Age-Specific Fecundity of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on Three Tree Species Infested in the United States

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ABSTRACT   The spread of *Anoplophora glabripennis* Motschulsky (Asian long horned bettle), in the United States is dependent on its rates of reproduction and dispersal among host-tree species. Therefore, investigations of the reproductive characteristics of *A. glabripennis*, including preovipositional period, age specific fecundity and survival, on Norway maple (*Acer platanoides* L.), red maple (*Acer rubrum* L.), and black willow (*Salix nigra* Marshall) were undertaken to quantify its reproductive capacity among these host-tree species under laboratory conditions. Differences were found in preovipositional period, fecundity, egg viability and survival among the host-tree species. Oviposition rate was positively correlated with beetle body size, but negatively correlated with beetle age, bolt area, diameter, and bark thickness. Collectively, results show that in terms of adult female *A. glabripennis* survival and reproductive capacity, Norway and red maple were more suitable than black willow, with Norway maple somewhat more suitable than red maple. We hypothesize bark thickness and woody-tissue characteristics (i.e., nutritional substances, secondary substances, structural features) caused, at least in part, the observed differences in *A. glabripennis* survival and reproduction. Comparison of the various measures of *A. glabripennis* reproductive capacity was made with other cerambycids, specifically species of the subfamily Lamiinae, and implications for development of management strategies in U.S. ecosystems are discussed.

KEY WORDS   *Anoplophora glabripennis*, intrinsic growth rate, age-specific fecundity, exotic invasive species, forest pest

Anoplophora glabripennis Motschulsky (Coleoptera: Cerambycidae: Lamiinae: Lamiini) is among a group of high-risk exotic wood borers native to Asia, specifically China and Korea (Nowak et al. 2001). *A. glabripennis* has been intercepted in 14 states in the United States, but established infestations are currently only known to exist in New York City and on Long Island (first discovered in 1996; Haack et al. 1997), and in Chicago, IL (first discovered in 1998; Poland et al. 1998). Using the only currently effective method for limiting its spread, ≈5,286 and 1,509 infested trees have been cut and removed in the New York and Chicago infestations, respectively, as of May 2001 (U.S. Forest Service 2001).

In China, *A. glabripennis* is considered one of the most important forest pests. It has been reported from 25 provinces in China, extending from 21 to 43° N latitude and 100 to 127° E longitude (Yan 1985). This region extends across climatic zones that correspond to the climatic zones in North America from southern Mexico to the Great Lakes, and includes virtually all of eastern United States. Feeding by larvae in the cambium and xylem causes widespread mortality among many deciduous broadleaf tree species in China (Yang et al. 1995), particularly *Populus* spp., *Salix* spp. and *Ulmus* spp. (Xiao 1992). Within the two U.S. infestations, *A. glabripennis* has thus far been reported to attack 18 deciduous tree species in 12 genera (Haack et al.1997, Cavey et al. 1998, U.S. Forest Service 2001). Most notably among these are maples (*Acer* spp.). In addition to the ability to attack and kill apparently healthy trees, *A. glabripennis* also structurally weakens trees, which poses a danger to pedestrians and vehicles from falling limbs or trees. Seriousness of the problem is further emphasized by the fact that ≈30% of all urban trees in eastern United States are maples (Nowak et al. 2001).

Although quarantines and eradication programs exist in New York and Chicago, *A. glabripennis* possesses the potential for introduction into the urban, suburban and forest landscapes, particularly in eastern United States. In so doing, this beetle could devastate, among others, the maple syrup industry and foliage tourism, worth ≈180 billion dollars annually (Haack et al.1997). The ecological disturbance and potential spread of this invasive species will depend upon its

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rates of dispersal and reproduction (Myers et al. 2000; Sharov and Liebhold 1998). Variation in reproductive success of individuals is critical to understanding natural selection, population dynamics, and pest management (Clutton-Brock 1988, Lomnicki 1988). There are a number of factors that may affect or influence reproductive success, including individual fitness and host characteristics and quality (Price 1997). Therefore, the goal of this study was to investigate the effect of host plant on the reproductive potential of *A. glabripennis.* The specific primary objective was to compare the preovipositional period, age-specific fecundity and survivorship, and the intrinsic rate of increase and associated population parameters of *A. glabripennis* on three tree species [Norway maple (*Acer platanoides* L.), red maple (*Acer rubrum* L.), and black willow (*Salix nigra* Marshall)] that have been recorded as hosts in the United States. *Salix* was also included in these studies because it is among the genera found infested in both the United States and China, where it is second only to *Populus* spp. in terms of susceptibility to *A. glabripennis.* Factors, including insect body size and age, and host tree characteristics (e.g., surface area, diameter and bark thickness) that may affect the biological characteristics were also of interest in the current study.

Materials and Methods

*Anoplophora glabripennis-***Infested Bolts.** *A. glabripennis*-infested branch sections (≈80 cm long and 10–20 cm in diameter) (primarily *A. platanoides* and *A. saccharinum* L.) were obtained from Chicago, IL, February 1999, and transported to the USDA Agricultural Research Service, Beneficial Insects Introduction Research (BIIR) quarantine facility (Newark, DE). Both ends of the bolts were sealed with melted paraffin wax and then placed into 189.2 liter metal trash cans (52 cm diameter, 66 cm height). Cans were vented on two sides through hardware cloth covered holes (15 cm diameter). A hole (15 cm diameter) was cut in the lid of each can and fitted with a plastic trap to facilitate collection of adult *A. glabripennis.* Cans were held under quarantine conditions at 22–25°C, 50–60% RH, and a photoperiod of 16:8 (L:D) h; and newly emerged *A. glabripennis* were collected daily.

Cages and Oviposition Bolts. Cages were 24 cm wide, 45 cm deep, and 41 cm high with a removable Plexiglas front door. Cage sides and top were screened with saran. Cages, open on the bottom, were placed atop metal trays (35 by 50 by 2 cm high) filled with fine, sterilized sand. Sand was kept moist daily and cages were held at 22–25°C, 50–60% RH, and a photoperiod of 16:8 (L:D) h.

Live healthy Norway maple, red maple, and black willow trees, ranging from 15 to 45 cm dbh (average diameter at breast height of 35.6, 17.8 and 30.5 cm, respectively) and within a 40-km radius from Newark, DE, were selected and felled weekly from 12 May to 10 October 1999. Bolts, 30 cm in length and ranging from 7.6 to 15.2 cm in diameter, were immediately cut from the branches or trunks of the freshly felled trees,

and returned to the BIIR quarantine facility. Tops of bolts were then sealed with paraffin wax and the unsealed end placed down into the moist sterilized sand. Bolts were then assigned at random to experimental cages within 24 h from the time the trees were felled and bolts cut. Newly emerged *A. glabripennis* (0–24 h after exiting branch sections), obtained from the *A. glabripennis*-infested branch sections, were randomly assigned to cages (one pair per cage), and a total of 15 pairs evaluated for each tree species (sample size was limited by the size of the BIIR facility). Because female *A. glabripennis* are normally longer lived than males, replacement males (1–3 d old) were provided so as to maintain mate availability. Freshly cut foliage bouquets of the same tree species (including current and 1-yr-old twigs) (Xiao 1992), in distilled water-filled flasks, were placed daily into their respective cages to provide an adequate amount of quality food for adult *A. glabripennis.*

Protocol. *A. glabripennis* uses both the mandibles and ovipositor to aid in oviposition (Xiao 1992), as do other species of the subfamily Lamiinae (Linsley 1961). Female beetles use their mandibles to chew holes through the bark surface and into the inner bark-sapwood interface. The subsequent process of oviposition includes ovipositor valve insertion, the possible introduction of a fluid (M.T.S., unpublished data) and the insertion of an egg at the interface of the inner bark and sapwood. The collective action of this process results, within ≈7 d, in a circular area between the inner bark and sapwood that becomes discolored and slightly sunken or depressed. Walsh and Linit (1985) similarly reported a roughly circular patch of discolored phloem tissue at the interface of the bark and phloem tissue into which *Monochamus carolinensis* (Olivier) places an egg.

Scars made by adult *A. glabripennis* on the surface of oviposition bolts were differentially marked and recorded daily (different color of liquid correction fluid each day). Oviposition bolts were replaced every 7 d with freshly cut bolts until death of the adult female beetle. Once replaced, the removed oviposition bolts were held (with their base in moist sand and under identical environmental conditions) for 21–28 d after which each scar was dissected and categorized as scars, aborted oviposition sites (interface of inner bark and phloem with a roughly circular area that was discolored or stained, and slightly sunken or depressed), nonviable eggs (not hatched), and viable eggs (presence of larvae and/or frass). Upon death, female body width (at the caudal end of the elytra) and body length (from the anterior end of the head to the terminal end of the abdomen) were measured, and body size was calculated as a cylinder ($\pi r^2 L$). Length and circumference of each oviposition bolt were also measured to calculate bolt surface area (square centimeters).

The data were used to test whether *A. glabripennis* reproduction or mortality varied among the three tree species. Analysis of variance (ANOVA) was used to test for an effect of tree species. Mean number oviposition sites produced by *A. glabripennis* on each of

the three tree species were then used to normalize the data and compared using Tukey's honest significant difference (HSD) test. A general linearized model was used to test for effects of bolt area, beetle size, and beetle age on female oviposition site production (Stat-Soft 1999). Differences in rates of change in age specific fecundity were tested using weekly oviposition and egg viability. These were analyzed with analysis of covariance (ANCOVA) of tree species with each week's reproduction as a covariate. A Kaplan-Meier analysis was performed to test for effects of tree species on adult survival (StatSoft 1999). Finally, a life table was calculated (Lee and Ahn 2000) with age-specific survival (l_x) and age-specific egg viability (m_x) of females. Because rearing techniques have not been fully developed for this univoltine species, viable eggs were used as a proxy for reproductive success. The net reproductive rate ($R_o = \Sigma\, l_x\, m_x$) and the intrinsic rate of increase ($\Sigma\, e^{-rx\, l}{}_x\, m_x$) were estimated for *A. glabripennis* on each of the three host-tree species.

Results

Oviposition Rate. A total of 9,074 scars was made by *A. glabripennis* on all bolts. However, only the 5,608 (61.8%) scars showing evidence of discoloration, depression, egg, larva, or frass were considered to have been made by female beetles, and thus included in the analysis as an oviposition site. This is supported by the fact that of all the oviposition sites that contained an egg, larva, or frass, 98.5% (98.6% on Norway maple; 98.0% on red maple; 99.1% on black willow) also showed evidence of a stain and/or depression on the xylem surface. Scars that lacked any of these signs were not included in the analysis because it was uncertain as to whether the female or male beetle had made the scars, either for reasons related to testing host quality or supplementary feeding.

Number of oviposition sites chewed per day by female *A. glabripennis* differed significantly among tree species ($F = 49.41$; df = 2, 42; $P < 0.01$; Fig. 1). Mean number of oviposition sites chewed per day was significantly higher on Norway maple (mean = 1.98 sites per day) than on red maple (1.09), which was in turn significantly higher than that on black willow (0.61). Lifetime number of oviposition sites chewed by female *A. glabripennis* also varied significantly among tree species ($F = 31.3$; df = 2, 42; $P < 0.01$; Fig. 1), with significantly greater lifetime number of oviposition sites chewed on Norway maple (mean = 213.6 sites per lifetime) than on red maple (108.0), which in turn was significantly greater than that on black willow (52.2).

Generalized linear model was used to test for differences in daily oviposition among tree species, using female body size as a covariate. Results showed that daily oviposition increased with female body size ($F = 7.56$; df = 1, 42; $P < 0.01$). However, body size, which averaged 13.8 cm³ overall (7.4–30.9 cm³), did not differ significantly among tree species ($F = 0.60$; df = 2, 42; $P = 0.55$). Mean body size was 14.9, 12.9, and 13.4
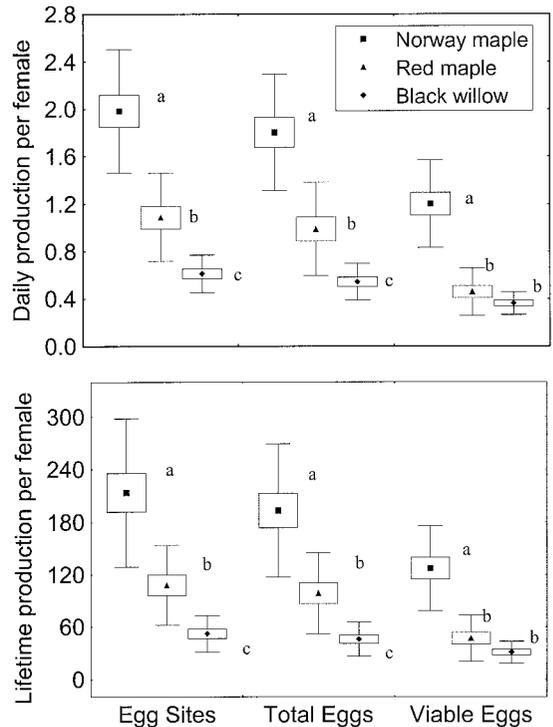

Fig. 1. (Top) Daily production of oviposition sites, and total eggs and viable eggs by *Anoplophora glabripennis* on Norway maple, red maple, and black willow, under laboratory conditions. (Bottom) Lifetime production of oviposition sites, and total eggs and viable eggs by *Anoplophora glabripennis* on Norway maple, red maple, and black willow, under laboratory conditions. Means, standard error, and standard deviation are represented by middle points, boxes, and whiskers, respectively.

cm³ on Norway maple, red maple and black willow, respectively. After accounting for body size effects, daily oviposition was found to differ significantly among tree species ($F = 45.6$; df = 2, 42; $P < 0.01$; Fig. 1). Daily oviposition was significantly higher on Norway maple (mean = 1.80 eggs per day), than on red maple (0.99), which was in turn significantly higher than that on black willow (0.54). Lifetime oviposition also varied significantly among tree species ($F = 35.1$; df = 2, 42; $P < 0.01$; Fig. 1), with significantly greater lifetime oviposition on Norway maple (mean = 193.3 eggs per lifetime) than on red maple (98.5), which in turn was significantly greater than that on black willow (45.9). It should be noted that *A. glabripennis* laid an egg in 90.3% of all oviposition sites (91.1, 90.8, and 89.3% on Norway maple, red maple, and black willow, respectively). Daily oviposition of viable eggs also differed significantly among tree species ($F = 51.20$; df = 2, 42; $P < 0.01$; Fig. 1). Using least significant difference (LSD) paired comparison tests with $P > 0.05$, daily oviposition of viable eggs was significantly higher on Norway maple (mean = 1.2 eggs per day) than on red maple (0.46) and black willow (0.36), while it did not differ significantly between the later
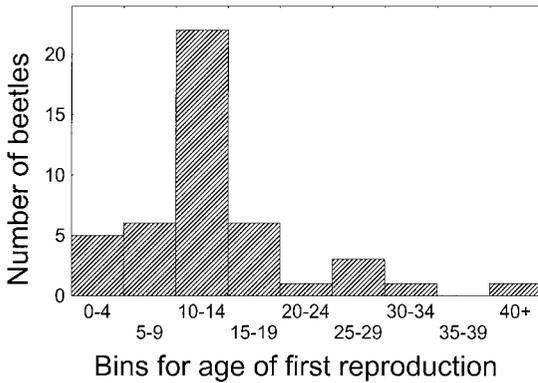
Fig. 2. Preovipositional period of *Anoplophora glabripennis* on Norway maple, red maple, and black willow under laboratory conditions, with data pooled across tree species (total of 45 female beetles).
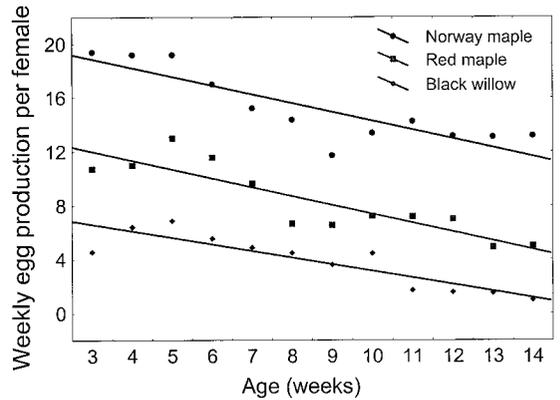

Fig. 3. Age-specific fecundity (all eggs) of *Anoplophora glabripennis* on Norway maple, red maple, and black willow under laboratory conditions.

two species. Lifetime oviposition of viable eggs also varied significantly among tree species ($F = 37.2$; df = 2, 42; $P < 0.01$; Fig. 1), with significantly greater lifetime oviposition of viable eggs on Norway maple (mean = 127.3 eggs per lifetime) than on red maple (46.8) and black willow (30.7). The latter two species did not differ significantly in terms of lifetime oviposition. It should be noted that percent egg viability differed significantly among tree species ($F = 8.46$; df = 2, 42; $P < 0.01$). Percent egg viability on Norway maple (60.4%) and black willow (60.5%) were not significantly different, but both were significantly greater than that on red maple (42.5%).

Preovipositional Period. The age at which oviposition (preoviposition) first occurred was subjected to ANOVA. Results showed that the mean adult age at which female beetles initiated oviposition (nonviable or viable) was 10.6, 16.7, and 15.8 d on Norway maple, red maple and black willow, respectively, which did not differ significantly among tree species ($F = 2.94$; df = 2, 42; $P = 0.06$). When data were pooled and grouped into age bins, analysis showed the beetles to be well synchronized in preoviposition time (Fig. 2), with the majority of beetles initiating oviposition between 10 and 15 d after emergence. Various distributions were also fitted to the preovipositional data ($y = 3{,}310$ lognormal [$7.6 + x$, 3.67, 0.96]; adjusted $R^2 = 0.79$). This alternative approach provided a precise estimate of preovipositional time (7.6 d). It should be noted that adult *A. glabripennis* are reported (Xiao 1992) to remain within their pupal chamber for 7 d and then exit the natal host, and therefore our data may underestimate preovipositional period.

Age Specific Fecundity. Weekly fecundity per female (post- and pre-ovipositional period) was analyzed with general linear model for an effect of tree species and bolt area (StatSoft 1999). While accounting for repeated measures of individual beetles, analysis showed that weekly fecundity was significantly affected by tree species ($F = 18.5$; df = 2, 42; $P < 0.01$; Fig. 3). Weekly fecundity of *A. glabripennis* was significantly higher on Norway maple than red maple,

which in turn was significantly higher than that for black willow (Tukey HSD pair wise comparisons; both $P < 0.01$). Regression of fecundity showed a weekly decline of 0.48 eggs per week ($F = 43.0$; df = 17, 714; $P < 0.01$). Rate of decline in fecundity did not differ significantly among tree species (ANCOVA, using Tukey's HSD test for paired comparisons; all $P > 0.05$).

Weekly proportion of viable eggs was significantly affected by tree species ($F = 32.0$; df = 2, 41; $P < 0.01$) (Fig. 4). *A. glabripennis* had lower weekly proportion of viable eggs on red maple than on Norway maple or black willow (Tukey HSD comparisons; both $P < 0.01$). Proportion of viable eggs increased by 4% per week ($F = 138.1$; df = 17, 697; $P < 0.01$). Rate of increase in proportion of viable eggs did not differ significantly among tree species (ANCOVA, using Tukey's HSD test for paired comparisons; all $P > 0.05$).

Longevity. Overall, beetle longevity ranged from 30 to 137 d. Adult female *A. glabripennis* longevity averaged of 103.9 (44–131 d), 97.2 (30–137 d), and 83.0 d (58–107 d) on Norway maple, red maple and black willow, respectively (Fig. 5). Kaplan-Meier survival analysis was used to compare the death rates among
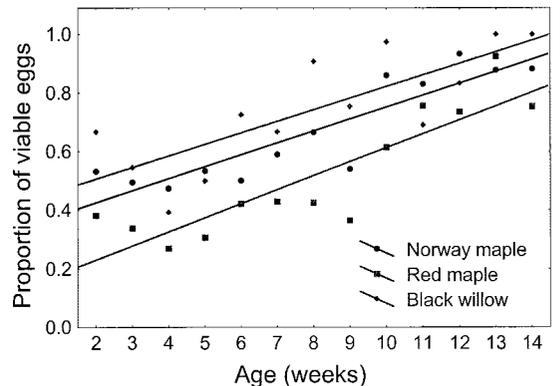

Fig. 4. Age-specific oviposition of viable eggs (percent) by *Anoplophora glabripennis* on Norway maple, red maple and black willow under laboratory conditions.
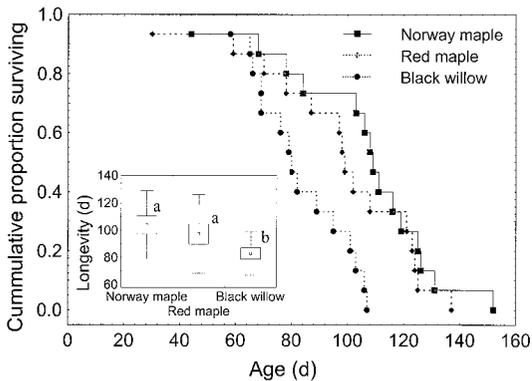
Fig. 5. Kaplan-Meier analysis of female *Anoplophora glabripennis* survival on Norway maple, red maple, and black willow under laboratory conditions. Inset: means, standard error, and standard deviation are represented by middle points, boxes, and whiskers, respectively.

each trees species ($\chi^2 = 7.89$, df = 2, $P = 0.02$; StatSoft 1999). Paired comparisons analysis (Cox 1970) showed that female longevity did not differ between the maples ($F = 1.38$, df = 30, $P = 0.19$) but had significantly lower longevity on black willow than on Norway maple ($F = 3.0$, df. = 30, $P < 0.01$) or red maple ($F = 2.2$, df = 30, $P = 0.02$).

Intrinsic Rate of Increase. Partial life tables were used to estimate intrinsic rates of increase among tree species, where tree species, listed in the order of declining 'r' values, were Norway maple, red maple and black willow (Table 1). These values likely over-estimate the net reproduction and intrinsic rate of increase because this study, by design, did not include larval and pupal mortality.

Bolt Area. Bolt area differed significantly among tree species ($F = 30.5$; df = 2, 524; $P < 0.01$). Average bolt area was 502.3, 583.6, and 628.7 sqcm per bolt, for Norway maple, red maple, and black willow, respectively.

Bolt Diameter. Bolt diameter differed significantly among tree species ($F = 30.6$; df = 2, 524; $P < 0.01$). Average diameter was 5.3 (range = 2.8–10.8), 6.2 (3.0–10.1), 6.7 (3.0–15.5) cm per bolt, for Norway maple, red maple, and black willow, respectively. All are significantly different (LSD < 0.05).

Bark Thickness. Average bark thickness was 2.2 mm (range = 1.5–7.7), 1.8 mm (0.97–4.2), and 3.4 mm (0.8–5.3), on Norway maple ($n = 2,682$), red maple (872), and black willow (422), respectively ($F = 4.13$,

Table 1. Reproductive capacity *Anoplophora glabripennis* on three host tree species under laboratory conditions

Host	Ro[a]	r[b]
Norway maple	61.2	4.1
Red maple	22.2	3.1
Black willow	14.6	2.7

[a] Net reproduction (total lifetime viable eggs per female).
[b] Annual intrinsic rate of increase (mean viable eggs per female).

df = 3973,2, $P < 0.016$). Although bark thickness did not differ between Norway maple and red maple, their bark was significantly thinner than that on black willow (LSD - both $P < 0.05$).

Discussion

Age specific survivorship and age specific fecundity are among the key population processes influencing the intrinsic rate of increase (Birch 1948). In the current study, significant differences were detected in oviposition rates (daily, lifetime and age-specific fecundity), and mortality rates among cohorts of adult *A. glabripennis* tested on the three different tree species. Collectively, the differences in these population processes resulted in differences in the relative intrinsic rate of increase.

Adult cerambycid that feed usually live 36–53 d (Hanks 1999). Lamiines are known to have a longer life span than species in other cerambycid subfamilies (Linsley 1959, Gandrade et al. 1971, Singh and Prasad 1985). Among lamiines, for example, adult life span has been reported to average 19 d for *Enaphalodes rufulus* (Haldemann) (Cerambycidae) on red oak logs (Donley 1978); 47.3 d for *Acalolepta vastator* (Newman) (Cerambycidae) on grapevine stems (Goodwin and Pettit 1994); and 38.3–61.4 d for *M. carolinensis* (Olivier) (Cerambycidae) on pine logs (Walsh and Linit 1985; Akbulut and Linit 1999a, 1999b). More specifically, longevity of female *A. glabripennis* was previously reported to average 42.5 d (14–66 d) on *Populus* spp. (Xiao 1992) and 73 d on *A. saccharum* Marsh (Keena 2000).

Fecundity and intrinsic rate of increase have been reported for some lamiine species. Daily and lifetime fecundity for *M. carolinensis* were reported to average 2.6–5.7 eggs per day and 116.5–200 eggs per female, respectively (Walsh and Linit 1985; Akbulut and Linit 1999a, 1999b), and 6.3 eggs per day and 119 eggs per female, respectively, for *E. rufulus* (Donley 1978). Lifetime fecundity of *A. glabripennis* was previously reported to average 35 eggs/female (30–80 eggs) on *Populus* spp. (Xiao 1992), and 68 eggs/female on *A. saccharum* (Keena 2000). Furthermore, intrinsic rate of increase was reported to range from 0.04 to 0.13 for *M. carolinensis* on pine logs (Akbulut and Linit 1999a, 1999b).

By comparison, adult female *A. glabripennis* longevity and fecundity found in the current study are generally greater than those previously reported for other lamiines, as well as those previously reported for *A. glabripennis.* In regard to bolt area and diameter, qualitative patterns showed that female *A. glabripennis* live longer and oviposit more on smaller bolts. Similarly, qualitative patterns showed that female *A. glabripennis* oviposit more on bolts with thinner bark. Edwards and Linit (1991) reported that the duration of time female *M. carolinensis* spent in excavating oviposition scars increased with bark thickness. Therefore, if one assumes that greater effort is required to oviposit into thicker bark, then the thicker bark of black willow may account, at least in part, for the lower rate of fecundity
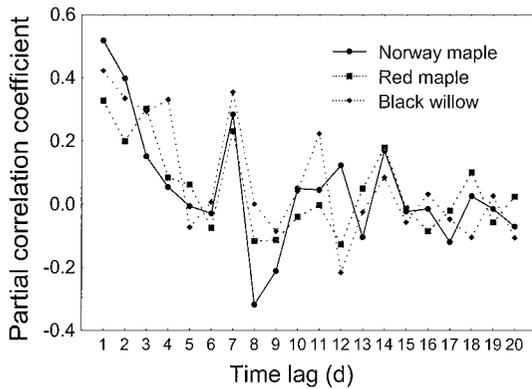
Fig. 6. Partial autocorrelation of oviposition rate of female *Anoplophora glabripennis* on Norway maple, red maple, and black willow under laboratory conditions.

of *A. glabripennis* caged on black willow in the current study. Furthermore, however, we hypothesize that differences in host-tree species and/or condition, environmental conditions (i.e., temperature), and/or provisioning of food, including foliage, may have contributed to the longer life span and/or higher reproductive rate of *A. glabripennis* in the current study. Furthermore, total fecundity has been shown to increase with female body size (Lauziere et al. 2000), specifically for *Plocaederus obesus* Gahan (Cerambycidae) (Khan 1993) and *Semanotus japonicus* Lacordaire (Cerambycidae) (Kato et al. 2000). Therefore, the large body size of *A. glabripennis* may have also contributed to higher rates of fecundity when compared with other lamiines. Finally, intrinsic rate of increase found in the current study likely overestimates *r* because larval and pupal mortality measurements were beyond the scope of this investigation.

Oviposition began for each cohort of *A. glabripennis* at a similar age in the current study. Once initiated, both oviposition and percent egg viability were found to be age dependent, with oviposition rate decreasing and percent egg viability increasing with age. These trends were present regardless of tree species, which may imply a compensatory relationship between these two parameters. It is worth noting that there was a strong correlation of reproduction over time (Fig. 6). The partial autocorrelation (an expression of the similarity of values of a variable, e.g., reproduction, at given intervals of time) shows a strong effect of the replacement of bolts at days seven and 8. This unexpected artifact shows that adult *A. glabripennis* exploit fresh bolts for oviposition, as depicted by the gradual daily decline in oviposition within each week, which may be due in part to the gradual daily decline in availability of suitable host substrate (surface area) as the female chews egg sites and lays eggs. Duffy (1953) reported that cerambycids are influenced more by the nature and condition of the host than by host species. However, Hanks et al. (1993) found that *Phoracantha semipunctata* females prefer host material that represents reduced competition for their progeny. Given the risk that *A. glabripennis* poses to hardwoods, the

attraction, acceptance and food quality of host-trees clearly require further investigation.

In the current study, adult female *A. glabripennis* were observed feeding on the subcortical tissues (defined herein as the inner bark, cambium, immature xylem) of bolts, shoots, petiole, and foliage (including veins and leaf tissue between veins). This is consistent with the fact that in nature, adult *A. glabripennis* feed on leaves, petiole, and twigs (M.T.S., unpublished data; Gao, personal communication; Xiao 1992). It has also been suggested (Gao, personal communication) that young adults may prefer to feed on subcortical tissues of twigs, while older adults may prefer to feed on similar tissues of the leaf and petiole. Similarly, among adult cerambycid species, most Lamiinae feed on bark of shoots, stems, twigs, branches and trunks, and foliage and leaf petioles (Linsley 1959, Goodwin and Pettit 1994, Hanks 1999).

Feeding as an adult for most cerambycid species is an essential prerequisite for egg maturation and oviposition (Linsley 1959). Although adults of many cerambycid species mate immediately after emergence, Hanks (1999) examined 21 lamiines and concluded that they required a mean maturation feeding period of 6.7 ± 1.2 d before mating, and a mean preovipositional period of 9.0 d. Both *M. carolinensis* and *M. titillator* were reported to require a 3-wk maturation feeding period before oviposition (Alya and Hain 1985). Dejia and Yining (1997) investigated the relationship between sexual development, age, supplementary feeding and copulatory behavior in *A. glabripennis*, and reported that while females could copulate upon emergence, adequate feeding was essential for maturation of the germanium. The germanium gradually reached maturity about 10 d after emergence, and supplementary feeding was reported to improve copulation. Results from the current study, where average preoviposition period ranged from 10.6 to 16.7 d, corroborate previous reports on *A. glabripennis* and other lamiines, and emphasize the importance of adult nutrition and its potential impact on longevity and reproduction.

Therefore, the nutritional quality of the subcortical tissue consumed by adult *A. glabripennis* during feeding may have contributed to the differences in the life processes (survival and reproduction) associated with the tree species cohorts of beetles used in this study. Although the three tree species were tested simultaneously during the growing season (May to October), differential seasonal changes in their respective nutritional quality may have also affected the reproductive potential of the cohorts of *A. glabripennis*. Seasonal changes in the nutritional quality of host plants have been shown to affect the reproductive potential of herbivorous insects, including *M. carolinensis* (Akbulut and Linit 1999a). In addition to nutritional substances, however, secondary substances, as well as structural and toughness features, are also among the woody-tissue characteristics that affect wood-feeder performance (Haack and Slansky 1987). Nutritional analyses of the subcortical tissues consumed by *A. glabripennis* were beyond the scope of this study.

However, our results suggest that host specific differences in nutritional quality, including secondary substances, and/or structural features (i.e., bark thickness), influenced the relative reproductive potential of the three cohorts of *A. glabripennis.*

The current study, in which the individual performance of adult female *A. glabripennis* was determined under controlled laboratory conditions, represents the first of the three basic steps in the research approach in nutritional ecology outlined by Price (1997). The species of host-tree colonized obviously plays an important role in the reproductive success and population dynamics of *A. glabripennis.* Reproductive success must be evaluated on available resources to assess the spread of an invasive species (without limiting natural enemies). In the current study we have quantified differences among three host-trees with respect to both adult reproduction and mortality, which represents the initial assessment of the impact of *A. glabripennis* following the framework of invasion by Parker et al. (1999). This new information provides insight into the reproductive strategy of *A. glabripennis.* By discriminating the potential effects of available trees on reproduction, one aspect *A. glabripennis* impact on various forest ecosystems in the United States is measured. Hanks (1999), in his review of the natural history and behavior of 81 cerambycid species, suggested that much more could be learned of the biology and behavior of cerambycids if key information were acquired in future research, such as adult feeding, precopulation and preoviposition period, adult longevity and fecundity, mechanisms of mate location and recognition, duration of mating and oviposition. Among these, preoviposition period, adult longevity and fecundity were examined in the current study. We suggest that studies of dispersal with respect to mating and food preference will further this assessment of invasion (Courchamp and Clutton-Brock 1999, Stephens and Sutherland 1999). Future studies should also include the evaluation of host suitability of various tree species in terms of development from egg to adult, with particular attention to host stress. Collectively, the current and suggested future studies will contribute to the development of management guidelines (eradication and otherwise) that are sensitive to insect-host interactions under various landscapes at risk in the United States.

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