. Spots on the elytra are highly variable in color, shape, and size. Males have longer antennae relative to their body and are generally smaller than females. The anterior elytra are smooth. (A) Asian longhorned beetle adult females. (B) Asian longhorned beetle adult males. Note the variation in sizes of males and females.

the United Kingdom (European and Mediterranean Plant Protection Organization [EPPO] 2013).

The Asian longhorned beetle has a broad distribution throughout China and the Koreas (Lingafelter and Hoebeke 2002, Williams et al. 2004a). It is most damaging in the Chinese provinces of Liaoning, Jiangsu, Shanxi, Henan, and Hubei (Yan 1985) and can be found in a much larger area spanning from 21°–43°N and 100°–127°E. Global warming has allowed the Asian longhorned beetle to spread northwards in China (Wang et al. 2011). Niche modeling indicates it is most likely to establish in central and eastern China, the Koreas, and Japan (Peterson et al. 2004), with a slight chance of establishment in southeast China and east India.

Niche modeling has been used to predict the susceptibility of U.S. forests to Asian longhorned beetle establishment. Most of the eastern United States is at risk (Peterson and Vieglais 2001, Peterson et al. 2004). Epidemic simulation models based on habitat suitability and known entry points (ports and warehouses) indicate that the Great Lakes region is most likely to be an initial invasion point (Peterson et al. 2004). Proximity to transportation corridors, such as roads, and a high probability of preferred host presence are significant predictors of an Asian longhorned beetle infestation (Shatz et al. 2013).

Given the lack of suitable hosts outside of urban areas, the western United States is less susceptible to establishment despite the greater volume of cargo arriving from Asia compared with other parts of the United States (Peterson et al. 2004). This species is not predicted to establish in Mexican or northern Canadian forests due to the general lack of the most preferred North American host trees. Cold temperatures are unlikely to limit the range of the Asian longhorned beetle. The beetle has a supercooling point of $-25.8°C$ and is freeze tolerant, with at least 92% of larvae being able to survive temperatures of $-25°C$ or lower for 24 h in laboratory experiments (Roden et al. 2009).

Life History. *Eggs.* After a female chews an oviposition pit in the bark during the summer or early fall, she lays an egg beneath the bark into the phloem. Mortality is highest in the egg and first instar, as these life stages occur close to the plant surface, leaving Asian longhorned beetles vulnerable to extreme temperatures, host responses, and natural enemies (Tang et al. 1996). Asian longhorned beetle eggs take 54.4 ± 0.7 to 13.3 ± 0.7 d to hatch at temperatures ranging from 15 to 30°C with less time needed at higher temperatures (Keena 2006). Percent egg hatch is the highest at 25°C ($63.6 \pm 6.8\%$) and rapidly decreases at temperatures above or below the optimum. Asian longhorned beetle eggs do not hatch if held at 5, 10 or 35°C and require
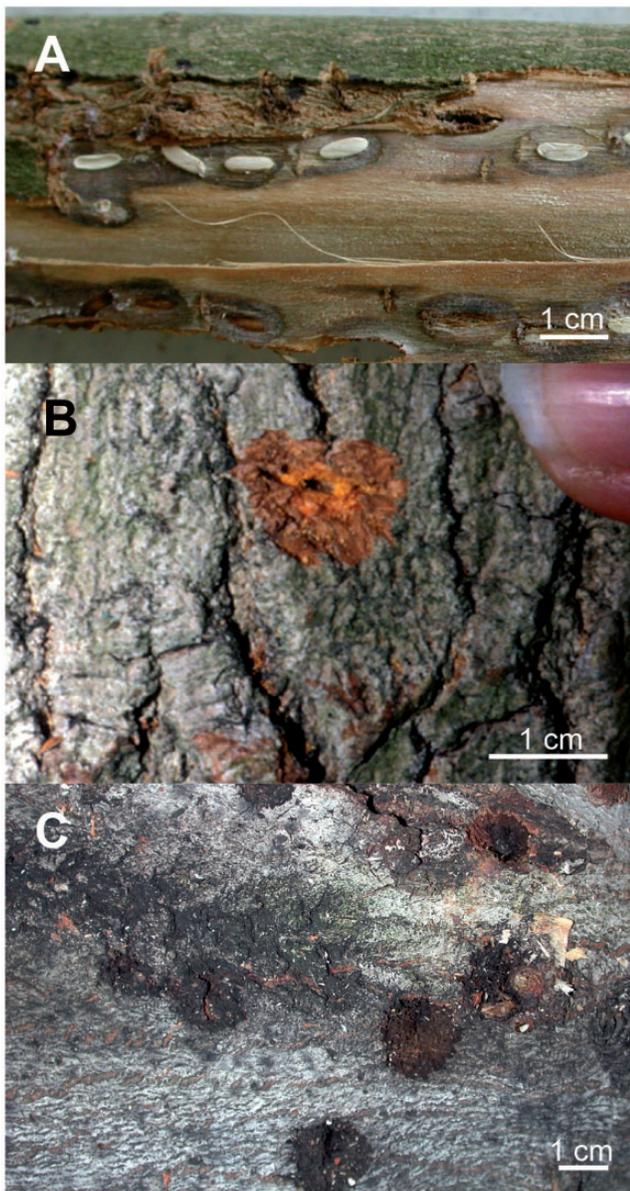
Fig. 3. Asian longhorned beetle oviposition sites and eggs. (A) *A. platanoides* bolt with bark removed showing eggs. Eggs are inserted beneath the bark. (B) An oviposition pit on *A. saccharum.* These pits can be found on branches and sometimes the main bole of infested trees. Fresh oviposition pits are red or light brown and may ooze sap. (C) Older oviposition pits on *Acer rubrum.* After a few months, oviposition pits darken.

239 degree-days for 50% of the eggs to hatch (Keena 2006, Table 1). Eggs that are laid in late summer or early fall do not have time to hatch; instead these eggs overwinter and hatch when it warms up again the next year. Females usually lay eggs only when the air temperature is between 15 and 30°C.

Larvae. Larvae require 1–2 yrs to develop before reaching a critical weight and pupating. In colder, northern regions of China, the Asian longhorned beetle is more likely to take 2 yrs to develop (Hua et al. 1992). There are five or more instars, which varies depending on host species, host condition, and temperature. In the laboratory, larval molts have numbered as high as 20 (Keena and Moore 2010). As with eggs, larval development time depends on host species (Smith et al. 2002) and temperature, with time in each instar shortening as temperatures

Table 1. Lower temperature development thresholds and degree-day requirements for various Asian longhorned beetle instars and life stages

Instar/Stage	T_L	DD_{50}
Egg	10.0	239
1	9.7	78.3
2	10.3	111.7
3	10.1	153.0
4	9.1	250.6
5	9.8	284.8
6	12.7	279.2
7	13.3	315.9
8	12.1	365.8
9	12.3	
Pupa	10.1	255.7

T_L, lower temperature development threshold measured in °C; DD_{50}, degree days needed for 50% of insects to complete each life stage. Excerpt from Keena and Moore (2010) and Keena (2006).
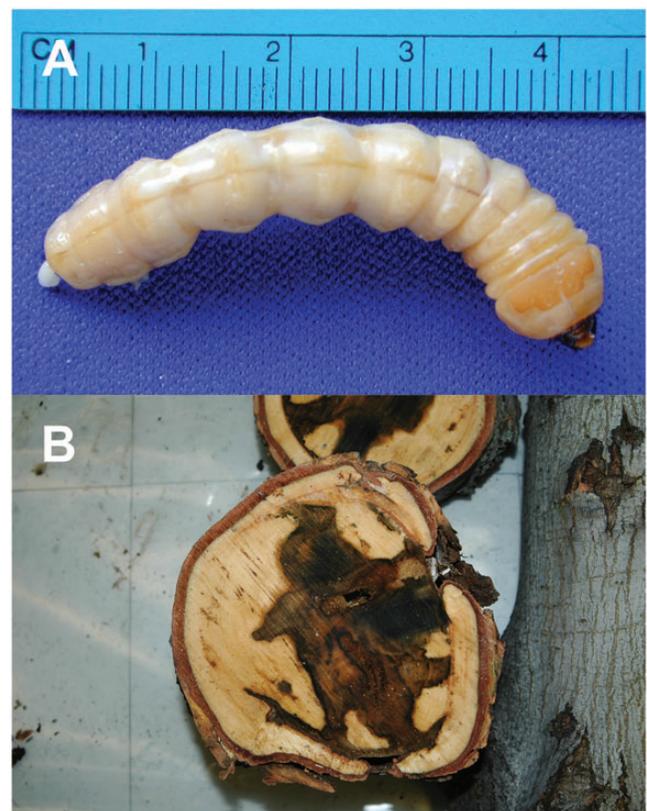
Fig. 4. Larval stages of Asian longhorned beetle. (A) An older larva. Notice the shape of the plate on the pronotum. (B) Galleries created by larvae in *Acer rubrum.* Older instars are able to tunnel into the heartwood.

increase up to 30°C and with no development occurring at ≤10 or ≥40°C (Keena and Moore 2010).

Pupae. Pupal eclosion is temperature-dependent and can take 12–50 d at temperatures ranging from 15–30°C (Keena and Moore 2010). Prepupae kept at low temperatures (10°C) may fail to pupate until exposed to higher temperatures. The lower temperature development threshold for pupae is estimated to be 10°C (Table 1). About 256 degree-days (lower threshold 10°C) are needed for 50% of pupae to develop into adults (Keena and Moore 2010).

Fig. 5. Asian longhorned beetle pupae. (A) Pupa in pupal chamber. Frass has been packed into the entrance tunnel with a partially prechewed exit tunnel from the chamber. (B) Various ages of pupae. Older pupae on the left have more sclerotized body parts compared with younger pupae on the right.

Fig. 6. Examples of Asian longhorned beetle look-alikes. (A) The invasive citrus longhorned beetle, *Anoplophora chinensis*. This beetle looks nearly identical to Asian longhorned beetle in shape and size but usually has rough, bumpy anterior elytra. Photo by Holly Raguza, Pennsylvania Department of Agriculture. (B) The white spotted sawyer, *Monochamus scutellatus.* This beetle is considerably smaller than Asian longhorned beetle and has a distinct, white scutellum. Asian longhorned beetle does not have a white scutellum. (C) The northern pine sawyer, *Monochamus notatus*, a native U.S. species, can be easily mistaken as Asian longhorned beetle. These beetles are generally smaller than Asian longhorned beetle and have longer antennae. The body of the northern pine sawyer is usually grayish-brown. Faint spots may be present on the elytra. (D) The cottonwood borer, *Plectrodera scalator*, can also be mistaken for Asian longhorned beetle. This beetle is native to the United States and found east of the Rocky Mountains. *P. scalator* has black spots against a yellow body.

Adults. Following adult eclosion, beetles spend 4–7 d undergoing sclerotization before initiating chewing out of trees, and another 4–5 d to complete emergence (Sánchez and Keena 2013). In Ningxia, China, peak emergence occurs from late June to early July, with a smaller peak occurring in mid-August (Zhang and Xu 1991). In the New York City infestation the first recorded beetles were found between June 26 and July 29; peak emergence generally also occurred during this time but some occurred even in September (Auclair et al. 2005).

Temperature and host species have significant effects on Asian longhorned beetle longevity and fecundity. In the laboratory, females and males can survive up to 158 and 202 d, respectively, when reared at 20 °C on *Acer saccharum* Marsh (Keena 2006). Optimal longevity occurs when beetles are kept at 18 °C (Keena 2006). Maximum fecundity occurs when beetles are kept between 23–24 °C, depending on their geographical origin, and more eggs hatch when held at 25 °C than at other temperatures. Using infested bolts cut from quarantine areas in New York and Chicago, fecundity of emerged females was evaluated under laboratory conditions. Lifetime production of viable eggs per female was 45–62 eggs on average (Keena 2002). In another laboratory-based study, the number of viable eggs laid increased with increasing female body size, but decreased as a function of beetle age, the diameter and area of the oviposition bolt, and the thickness of the bark (Smith et al. 2002). Females fed on twigs of *Acer platanoides* L. or *Acer rubrum* L. had longer survival and greater fecundity than females fed on *Salix nigra* Marshall (Smith et al. 2002).

Adults remain inactive and perch in tree crowns during the early morning and late afternoon, and are inactive during inclement weather and high temperatures (Zhou et al. 1984). Under greenhouse conditions, adults were least active in the morning when it was cool, rested in the shade during the heat of the day, and were most active later in the day from 8 p.m. to midnight (Morewood et al. 2004). Both sexes spent most of their time "in decreasing frequency" resting, walking, or feeding. Males mate multiple times with multiple females and guard inseminated females for several hours. Adults feed on leaf petioles and debark small branches, also feeding on the cambium. Adults tend to re-infest their natal host as long as it is alive, rarely fly, and instead walk as their primary means of locomotion (Zhou et al. 1984). Possible reasons that beetles fly are in response to declining host quality (M.K., unpublished
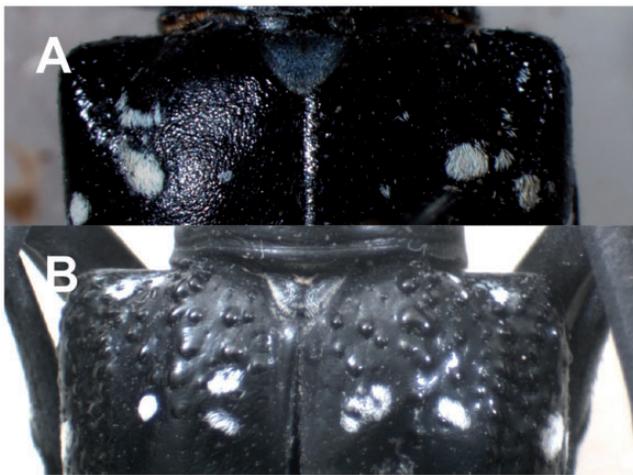
Fig. 7. Comparison of anterior elytra of Asian longhorned beetle and *A. chinensis.* (A) The anterior elytra of Asian longhorned beetle are smooth. The scutellum is covered with dark hairs. (B) The anterior elytra of *A. chinensis.* Note the bumps present in this area. The scutellum is also covered with white hairs. Photo by Holly Raguza, Pennsylvania Department of Agriculture.

Table 2. Tree genera (families) that serve as larval hosts for Asian longhorned beetle

Genera	Common name
Acer (Sapindaceae)	Maple
Aesculus (Sapindaceae)	Buckeye and horse chestnut
Albizia (Fabaceae)	Silk tree
Betula (Betulaceae)	Birch
Carpinus (Betulaceae)	Hornbeam
Carya (Juglandaceae)[a]	Hickory
Cercidiphyllum (Cercidiphyllaceae)	Katsura
Crataegus (Rosaceae)	Hawthorn
Elaeagnus (Elaeagnaceae)	Silverberry
Fagus (Fagaceae)	Beech
Firmiana (Sterculiaceae)	Parasol tree
Fraxinus (Oleaceae)	Ash
Koelreuteria (Sapindaceae)	Golden-rain tree
Malus (Rosaceae)	Apple tree
Platanus (Platanaceae)	Planes, sycamore
Populus[b] (Salicaceae)	Poplar, aspen, cottonwood
Prunus (Rosaceae)	Stone fruit tree
Salix (Salicaceae)	Willow
Sorbus (Rosaceae)	Mountain-ash
Tilia (Malvaceae)	Linden, basswood
Ulmus (Ulmaceae)	Elm
Xanthoceras (Sapindaceae)	Yellowhorn

[a]Only one report of a single species from this genus reported as infested.
[b]Susceptibility to Asian longhorned beetle varies greatly in *Populus* spp.

data), in response to landing on nonpreferred hosts, after experiencing an aggressive encounter with a conspecific (M.K., unpublished data), to locate a mate, when disturbed by a potential predator, or to find suitable environmental conditions.

Ecology. Larvae live in and consume the sapwood and heartwood of susceptible host species. A single Asian longhorned beetle larva can consume 1,000 cubic cm of wood (Yan and Qin 1992). When 3-yr-old *Populus euramericana* Guinier trees were infested with Asian longhorned beetles for 3 yrs, they had a 22–49% and 5–25% decrease in the diameter of the truck at breast height (DBH) and vertical height, respectively (Gao et al. 1993). Mounting evidence suggests that the beetle is able to thrive in the sapwood and heartwood of healthy trees by harboring a diverse gut microbial community that facilitates lignocellulose degradation and nutrient acquisition (Geib et al. 2008, 2009; Scully et al. 2013; Ayayee et al. 2014).

The Asian longhorned beetle typically begins attacking the crown of a host tree along main branches (Haack et al. 2006), making it difficult to detect in the first year or two of the infestation. Eggs are laid in an aggregated pattern along main branches and the lower crown (Li et al. 2012, Ma et al. 2012). In heavily infested trees or those with continuous branches beginning at the base, beetles oviposit on the lower trunk. A female-produced trail pheromone is hypothesized to act as a spacing pheromone that may deter repeated oviposition in the same location (Hoover et al. 2014). Asian longhorned beetles also begin attacking the trunk as the crown dies from a heavy infestation (Lingafelter and Hoebeke 2002).

Adult Dispersal. Spread of the Asian longhorned beetle within a given location has been modeled; in a 30-d mark, release, recapture study in China, the average dispersal of Asian longhorned beetles from the center of a field was 106.3 m (Junbao et al. 1988). Weekly sampling of forest trees in Liu Hua, China, for 3.5 mo revealed that male and female beetles can disperse up to 1,029 and 1,442 m, respectively (Smith et al. 2001). Ninety-eight percent of the recovered beetles were captured within 560 m of the release site. In a follow-up study performed at the same location with more distant recapture points, dispersal potential for males and females was calculated to be 2,394 and 2,644 m, respectively, but 98% of beetles were recaptured within 920 m from the release point (Smith et al. 2004). A study utilizing harmonic radar showed that beetles moved an average of 14 m in a 9–14-d interval with a bimodal distribution of 0 and 90+ meters; males moved six times the distance compared with females (Williams et al. 2004b). Recaptured beetles tend to move upwind (Li et al. 2010), perhaps in

response to plant or conspecific odors. USDA-APHIS requires quarantine boundaries to extend 2,400 m from the nearest infested tree, which encompasses the dispersal potential of nearly 100% of Asian longhorned beetles ([USDA-APHIS-PPQ] 2014).

In poplar forests, the Asian longhorned beetle is more likely to be found along forest edges than in the forest interior (Liu et al. 2012). High canopy density and high vegetation coverage reduce Asian longhorned beetle densities. In Ningxia, China, populations were lowest 12 m inside a *Populus alba* L. stand and peaked 2 m from the forest edge (Wei et al. 1997). Trees on the eastern side of the stand were the least damaged by the Asian longhorned beetle. In mixed stands, the distribution of Asian longhorned beetles can vary according to tree species composition (Wang et al. 2006). For example, in a stand containing *P. alba* var. *pyramidalis* and *Acer negundo* L., damage by Asian longhorned beetles followed an aggregated distribution. The oldest oviposition pits were found on the outside of the stand, while the active frass holes were in the center of the stand, indicating the infestation started on the margins and moved toward the center of the stand. In a pure stand of *Populus simonii* x *Populus nigra* var. *italica*, damage caused by the Asian longhorned beetle was randomly distributed. In closed canopy mixed hardwood stands in the Worcester, Massachusetts, regulated area, Asian longhorned beetle-infested *Acer* trees were found throughout the stand, indicating that although they may have started along the edges, they can quickly move into a stand (Dodds et al. 2014). In addition, in these stands the codominant and dominant size classes of *Acer rubrum* L. were more frequently attacked compared with other *Acer* species and size classes that were present.

Hosts. The Asian longhorned beetle is known to attack >100 different tree species in the wild with preference for those in the genera *Acer*, *Populus*, *Salix*, and *Ulmus* (MacLeod et al. 2002, Haack et al. 2006, Hu et al. 2009). See Table 2 for a list of genera known to serve as Asian longhorned beetle larval hosts (one of which has a single documented infestation on one species) and Supp Table 1 (online only) for an extended list of tree species on which Asian longhorned beetle feeds, oviposits, or completes development under field conditions. (Wu and Zhang 1966; Gao et al. 1993; Lou et al. 1993; Zhao et al. 1993; Wang and Zhou 1994; Tang et al. 1996; Gao et al. 1997; Bai and Zhang 1999; Wang et al. 2000b, 2009; Maspero et al. 2007; Qiao et al. 2007; Tomicezk and Hoyer-Tomiczek 2007; Guo 2008; Yan et al. 2008; Hu et al. 2009; Jin and Sun 2009; Tian et al. 2009; Zhao et al. 2011; Bund

Fig. 8. Signs of Asian longhorned beetle infestation in *Betula platyphylla* Suk in Harbin, China. (A) Oviposition pits concentrated along a main branch and the trunk in the lower crown. In *Betula* spp., oviposition pits become black by the following season. Recently chewed pits are brown colored. (B) Frass being extruded from oviposition pits. Frass will also accumulate on the ground beneath a tree. (C) Perfectly round exit hole on a small branch. This is uncommon. Exit holes are typically found on larger branches and the main trunk. (D) Adult feeding damage on *A. rubrum* twigs. Beetles debark twigs to gain access to the cambium.

Schweizer Baumpflege [BSB] 2012; Jiang et al. 2012; Yan and Liu 2012; U. S. Department of Agriculture, Forest Service [USDA-FS] 2012; CFIA 2013; EPPO 2013; Dodds et al. 2014; CABI 2014; USDA-APHIS-PPQ-CPHST 2015). In the United States, the Asian longhorned beetle has also been documented to infest tree species in the genera *Aesculus*, *Hibiscus*, and *Betula* (Haack et al. 1996), but strongly prefers maples, which are ubiquitous across the American landscape, including *Acer platanoides* L. (Norway maple), *Acer saccharum* Marsh (sugar maple), *Acer saccharinum* L. (silver maple), *Acer rubrum* (red maple), and *Acer negundo* (boxelder) (Haack et al. 2006). The most recent new host record was recorded in Worcester, Massachusetts, the katsura tree in the genus *Cercidiphyllum* (U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine [USDA-APHIS-PPQ] 2010). In China, the beetle is a major pest in monoculture *Populus* plantations and has been referred to as the "forest fire without smoke" (Li and Wu 1993), but susceptibility among poplar species and hybrids varies considerably (Hu et al. 2009).

Sampling or Scouting Procedures

Signs of Asian Longhorned Beetle Infestation. Signs of Asian long-horned beetle infestation include oviposition pits (Figs. 3B and C and 8A), frass (Fig. 8B), exit holes (Fig. 8C), oozing sap, twigs with stripped bark (Fig. 8D), and galleries in the sapwood and heartwood (Haack et al. 2010, Fig. 4B). Thus, severe infestations can compromise the structural integrity of a tree. Since older (and bigger) larvae spend most of their time in the heartwood, trees can sustain infestations with-out visible signs of attack. Asian longhorned beetle infestations are often first detected and brought to the attention of government officials by members of the public.

Detection and Eradication Methods. Several methods have been developed to detect and delimit Asian longhorned beetle populations. The most commonly used approach utilizes specialized ground sur-veyors equipped with binoculars to locate signs of Asian longhorned beetle damage on a tree. During these surveys all trees with a stem diameter of >2.5 cm are inspected (Ric et al. 2007), as this beetle has been found in trees as small as 8 cm in diameter in the United States (Haack et al. 2006) and as small as 3.3 cm in diameter in Canada (Kimoto and Duthie-Holt 2004). According to USDA environmental assessment reports, accuracy of detection by ground surveyors is about 30% as determined by quality assurance checks (USDA-APHIS 2013a). Effectiveness of ground surveyors in detecting trees with signs was found to improve when sign density increased, signs were below 2.5 m in height on the tree, and when oviposition pits were located on boles and exit holes on branches (Turgeon et al. 2010). Tree climbers can detect signs of Asian longhorned beetle infestation with higher rates of accuracy, ranging from 60 to 75% (USDA-APHIS 2013a), but this method is more costly and slower than ground surveys (Hu et al. 2009). Hydraulic lifts are also used to survey for evidence of Asian longhorned beetle infestation and are more effective than ground surveys alone.

Lure-baited traps can be used to detect Asian longhorned beetles in the field. A two-component volatile male-produced pheromone consist-ing of a 1:1 ratio of 4-(n-heptyloxy)butanal and 4-(n-heptyloxy)butan-1-ol was identified (Zhang et al. 2002) and has been under evaluation for several years. The pheromone alone is not significantly attractive (Nehme et al. 2009), but addition of a plant kairomone mixture contain-ing (-)-linalool, (Z)-3-hexen-1-ol, and *trans*-caryophyllene with or without addition of *trans*-pinocarveol or linalool oxide significantly increased trap catches of female Asian longhorned beetle in field

studies (Nehme et al. 2010, 2014). This finding is consistent with several cerambycid trapping studies that demonstrated a synergistic effect when pheromone and host plant kairomones were released together, resulting in a larger number of beetles being captured compared with traps baited with pheromone or plant kairomones alone (Pajares et al. 2004, 2010; Reddy et al. 2005).

In a recent field study in China, increasing the release rate of plant volatiles in combination with the male-produced pheromone increased the number of female beetles trapped compared with lower release rates (Meng et al. 2014). Other semiochemicals produced by Asian longhorned beetle include a female-produced, sex-specific trail pheromone (Hoover et al. 2014), a female-produced contact pheromone (Zhang et al. 2003), and a punitive third component to the male-produced pheromone (Crook et al. 2014), but whether these semiochemicals would have any use in management has not been determined.

Acoustic detection of the Asian longhorned beetle has been investigated by two different groups. When Asian longhorned beetle larvae feed inside of trees they produce distinctive sounds that can be picked up by sensors attached to the infested tree and distinguished by use of software calibrated for the particular frequency and pattern of sounds (Haack et al. 2001, Mankin et al. 2008).

Sniffer dogs have been trained to detect the Asian longhorned beetle and *A. chinensis* in the United States and Europe (Errico 2012, Hoyer-Tomiczek and Sauseng 2013). Dogs can detect frass odors on tree trunks and exposed roots. A team of four dogs can inspect 15,000 *Acer* seedlings in a nursery in 3 d (Hoyer-Tomiczek and Sauseng 2013), and a team of three dogs can search a 5-acre neighborhood in 20 min (Errico 2012). In controlled double-blind laboratory trials, trained dogs were able to detect Asian longhorned beetle frass 80–90% of the time (Errico 2012).

The only effective method to eradicate Asian longhorned beetle is to completely remove and chip or burn infested trees and grind stumps (Wang et al. 2000a,b). From 1998 to 2006, the costs to detect, remove, and prophylactically treat host trees with imidacloprid was US$249 million dollars in the United States alone (United States Government Accountability Office [GAO] 2006). Full host removals of infested and adjacent healthy trees may prevent the spread of the Asian longhorned beetle but are controversial with the public. Early detection of invasive pests both increases the likelihood of successful eradication as well as decreases control costs (Mehta et al. 2007). The Asian longhorned beetle infestation in Worcester, Massachusetts, was not detected until 8–10 yrs after the beetle's likely introduction (USDA-APHIS 2010). As of 2013, the quarantine area now spans 110 square miles in six jurisdictions. Thus, there is a strong need for developing sensitive Asian longhorned beetle detection methods that can delimit the extent of the beetle infestation before it becomes unmanageable.

A review of the Asian longhorned beetle eradication programs suggests that emphasis on minimizing potential pathways for new introductions, maintaining public awareness, and continuing to develop methods for early detection and rapid response are key to reducing the threat posed by this insect (Smith et al. 2009). Public outreach is critical (GAO 2006, Ciampitti and Cavagna 2014). Members of the public have been responsible for locating and bringing to authorities' attention the beetle or its signs in each North American location that a breeding population has been found. In addition, cooperation from the public and local governments is critical to eradication efforts.

Management Options

Cultural or Mechanical Control. Cultural control methods to manage the Asian longhorned beetle have been developed in China. *Elaeagnus angustifolia* L. and *Acer mono* Maximowicz are planted in *Populus* plantations as trap trees and then cut down and burned prior to adult emergence (Feng et al. 1999). *Acer negundo* can be used to protect *Salix* plantations from the Asian longhorned beetle and *A. chinensis* by luring the beetles to a centralized location and then manually

removing trees (Xu and Wu 2012). Trap trees not removed from plantations may cause a temporary reduction in Asian longhorned beetle populations for 1 yr and then lead to a sharp increase in beetle populations the following year (Xu and Wu 2012). *Tilia mongolica* Maximowicz is another trap tree that can be used to help control the Asian longhorned beetle because it draws adults from up to 10 m away and then inhibits egg and larval development (Tian et al. 2009).

Host Plant Resistance. Considerable efforts have been devoted to breeding poplar cultivars resistant to borers. *Populus deltoides* 'Lux (I-69/55)' has a high water content in the sapwood that confers resistance to Asian longhorned beetles (Qin et al. 1996). Egg chambers fill with sap, which inhibits insect development or may kill the eggs. On other resistant poplars, callus tissue overgrows the oviposition wounds quickly and can prolong egg hatch or kill eggs (Wang and Zhou 1994). Planting mixed stands of susceptible and resistant poplar cultivars can dramatically reduce the proportion of infested trees (Jia and Li 2008). In the United States, a list of trees to use for replanting in Asian longhorned beetle-infested areas and a list of nonhosts have been compiled (USDA FS 2014 and Supp Table 2 [online only] (Wang et al. 2000b, 2009; Lazarus 2003; Morewood et al. 2004; USDA-FS 2014, respectively).

Biological Control. Entomopathogens and other biological control agents have been evaluated for their efficacy against the Asian longhorned beetle and may be environmentally safer than conventional control methods utilizing pesticides. However, in regulated areas in North America and Europe where eradication is the goal, classical biological control is not the first option. In its native range in China, biological control has been incorporated into an integrated pest management approach. Unfortunately, several of the biological control agents have a broad host range and would be capable of attacking native woodborers if introduced to North America or Europe.

Several entomopathogens have been evaluated for their efficacy against the Asian longhorned beetle and other invasive species (Hajek and Tobin 2010). *Beauveria brongniartii* (Saccardo) Petch is a fungus native to North America that has been shown to increase mortality and decrease fecundity in the Asian longhorned beetle (Dubois et al. 2004a,b). However, the commercial strain of *B. brongniartii* from Japan was found to belong to the taxon *Beauveria asiatica* (Saccardo) Petch (Goble et al. 2014). Given the reclassification of *B. asiatica* and lack of natural North American isolates, introduction of this strain as a biological control in the United States is unlikely. The pathogenicity of *Metarhizium anisopliae* was also tested against the Asian longhorned beetle but was less promising than the two aforementioned *Beauveria* spp. (Hajek et al. 2006).

Goble et al. (2014) found that exposure to *Metarhizium brunneum* and *B. asiatica* decreased median adult beetle survival time to 7.5–9.5 d compared with 24–31 d for *B. brongniartii*. Given the high virulence of *M. brunneum* against Asian longhorned beetle adults and its current registration in the United States, research has focused on the formulation and delivery of this fungus using oil, agar, and different fungal band textures (Ugine et al. 2013a,b). Finding an entomopathogenic fungal biological control agent for this beetle that can be used in the United States is still a possibility, but as with all fungi, efficacy when exposed to high temperature and low humidity environments may be diminished.

Bacillus thuringiensis Berliner toxins have been tested in a laboratory setting and were found ineffective against the Asian longhorned beetle when incorporated into artificial diet or delivered directly to beetles with a micropipette (D'Amico et al. 2004). The entomopathogenic nematodes *Steinernema feltiae* (Filipjev) Wouts, Mracek, Gerdin & Bedding; *S. glaseri* Ssteiner; *S. riobrave* Cabanillas, Poinar & Raulston; *S. carpocapsae* (Weiser) Wouts, Mracek, Gerdin & Bedding; and *Heterorhabditis marelata* Liu and Berry were tested against early instar Asian longhorned beetles (Xixiang et al. 1988, Fallon et al. 2004). Only *S. feltiae* and *S. carpocapsae* were effective, and only against mid- to late-instars. Methods to apply the nematodes to infested

trees so that they can survive and find the beetle larvae successfully are still needed to make this a viable option.

Predators and parasitoids in the native range of the Asian longhorned beetle have also been evaluated for control potential. *Dastarcus helophoroides* (Fairmaire) is a parasitoid of cerambycids in China with a broad host range and has been used to control the Asian longhorned beetle in its native range (Li et al. 2007, Wei et al. 2009). Populations of this parasitoid from different regions of China are differentially attracted to Asian longhorned beetle frass (Wei and Jiang 2011). *D. helophoroides* also parasitizes *Monochamus alternatus* Hope, a vector of the pinewood nematode (*Bursaphelenchus xylophilus* (Steiner & Buhrer) Nickle, Miura et al. 2003). Because *D. helophoroides* has a wide host range, it would be an unlikely candidate for classical biological control. *Sclerodermus guani* Xiao and Wu, a hymenopteran parasitoid, is highly effective against Cerambycidae in China and can reduce Asian longhorned beetle populations up to 45% in *Populus* plantations (Fu et al. 2010). However, this parasitoid is known to attack and develop in honey bees so it would not be considered for use in the United States (Yao and Yang 2008).

Some native European hymenopteran parasitoids that immobilize and feed on the outside of Asian longhorned beetle larvae (idiobiont ectoparasitoids) have been found to host-shift to Asian longhorned beetles and could be candidates for biological control. The most common parasitoids of Asian longhorned beetle larvae in Italy were *Spathius erythrocephalus* Wesmael and *Trigonoderus princeps* (Westwood) (Hérard et al. 2013). No Asian longhorned beetle egg parasitoids were found in Italy. Similar studies are ongoing in the United States and three natural enemy species can complete some development in Asian longhorned beetle (Smith et al. 2007).

Woodpeckers are well known to prey on Asian longhorned beetle in China (Gao et al. 1994); artificial cloth bird nests can be used to attract the woodpecker *Dendrocopos major* L. to susceptible trees (Cheng et al. 2010), but woodpeckers alone cannot eliminate the Asian longhorned beetle. Woodpecker activity has been observed in the United States on trees infested with Asian longhorned beetle and can indicate potential infestations.

Chemical Control. Conventional methods using insecticides to control the Asian longhorned beetle have been used in both the native and introduced ranges. In China, cypermethrin is widely used to kill adult Asian longhorned beetles in host tree canopies (Liu et al. 1999). Clothianidin, dinotefuran, and thiamethoxam can also be used to control Asian longhorned beetles via ingestion, contact, and antifeedant effects (Wang et al. 2005).

Neonicotinoids for control of the Asian longhorned beetle have been studied in the laboratory and field for several years. In laboratory studies, 60% of larvae that were fed artificial diet treated with 50 ppm azadirachtin or 1.6 ppm of imidacloprid showed decreased longevity (Poland et al. 2006a). One hundred percent of Asian longhorned beetle adults died in 13 and 20 d while feeding on maple twigs dipped in 150 and 15 ppm of imidacloprid, respectively. This contrasts with a report by Ugine et al. (2011) who reported that adult female Asian longhorned beetles fed 1 μl of 10 or 30 ppm of imidacloprid per day failed to die faster than control beetles, but laid 23–38% fewer viable eggs because they spent time recovering from intoxication. However, females administered 1 μl of 40 or 50 ppm of imidacloprid per day died faster than control beetles and laid significantly fewer eggs.

In field studies performed in 2000 and 2001 in China, tree injection with imidacloprid and thiacloprid reduced populations of Asian longhorned beetles in several host species (*Salix* spp., *Ulmus* spp., and *Populus* spp.), but the efficacy declined over time following treatment (Poland et al. 2006b). In a separate study in the United States, beetles were fed twigs from *A. platanoides* trees that were trunk-injected with imidacloprid in the Worcester, Massachusetts, infestation. Adult beetles fed twigs from treated trees had significantly lower fecundity and survival compared with beetles fed untreated twigs, with an LC_{50} over 21 d of 1.3 ppm; yet, during the course of the study, only 35% of all

beetles died (Ugine et al. 2012). Imidacloprid concentrations in twig samples varied widely, both seasonally and between trees (Ugine et al. 2012). During the course of the study, over half of twig samples from injected trees contained <1 ppm of imidacloprid and 37% contained no detectable levels. Twigs from trees injected in the spring also showed a decline in insecticide concentration as the season progressed into the fall. Leaves were only sampled in the fall and had a higher concentration of imidacloprid than twigs; adult Asian longhorned beetles feed on both twigs and leaves.

Imidacloprid seemed to produce an antifeedant response in Asian longhorned beetle larvae in the study by Poland et al. (2006a). However, in a choice test from a different study, adults did not have a stronger preference for control twigs compared with those obtained from imidacloprid-injected trees (Ugine et al. 2012). The discrepancies between these two studies may reflect differences in either methods or host tree species characteristics (e.g., size, species, soil conditions).

Although imidacloprid and other neonicotinoids may be an option to prophylactically treat and protect susceptible trees, these pesticides do not translocate evenly or quickly within a tree and have sublethal effects on nontarget organisms (Tattar et al. 1998, Kreutzweiser et al. 2008), with particular concern for pollinators (Biddinger et al. 2013), although many Asian longhorned beetle hosts are wind pollinated. In addition, a study of the nearly 250,000 at-risk trees treated in the New York, Illinois, and New Jersey regulated areas found that 11 trees had strong evidence that some Asian longhorned beetles may have escaped the effects of imidacloprid treatments resulting in nine adults emerging (Sawyer 2006). Given the high cost of treating large numbers of trees with systemic insecticides and the potential for nontarget effects, additional controlled studies on a broader scale in the United States are needed to maximize the likelihood of successful control in the context of complex environmental and biological factors that can impact this approach.

Summary of Management Options. Successful eradication efforts for the Asian longhorned beetle hinge on accurate and timely detection of infested trees, methods to kill the beetle in infested trees, and ways of preventing it from spreading. Currently, detection of infested trees is accomplished through ground and tree-climbing surveys, but over the past decade a lure and trap combination has been developed that can aid pest management practitioners and eradication programs in locating infestations and allocating resources to halt the beetle's spread. Control options beyond cutting down infested trees are limited. To date, the parasitoids and predators that have been found attacking this beetle have broad host ranges and are unlikely to be approved for release in the United States or Europe. An effective delivery system under development for entomopathogenic fungi seems promising. Systemic insecticides have been widely used in the United States, primarily to protect trees from becoming infested, but the ability of these chemicals to reach lethal doses in the crown of large trees is disputed by some scientists, and the potential nontarget effects, especially on pollinators, raise concerns. Managing Asian longhorned beetle via other chemical methods holds some promise, but widespread chemical treatments would be cost prohibitive and could cause unpredictable nontarget effects.

Concluding Remarks. Failure to eradicate Asian longhorned beetle where it has been introduced or to control it in altered habitats in the native range could be devastating to both forest and urban trees. In its native China, Asian longhorned beetle causes nearly 12% of the total losses attributable to forest pests, costing an estimated US$1.5 billion annually (Hu et al. 2009). In the United States, it is estimated that 12–61% of all urban trees are at risk, with total estimated value of US$669 billion dollars (Nowak et al. 2001). In 2002, two of the maple hosts favored by Asian longhorned beetle were among the top 10 most common forest trees in U.S. forests: *Acer rubrum* (7.6% of all trees) is the most common, and *Acer saccharum* (3.1% of all the trees) the sixth most common (USDA-FS 2002). Thus, the value of the trees at risk in

the United States alone if the Asian longhorned beetle were to freely infest all susceptible hosts is monumental, serving as an important factor in the decision to eradicate this insect where it has been introduced both in North America and Europe.

Supplementary Data

Acknowledgments

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