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Timing and duration of the life cycle of Asian longhorn beetle *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in southern England

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Abstract

1 In March 2012, an outbreak of Asian longhorn beetle *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae), a quarantine pest that is highly damaging to broadleaved trees, was discovered at Paddock Wood in southern England.

2 Infested trees were felled as part of an eradication programme, but material that contained *A. glabripennis* life stages was retained and analyzed to provide information on the timing and length of the life cycle, as an aid to future management and surveillance.

3 A total of 366 *A. glabripennis* larvae were recovered, including 69 first- and second-instar larvae found in June and July before any adults were found in the samples or had emerged, which indicated that the majority of eggs were laid in the previous autumn and over-wintered before hatching.

4 Tree ring analysis and predictions of the timing of adult emergence based on degree-day accumulation also indicated that adults emerged late in the season, from August onwards, when lower temperatures would have caused most eggs to delay hatching until the next year.

5 Two cohorts of older, established larvae were present in the samples, corresponding to larvae that had over-wintered once and twice, respectively. Thus, most larvae required two seasons to complete their development after hatching and a total of 3 years to complete the full life cycle from egg to adult.

Keywords *Anoplophora glabripennis*, degree-days, invasive species, life-cycle variation, overwintering, voltinism.

Introduction

Around the world, an increasing number of insect pests and plant diseases are being introduced into new regions outside their natural areas of distribution, as a direct result of the increase in global trade that has occurred in recent years and because of changes in the climate (Smith *et al.*, 2007; Hulme, 2009; Santini *et al.*, 2013). Trade facilitates the transport of species between regions, whereas changes in climate are enabling species to survive and gain a foot-hold in regions where once they would have been considered unable to establish (Roques, 2010; Boyd *et al.*, 2013). In the U.K., several new insect pests and diseases that are harmful to trees have been introduced in recent years, including the Asian longhorn beetle *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae), which was discovered breeding at Paddock Wood in Kent in 2012 (Leather, 2013; Straw *et al.*, 2015). The population of *A. glabripennis* at Paddock Wood had become established in trees next to offices and a warehouse where a company had previously imported stone and slate from China. *Anoplophora glabripennis* is native to China and Korea and has been transported around the world in untreated wood packaging material (Hu *et al.*, 2009; Haack *et al.*, 2010), and this is likely to have been the pathway that brought the beetle into the U.K.

Anoplophora glabripennis is extremely damaging to a wide range of deciduous broadleaved trees, especially species of *Acer*, *Aesculus*, *Populus*, *Salix* and *Ulmus*, and it is included in the European Union (EU) Annex 1 list of quarantine pests that require regulation (MacLeod *et al.*, 2002; EPPO, 2013a). Consequently, immediately after *A. glabripennis* was discovered at Paddock Wood, a series of delimiting surveys was established

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to determine the extent of the infestation, and an eradication programme was put in place, which involved felling and burning all of the infested trees and any other trees within a radius of 100 m that could have acted as a host for the beetle (Straw *et al.*, 2015). Sixty-six trees were infested by *A. glabripennis* at Paddock Wood, primarily sycamore trees *Acer pseudoplatanus* L., and these trees and a further 2163 trees were felled and destroyed during the eradication programme (Straw *et al.*, 2015).

The surveys and eradication programme at Paddock Wood followed protocols and best practice that were developed in the U.S.A. and Canada, where *A. glabripennis* was introduced in the 1990s (USDA APHIS, 2008; Smith *et al.*, 2009; Haack *et al.*, 2010), and in other parts of Europe where *A. glabripennis* has been found established outdoors on a number of occasions (Hérard *et al.*, 2006, 2009a; Krehan, 2008; Forster & Wermelinger, 2012; Faccoli *et al.*, 2014). The procedures for dealing with *A. glabripennis* outbreaks in Europe have subsequently been standardized and were published recently by the European and Mediterranean Plant Protection Organisation (EPPO, 2013a). The standardized procedures formalize the requirement to carry out surveys as soon as possible after an *A. glabripennis* outbreak is discovered, to fell all host species out to a distance of at least 100 m, and to carry out subsequent monitoring for several years to detect and eliminate any residual infestation. Current EU policy states that an outbreak can only be declared to have been eradicated if annual surveys have been carried out for at least 4 years, or a period of twice the length of the pest's life cycle, which ever is longer, without any further infestation being found (EPPO, 2013a).

These recommendations are based on field experience of how quickly *A. glabripennis* populations tend to increase and spread (Haack *et al.*, 2010). Generally, compared with other insect pests, *A. glabripennis* populations increase and spread relatively slowly because the larvae, which feed within the woody tissues of the host, require 1 or 2 years to complete their development. The adult females also prefer to lay their eggs on the same tree from which they emerged, or on adjacent trees, and only a small proportion of adults travel more than 200–300 m (Smith *et al.*, 2004; Bancroft & Smith, 2005; Sawyer *et al.*, 2010). Adults are more active, however, and disperse farther when temperatures are higher (although, on very hot days above 30 °C, adults may become less active and seek places to rest in the shade) (Lingafelter & Hoebeke, 2002; Bancroft & Smith, 2005) and higher temperatures generally lead to shorter development times and a reduction in the length of the life cycle (Keena, 2006; Keena & Moore, 2010), which together might be expected to increase the rate at which a population might multiply and spread. In the warmer parts of its range therefore, there is a greater need to implement control programmes against *A. glabripennis* earlier rather than later, to prevent populations increasing rapidly, and to survey outwards to a greater distance to ensure that all pockets of infestation are detected.

In China, the U.S.A. and Canada, *A. glabripennis* has a 1-year (univoltine) or 2-year (bivoltine) life cycle (Fan *et al.*, 1997; Haack *et al.*, 2006, 2010; Hu *et al.*, 2009; Keena & Moore, 2010). In Europe, climate-matching studies (CLIMEX analysis) suggest that *A. glabripennis* could establish across most of the region and would cause significant damage, and that it would have a 1-year life cycle in southern France and Italy and in other countries around the Mediterranean, as well as in south-east Europe, and a 2-year life cycle in central Europe and further north, perhaps even a 3-year life cycle in the most northerly areas (Macleod *et al.*, 2002, 2012; de Boer, 2004). There is little direct information, however, on the length of the life cycle of *A. glabripennis* in Europe and the time of year when adults are active and eggs are laid, even though this information is important for effective management and for predicting how quickly populations might increase and spread (Faccoli *et al.*, 2014). Part of the problem is that, when outbreaks have been discovered, the priority has been to eradicate the pest as soon as possible to prevent further spread, and this has limited the opportunities for detailed study and research. At Paddock Wood, however, all of the material that contained *A. glabripennis* was collected and analyzed to determine the range and character of the life stages that were present. The present study describes the life stages found in the samples and uses this information, as well as estimates of when the adults are likely to have been active during the year, to identify the length of the life cycle in this part of southern England and the implications for the eradication programme and future monitoring.

Materials and methods

Study site and collection of sample material

The outbreak of *A. glabripennis* at Paddock Wood (latitude 51°11′ north, longitude 0°24′ east) was located 1.5 km north of the town, in a rural area consisting of a mixture of agricultural fields, sheep grazed pastures, small woodlands and a scattering of houses and gardens, with a small number of light industrial units (Straw *et al.*, 2015). This area of Kent is low-lying and flat, at around 14 m a.s.l., and has mean January and July temperatures of 5.2 and 17.6 °C, respectively, and a mean annual rainfall of 660 mm (data for 2000–2012 from East Malling Research Station, 12 km north of Paddock Wood).

The programme of felling trees at Paddock Wood started on 16 April 2012 and was completed by 3 August 2012. As each tree was felled, it was searched meticulously for signs of infestation, and any stems and branches that contained *A. glabripennis* life stages, or which showed evidence of damage, were cut into 20–40-cm long sections and labelled and packaged securely. Later on the same day, or early on the next day, the samples were transported under licence (FERA Scientific Licence 6647/198760/0) to the Forest Research laboratories at Alice Holt, where they were stored at 15 °C in a secure quarantine facility until processed. All other material from the felled trees was destroyed on site at Paddock Wood (Straw *et al.*, 2015).

A small series of samples containing *A. glabripennis* was also collected at Paddock Wood between 12 March and early April 2012, when the nature and scale of the outbreak was first being identified, and before the main eradication programme got under way. These samples were also returned to Alice Holt and added to the samples collected during the main tree-felling programme.

Life stages recovered from the samples

Anoplophora glabripennis attacks healthy and stressed trees, and it passes through a series of clearly recognizable stages during its development, which produces a distinctive pattern of damage (Ric *et al.*, 2007; Hérard *et al.*, 2009b). Adult females chew oviposition pits in the bark of live stems and branches through which they insert a single egg into the cambium tissues between the bark and the sapwood. The tissues around the egg soon die, resulting in the formation of a distinctive oval patch of dark stained tissue, on average 0.9 × 2.1 cm in size, beneath the bark on the surface of the sapwood (Smith *et al.*, 2002; Ric *et al.*, 2007; Haack *et al.*, 2010). The first-instar larva feeds on the dead cambial tissue within this oval patch, and only after it has moulted into the second instar does it start to feed laterally on undamaged phloem and xylem (Yan & Qin, 1992; Lingafelter & Hoebeke, 2002; Hu *et al.*, 2009).

Second- and third-instar larvae excavate a flat gallery underneath the bark, which becomes packed with fine, dark coloured frass. Later, toward the end of the third instar or when the larva has moulted into the fourth instar, the larva tunnels into the wood and for the remainder of its development the larva feeds within the woody tissues (xylem), although it may return occasionally to the gallery under the bark, either to feed or to push frass out of the tunnel (Lingafelter & Hoebeke, 2002; Hu *et al.*, 2009; Haack *et al.*, 2010). Larvae generally tunnel upwards for 10–30 cm and when fully grown; they excavate a slightly enlarged chamber at the end of the tunnel in which to pupate. The adult beetle emerges from the pupa inside the pupal chamber and, after waiting 12–14 days to harden its exoskeleton, it chews its way to the outside leaving behind a perfectly circular exit hole that is typically 10 mm in diameter (Haack *et al.*, 2010; Sánchez & Keena, 2013).

The stem and branch samples from Paddock Wood were processed by measuring their length and diameter and noting whether the wood was alive or dead. The sample was then examined and the numbers of oviposition pits, exit holes and other signs of damage visible on the surface were recorded. When this had been completed, the sample was taken apart piece by piece and all of the *A. glabripennis* life stages were extracted and counted. Larval tunnels were traced from their beginning to their end, so that the fate of each larva could be determined and all adult exit holes, both current exit holes visible on the surface and old exit holes formed in previous years but now calloused over, were identified and retained. Live and dead life stages (larvae, pupae and teneral adults) were preserved individually in 70% industrial methylated spirits and were labelled with the sample number and the dates when the sample was collected and processed. Sample processing started as soon as the first samples were brought in from the field in March and April, and continued throughout the summer and was completed by 18 September 2012.

For the purposes of analysis, *A. glabripennis* life stages were divided into groups depending on the month in which the sample from which they were recovered was processed, and the body length and head capsule width of the larvae were measured and recorded. Based on these measurements, the larvae were separated into first- and second-instar larvae, which were considered not yet to have firmly established, and older larvae, primarily third-instar larvae and later instars, that were clearly well established in galleries under the bark or in tunnels in the wood. First and second instars were recognized by their small size (a body length of 7–10 mm and approximately 9–12 mm, respectively), their location within or next to the oval patch of stained tissues surrounding the original oviposition site, with no more than the beginnings of a lateral gallery, and their small head capsules. First- and second-instar *A. glabripennis* larvae have a mean head capsule width of 0.93–0.99 mm and 1.34–1.47 mm, respectively (Keena & Moore, 2010) and there is very little overlap in the range of head capsule widths between the two instars. The head capsule widths of second-instar larvae also show little overlap with the head capsule widths of third-instar larvae. The head capsules of third-instar larvae (mean width: 1.79–2.21 mm), fourth-instar larvae (mean width: 2.36–3.03 mm), fifth-instar larvae (mean width: 3.01–3.75 mm) and later *A. glabripennis* larval instars overlap to a greater and increasing extent (Keena & Moore, 2010).

The distributions of head capsule widths of the older, established larvae (third-instar larvae and later instars) that were observed in March/April, May, June/July and August/September were analyzed using Hartigans' Dip Test (Hartigan & Hartigan, 1985) to determine whether the larval size distribution was unimodal or deviated significantly from a unimodal distribution. A non-unimodal distribution of larval sizes would provide evidence that more than one larval age cohort was present in the samples. Hartigans' test calculates a dip statistic (D), which, if significant, indicates a non-unimodal distribution.

This analysis was followed by fitting normal mixture models to the data to determine whether they were represented better by a single normal distribution (Model 1) or a mixture of two normal distributions with either a common variance (Model 2) or separate variances (Model 3). For each model, Akaike's information criterion (AIC) and bias-corrected information criterion (AICC) were calculated, and the model with the smallest AIC and AICC values was selected as the best fit to the data. Both the dip test and normal mixture models were applied using R statistical software (R Development Core Team, 2013). The model fit criteria were calculated using the finite mixture models procedure in SAS (SAS Institute Inc., 2013), using the parameter values provided by the R analysis.

Timing of adult emergence

If the stem or branch from which an adult *A. glabripennis* emerges remains alive and continues to grow, then the formation of new annual rings of woody tissue eventually grows over the exit hole and hides it from view. Old exit holes become buried completely within the woody tissues and this process can be quite rapid. In stems that are growing relatively quickly, exit holes can become calloused over within just one or two seasons. Once the exit hole has been calloused over, the only external sign that the hole is present is a small irregularity in the surface of the bark, although this also disappears with time.

When the samples from Paddock Wood were processed, those samples that contained exit holes, whether visible on the surface or concealed within the wood, were retained and dried at room temperature. Once dry, the samples were cut transversely with a band saw through the middle of each exit hole, and the cross-section was polished using a series of fine sandpapers to reveal the annual growth rings formed before and after the adult *A. glabripennis* had emerged. For old exit holes concealed within the wood, the position of the outer edge of the exit hole relative to the inner and outer surfaces of the annual growth rings provided information on the time of year when the adult beetle emerged. Exit holes cut in the early spring or late summer or autumn, either before or after the period when wood was being formed in the stem, would be expected to leave an edge that was flush with the line separating the individual growth rings (Copini *et al.*, 2013a). By contrast, exit holes produced during the growing season, when wood formation was still taking place, would be expected to show some degree of callous formation and in-growth into the exit hole cavity before growth for the year was completed (Favaro *et al.*, 2013; Copini *et al.*, 2013a).

The time of year when adult *A. glabripennis* were likely to have emerged and laid eggs was also estimated by calculating the number of degree-days accumulated over the season. Smith *et al.* (2004) have shown that peak numbers of adult *A. glabripennis* occur in the field once 800–900 degree-days have been accumulated above a base threshold of 10 °C from 1 January. The dates when 800 and 900 degree-days were accumulated at Paddock Wood were calculated for the years 2000–2012 using daily maximum and minimum temperatures recorded at East Malling Research Station. Temperature data were obtained from the British Atmospheric Data Centre (University of East Anglia Climatic Research Unit, 2014) and degree-days were calculated using the sine wave method (Allen, 1976; Smith *et al.*, 2004).

To place the timing of adult emergence and activity at Paddock Wood in a wider context, degree-days were also calculated for Central Park in New York City, U.S.A. (latitude 40.8°N, longitude: 74.0°W; 40 m a.s.l.), Chicago O'Hare airport in Illinois, U.S.A. (latitude, 42.0°N, longitude, 87.9°W; 204 m a.s.l.) and Burlington International airport in Vermont, U.S.A. (latitude, 44.5°N, longitude, 73.1°W; 101 m a.s.l.). New York and Chicago have climates considered to be optimal for *A. glabripennis* and are representative of areas where the beetle has a 1-year life cycle (MacLeod *et al.*, 2002; Keena, 2006; Keena & Moore, 2010). Burlington in Vermont, in contrast, has a cooler climate where *A. glabripennis* has a predominantly 2-year life cycle (Roden *et al.*, 2008). Temperature data for these locations were downloaded from the U.S. National Oceanic & Atmospheric Administration Climatic Data Centre (NOAA, 2014) and degree-days were calculated using the same method as for Paddock Wood.

Results

Anoplophora glabripennis life-stages recovered from the samples

A total of 1346 samples were returned to Alice Holt from Paddock Wood, of which 256 samples (19%) contained live or dead *A. glabripennis* larvae, pupae or adults and 247 samples (18%) contained *A. glabripennis* exit holes. The large number of samples that did not contain *A. glabripennis* suggests that very little of the infestation was missed and the majority, if not all, of the life-stages and exit holes were recovered. This is supported by there having been no further findings of *A. glabripennis* at Paddock Wood subsequent to the eradication programme being completed in 2012.

The *A. glabripennis* life-stages included 366 live larvae, 52 larvae that had died *in situ*, 33 pupae and three adult beetles. In addition, there were 82 instances where a current gallery or tunnel was found, with evidence that feeding had taken place recently but in which the larva had disappeared. In 38 of these cases, there was no obvious reason why the larva was absent and the larva was recorded as missing. In the other 44 cases, the larva had been taken by a woodpecker (Straw *et al.*, 2015).

Eighteen of the live larvae were damaged when the samples were collected in the field or when they were processed in the laboratory and could not be measured. Consequently, 348 larvae were measured and separated into different size classes (Table 1). Larvae varied widely in size, although 78 first-instar larvae and six second-instar larvae with a mean body length of 7.3 ± 0.3 mm and mean head capsule width of 0.95 ± 0.04 mm (mean ± 95% confidence limits, range: 0.7–1.5 mm, $n = 84$) were clearly distinguishable from older, established larvae that had a body length of > 10 mm and a head capsule width of > 1.8 mm (Fig. 1 and Table 1). Only small numbers of first- and second-instar larvae were found in the samples processed in March, April and May, whereas much higher numbers were found in June and July, before numbers decreased again in August (Fig. 1 and Table 1). Older, established larvae with a body length of > 10 mm, in contrast, were well represented in every month and their numbers varied less dramatically over the course of the season (Table 1).

Anoplophora glabripennis pupae were found in June, July and August, and three adult beetles were found in August and September (Table 1). The adult found in August and one of those found in September were still inside their pupal chambers but had started to chew an exit hole to the outside. The other adult found in September had emerged into the sample bag.

Larval size distributions

Analysis of larval size distributions was restricted to established larvae (third-instar larvae and later instars) and was based on head capsule width, rather than body length, because preserving the larvae in industrial methylated spirits tended to distort the body and slightly alter its length. By contrast, the head capsule is more heavily sclerotized and its width was less likely to have been affected by the storage conditions. There was a close correlation however, between body length (BL) and head capsule width (HW):

$$\mathrm{BL} = 13.157\,(\mathrm{HW}) - 7.427\ \left(n = 260, r^2 = 0.66, P < 0.001\right) \tag{1}$$

At the beginning of the season, in March and April, the head capsule widths of larvae recovered from the samples did not fit a single normal distribution (Hartigan's dip test, $D = 0.072$, $n = 66$, $P = 0.013$), but were better described by two normally distributed, but partly overlapping distributions, with a common variance and modes at 2.35 mm ($n = 36$; 55% of the larvae) and 3.70 mm ($n = 30$; 45% of the larvae) (SD = 0.35) (Fig. 1a and Table 2, Model 2). From Eqn 1, the corresponding body lengths of these two head capsule distributions were 10–35 and 35–55 mm, respectively.

Head capsule widths of the smaller sample of larvae recovered during May showed an irregular distribution that did not

Table 1 Total numbers of larvae, pupae and adults of *Anoplophora glabripennis* recovered each month from the samples brought back from Paddock Wood in 2012

	Month					
Body length (mm)	March to April	May	June	July	August	September
0.0–10.0	1	5	50	19	9	–
10.1–20.0	12 (18.4)	6 (12.2)	8 (10.1)	3 (13.0)	4 (6.6)	–
20.1–30.0	23 (35.4)	18 (36.7)	17 (21.5)	1 (4.3)	8 (13.1)	5 (21.7)
30.1–40.0	13 (20.0)	16 (32.7)	17 (21.5)	9 (39.1)	17 (27.9)	9 (39.1)
40.1–50.0	12 (18.5)	8 (16.3)	12 (15.2)	5 (21.8)	16 (26.2)	7 (30.5)
50.0+	5 (7.7)	1 (2.1)	3 (3.8)	–	9 (14.8)	–
Pupae	–	–	22 (27.9)	5 (21.8)	6 (9.8)	–
Adults	–	–	–	–	1 (1.6)	2 (8.7)
Total established larvae	65	49	79	23	61	23
Number of samples processed	123	283	474	200	231	35

The percentage of the total numbers of established larvae represented by larvae in each size class and by pupae and adults is given in parenthesis. Established larvae = total number of larvae greater than 10 mm in length + pupae + adult beetles.

differ significantly from a unimodal distribution (Hartigan's dip test, $P > 0.05$) and applying the dip test to head capsule widths in June–July also produced a nonsignificant result ($P > 0.05$). Normal mixture models, however, indicated that the June–July head capsule data were described better by a combination of two normal distributions rather than a single normal distribution, although the improvement in describing the data when a bimodal distribution was fitted was less than that observed when a bimodal distribution was fitted to the March–April data (Table 2). The AIC estimates indicated that two normal distributions with separate variances (Model 3) were the best fit to the data, with modes at 2.38 mm ($n = 25$ larvae; SD = 0.27) and 3.49 mm ($n = 49$ larvae; SD = 0.45), whereas the AICC estimates indicated a better fit with two normal distributions and a common variance (Model 2) with modes at 2.51 and 3.58 mm ($n = 29$ and 45 larvae, respectively; SD = 0.39) (Fig. 1b and Table 2). The modes of these distributions were similar to the modes of the distributions observed in March–April.

By contrast, larvae recovered in August–September did not show any dichotomy in size. The distribution of head capsule widths in this time period was unimodal (Hartigan's dip test, $P > 0.05$) and was described best by a single normal distribution (AIC and AICC values lowest for Model 1).

Timing of adult emergence

In total, 564 *A. glabripennis* exit holes were found in the samples from Paddock Wood. Forty-six percent of the exit holes ($n = 260$) were found in stems and branches that were alive, and 54% ($n = 304$) were found in stems and branches that had died either before or after the adult had emerged. Amongst the exit holes found in live wood, 180 had been formed before 2011 and the exit hole had been either partially or completely calloused over by subsequent growth. In almost all of these cases, the outer edge of the exit hole occurred in line with the boundary between successive growth rings (Fig. 2). There was no sign of any callous tissue growing into the exit hole cavity before the end of the season and therefore no evidence that the exit holes had been formed when wood formation was still taking place. Because adult beetles did not emerge in the spring before stem radial growth commenced, it appears that they emerged relatively late in the year, after wood formation had ceased.

The calendar dates on which 800 and 900 degree-days were accumulated at Paddock Wood are shown in Fig. 3. On average, 800 and 900 degree-days were accumulated on 24 August and 10 September, respectively, although there was considerable variation between years. The years 2003–2006 were noticeably warmer compared with the 3 years before and 6 years afterwards and, in these years, 800–900 degree-days were attained on dates between 10 August and 4 September. By contrast, 2012 was a particularly cool year, with 800–900 degree-days not being reached until 4–28 September (Fig. 3).

Mean summer temperatures at Paddock Wood are 5–7 °C lower than summer temperatures in New York and Chicago (Tables 3 and 4) and, at these locations in the U.S.A., 800–900 degree-days are accumulated much earlier in the season. For example, from 2000 to 2012, 800 and 900 degree-days were accumulated in Central Park in New York City by 7 July and 14 July, on average, respectively, and at Chicago O'Hare airport by 15 July and 23 July, on average, respectively.

Summer temperatures at Burlington in Vermont are intermediate between New York and Chicago and Paddock Wood (Tables 3 and 4). Degree-day accumulation predicts that, at Burlington, during 2000–2012, peak adult abundance would have occurred between 30 July and 8 August.

Discussion

Life-cycle variation in A. glabripennis

The life cycle of *A. glabripennis* is well known to vary in terms of timing and duration depending on regional and local climatic conditions. In the warmer parts of its range, in south, central and eastern China, the U.S.A. (e.g. New York and Chicago) and southern Europe (Italy), *A. glabripennis* adults start to emerge in April or May and peak adult activity occurs in late May, June or July (Hua *et al.*, 1992; Li & Wu, 1993; Hu *et al.*, 2009; Hérard *et al.*, 2009a; Haack *et al.*, 2010; EPPO, 2013a; Faccoli *et al.*, 2014). The adult females mate and lay eggs, and the eggs hatch within 1–2 weeks (Haack *et al.*, 2010). The larvae feed

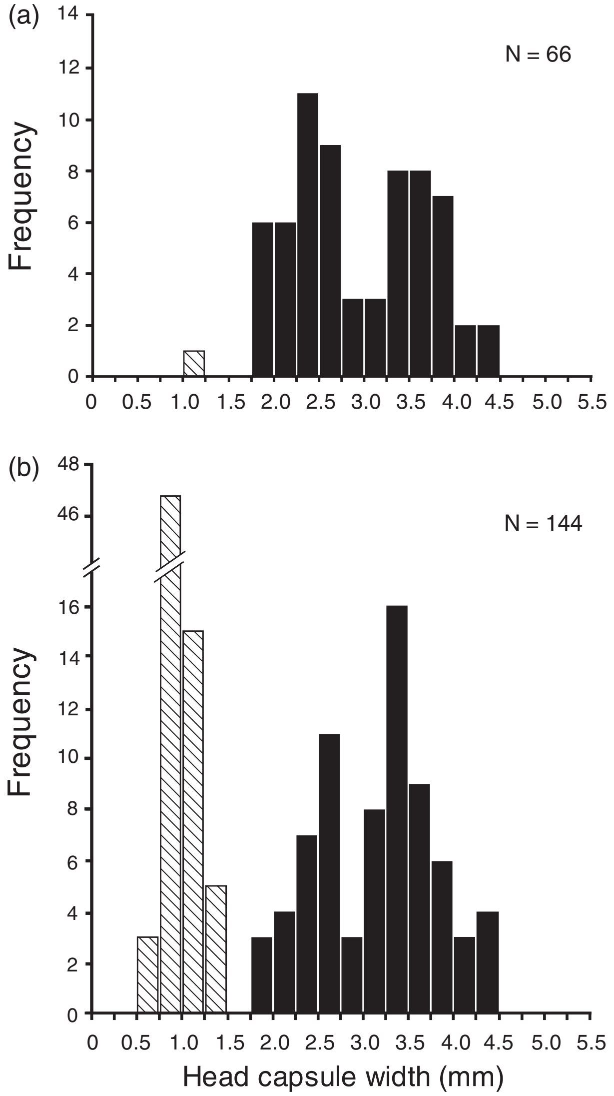

Figure 1 Frequency distribution of head-capsule widths of *Anoplophora glabripennis* larvae recovered from Paddock Wood during (a) March and April 2012 and (b) June and July 2012. Hatched columns indictate the head capsules of first- and second-instar larvae; black columns indicate the head capsules of third-instar larvae and later instars that were well established in feeding galleries under the bark and in tunnels in the wood.

and develop through the remainder of the summer and into the autumn, until falling temperatures cause activity to cease. Once the larvae have over-wintered, they complete their development during the next spring (Lingafelter & Hoebeke, 2002; Haack *et al.*, 2006, 2010). Thus, in regions where the climate is optimal for *A. glabripennis*, eggs hatch soon after they are laid, larvae are the main over-wintering stage and the life cycle is completed within 1 year (Fig. 4, life cycle 1).

In areas where summer temperatures are lower, for example, in northern China, in cooler areas within the U.S.A. (e.g. Vermont) and Canada, and in central Europe, adult emergence and the period when most eggs are laid is shifted to later in July and into August (Li & Wu, 1993; Zhao & Yoshida, 1999; Pan, 2005; Ric *et al.*, 2007; Roden *et al.*, 2008; Hu *et al.*, 2009). For example, in central Europe (Austria, Germany, France and Switzerland), adults of *A. glabripennis* have been captured or observed in the field during July (Hérard *et al.*, 2006; Krehan, 2008; Hugel & Brua, 2009; EPPO, 2014) and August (EPPO, 2010; Forster & Wermelinger, 2012) and occasionally later in the year (Krehan, 2008; EPPO, 2013b). Eggs that are laid in July and August still hatch soon afterwards and the larvae feed during the rest of the summer and into the autumn, but the larvae have less time to develop before the winter and, because temperatures are generally lower and development is slower, fewer larvae reach a size sufficient to enable them to pupate in the following spring. Larvae of *A. glabripennis* need to reach a threshold weight of at least 500 mg, or more typically 1000–2000 mg, before they will pupate, and larvae that do not reach this critical size by the autumn continue to feed during the next year and over-winter for a second time (Benker & Bögel, 2008; Keena & Moore, 2010). The result is a life cycle that takes 2 years (Fig. 4, life cycle 2a).

Adult *A. glabripennis* are quite long-lived (females live for up to 43–137 days; males for up to 98–145 days; Yan & Qin, 1992; Keena, 2002, 2006; Smith *et al.*, 2002) and some individuals are active in the field as late as October and even into December (Lingafelter & Hoebeke, 2002; Haack *et al.*, 2006, 2010; Krehan, 2008). A small proportion of *A. glabripennis* adults also emerge late in the year, after the main peak in adult activity, and lay eggs in the autumn. Eggs laid this late, in the autumn, appear to overwinter and do not hatch until the next summer, and this may be another reason why the life cycle sometimes takes 2 years (Fig. 4, life cycle 2b) (Hua *et al.*, 1992; Yan & Qin, 1992; Fan *et al.*, 1997; Lingafelter & Hoebeke, 2002; Haack *et al.*, 2006; Keena, 2006; Keena & Moore, 2010). Eggs laid in the autumn probably delay hatching because of the decrease in temperatures. Eggs of *A. glabripennis* do not hatch once temperatures fall below 10 °C (Keena, 2006). Thus, even in regions where the life cycle is usually completed in 1 or 2 years and most eggs are laid in the summer and hatch soon afterwards, a small proportion of individuals, derived from eggs laid late in the year, which then over-winter, will require an extra season to complete their development.

Timing of adult emergence at Paddock Wood

Smith *et al.* (2004) have shown that peak adult activity in *A. glabripennis* occurs when 800–900 degree-days have been accumulated from the beginning of the year. In their study area in Gansu province in north central China, where day-time temperatures in the summer reached 30–35 °C and *A. glabripennis* was univoltine (Bancroft & Smith, 2005), this number of degree-days was accumulated by mid-July, which was the time when peak numbers of adult *A. glabripennis* were observed in the field. Similarly, in New York and Chicago, where *A. glabripennis* also has a 1-year life cycle, degree-day accumulation predicts that peak adult activity should occur during the middle 2 weeks of July.

At Paddock Wood, in contrast, 800–900 degree-days were not attained before late August or September, or mid-August in the warmest years, indicating that adult *A. glabripennis* would not have emerged and laid eggs at this location until relatively late in the year. Keena and Moore (2010) reared *A. glabripennis* larvae at different constant temperatures in the laboratory and

Table 2 Parameters and estimates of the model fit criteria for the normal mixture models that were applied to the distributions of head capsule widths of larvae recovered from the Paddock Wood samples in (a) March and April and (b) June and July

Model	Parameters[a]	*n*	*P*	Log-likelihood (L)	AIC	AICC
(a) March to April						
Model 1	m, s	66	2	−75.1	154.3	154.5
Model 2	m1, m2, s, l	66	4	−65.2	138.4	139.1
Model 3	m1, m2, s1, s2, l	66	5	−65.1	140.1	141.1
(b) June to July						
Model 1	m, s	74	2	−73.2	150.4	150.6
Model 2	m1, m2, s, l	74	4	−70.1	148.2	148.7
Model 3	m1, m2, s1, s2, l	74	5	−68.9	147.9	148.8

[a] m1, mean 1; m2, mean 2; s1, variance 1; s2, variance 2; l, mixing parameter.
n, sample size, *P*, number of parameters.

found that 50% of adults emerged from the wood once 925 degree-days had been accumulated. At Paddock Wood, during the years 2000–2012, 925 degree-days were not accumulated until 20 August to 3 September, even when 2 °C were added to ambient temperatures to adjust for the larvae being enclosed within the host's tissues (Keena & Moore, 2010).

The emergence of adult *A. glabripennis* during late August and September at Paddock Wood is supported by the sample material brought back from the outbreak site. Adult beetles were only recovered from the samples in August and September. Emergence from the samples may have been delayed by storing the material at 15 °C, although this temperature was not much lower than outdoor temperatures in 2012, and the delay in emergence was likely to have been small (mean monthly temperatures at East Malling in May, June, July, August and September 2012 were 13.1, 14.5, 16.4, 17.7 and 13.9 °C, respectively; the mean May–September temperature was 15.1 °C). Prior to the outbreak of *A. glabripennis* being discovered at Paddock Wood, a single adult beetle was captured in an adjacent garden (Straw *et al.*, 2015). This adult was found on 12 October 2009 and, if it had emerged from one of the infested trees growing nearby, then it also indicates that adult *A. glabripennis* at Paddock Wood were active late in the year.

The first pupae were found in the samples in mid June. The pupal stage in *A. glabripennis* lasts 47–54 days at 15 °C and, after eclosion, the adult remains in the pupal chamber for a further 12–14 days (at 20 °C) before it chews its way out and emerges from the wood (Keena & Moore, 2010; Sánchez & Keena, 2013). Thus, the individuals found as pupae in June are unlikely to have emerged as adults before mid-August, and those pupae found in the samples in July and August would not have emerged and laid eggs until even later in the season.

Analysis of growth rings in the stems and branches from which adults emerged also indicated that adults emerged late in the year. Almost all of the exit holes in the samples had been formed after growth had finished and, even in the very few cases where

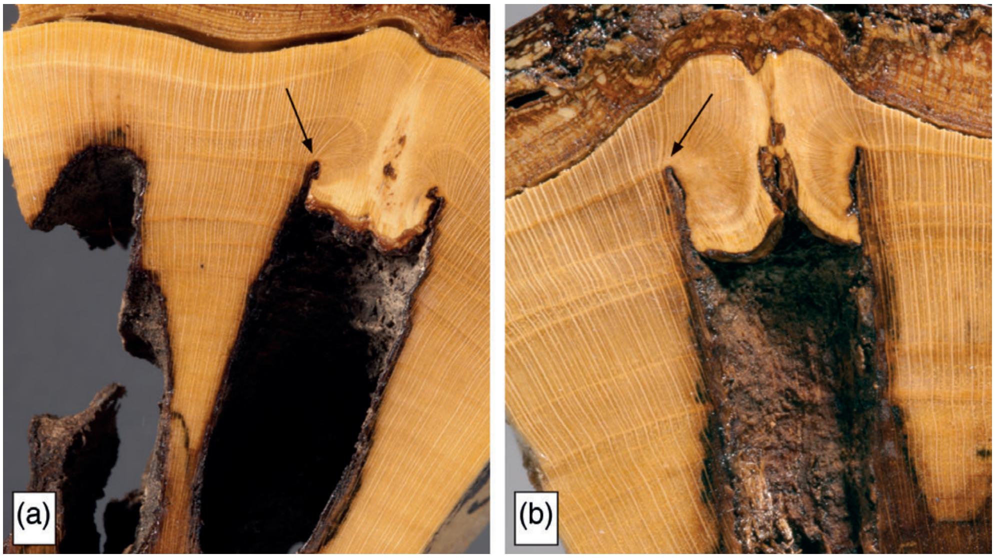

Figure 2 Transverse sections through *Anoplophora glabripennis* pupal chambers and exit holes in stems of sycamore *Acer pseudoplatanus* L. collected from Paddock Wood on 25 May 2012: (a) an exit hole formed in 2008 and (b) an exit hole formed in 2010. In both examples, the outer edge of the exit hole (marked by an arrow) occurs at the junction between successive growth rings and there is no in-growth of callous tissues before the end of the growing season.

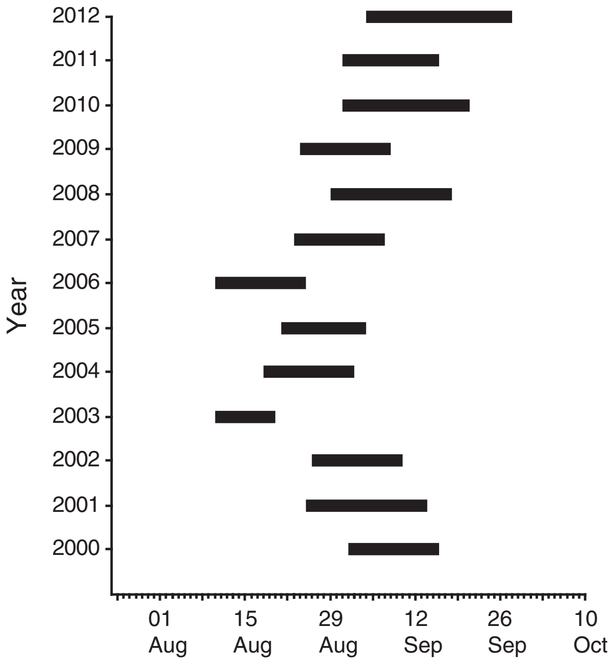

Figure 3 Timing of adult activity at Paddock Wood as predicted by the number of degree-days accumulated from the beginning of the year. Horizontal bars represent the period when 800–900 degree-days were accumulated above a base threshold of 10 °C from 1 January in each year, and indicate the period when most *Anoplophora glabripennis* adults would have been active (for further details, see text).

there appeared to be some radial growth after the exit hole had been cut, the amount of growth was very small. In northern temperate regions, wood formation in the stems of deciduous, broadleaved trees begins in late March or April, is at a maximum in May and June, and then decreases during July and is usually completed by the end of August (Fritts, 1976; Schmitt *et al.*, 2000; Skomarkova *et al.*, 2006; Michelot *et al.*, 2012; Copini *et al.*, 2013a). Therefore, on this basis also, it would appear that most adult *A. glabripennis* at Paddock Wood emerged either during late August or in September.

Similar observations are reported from the Netherlands. A small outbreak of *A. glabripennis* was discovered at Almere in the Netherlands in 2012 and analysis of growth rings in the trees from which adult *A. glabripennis* emerged indicated that, at this location, which has a climate similar to that in southern England, exit holes had also been formed at the end of the growing season (Loomans *et al.*, 2013; Copini *et al.*, 2013b).

Life cycles of 2 and 3 years duration at Paddock Wood

The sudden appearance of large numbers of first- and second-instar larvae in the samples from Paddock Wood in June and July, when very few had been found in March, April and May, suggests that these larvae had hatched recently, either in late May, June or early July. This was before any adults emerged and were present in the field and therefore the eggs from which the larvae hatched could not have been laid in the same year and must have been laid in the previous year and over-wintered. The presence of *A. glabripennis* eggs was not recorded when the Paddock Wood samples were processed, because it was assumed that any eggs would have hatched in the previous year, as documented in other studies, and that they would have been destroyed by the subsequent feeding activities of the larvae. In retrospect, those eggs that were found, and which at the time were classed as either infertile or to have died, should have been examined more carefully and recorded.

Larvae hatching from the eggs in May–July may have grown sufficiently by the autumn to pupate and emerge as adults during the next year (Fig. 4, life cycle 2b), although it is more likely, given the relatively cool climate at Paddock Wood, that most larvae would over-winter for a second time and emerge as an adult after 3 years (Fig. 4, life cycle 3). Significantly, when eggs over-winter, only the 3-year life cycle results in there being two cohorts of older, established larvae present in March and April: a cohort of smaller larvae (Ls) that have over-wintered once, and a cohort of larger larvae (Lm) that have overwintered twice and which are nearing pupation (Fig. 4, life cycle 3). Two cohorts of *A. glabripennis* larvae were evident in the samples from Paddock Wood, and these cohorts are likely to have represented larvae in their second and third years, respectively, indicating that most larvae were taking 3 years to complete their development.

The presence of a second-instar *A. glabripennis* larvae in one of the Paddock Wood samples in April (Fig. 1a) suggests that some eggs may have hatched in the previous autumn and the small larva over-wintered (Fig. 4, life cycle 2c). If these larvae grew sufficiently large by the autumn, then it is conceivable that they could have pupated and emerged during the next summer (i.e. after 2 years). A life cycle completed this quickly, however, would result in very small larvae being present in the spring (March–April) alongside a single cohort of large, mature larvae, which was not the general pattern observed at Paddock Wood. Alternatively, if larvae that hatched in the autumn over-wintered for a second time and took 3 years to complete development, then two cohorts of older, established larvae (Ls and Lm) would be observed in the spring, as seen at Paddock Wood. Thus, even if a proportion of eggs hatched in the autumn, the presence of two cohorts of older, established larvae suggests that most individuals were still taking 3 years to complete their development.

Even though two cohorts of *A. glabripennis* larvae could be identified in the samples, there was considerable overlap in larval sizes and 8–26% of the larvae were intermediate in size and could have been allocated to either cohort. The overlap between the cohorts probably reflects variation in the growth rate of individual larvae, although it may also indicate the presence of larvae that were completing their life cycle in 2 years and which were genuinely intermediate in size. The proportion of larvae able to complete their development within 2 years may have varied depending on annual temperatures. The summers of 2011 and 2012 at Paddock Wood were relatively cool. Mean June–August temperatures in 2011 and 2012 were 15.8 and 16.2 °C, respectively, compared with the 2000–2012 average of 17.0 °C, and, in these years, a 3-year life cycle appears to have predominated. In warmer years (e.g. 2003–2006) (Fig. 3), a greater proportion of eggs may have hatched soon after being laid and some larvae may have been able to complete their development within 2 years. Therefore, the population of *A. glabripennis* at Paddock Wood probably contained a mixture

Table 3 Mean monthly mean temperatures from May to November at Central Park, New York City (U.S.A.), Chicago O'Hare airport (U.S.A.), Burlington International airport (Vermont, U.S.A.) and East Malling Research Station (U.K.): 30-year mean surface air temperatures, 1981–2010

	Monthly mean temperature (°C)			
Month	New York	Chicago	Vermont	East Malling
May	17.1	15.0	13.5	12.2
June	22.1	20.5	18.8	15.3
July	24.9	23.3	21.5	17.7
August	24.2	22.4	20.4	17.6
September	20.2	18.0	15.9	14.7
October	14.1	11.4	9.0	11.4
November	8.9	4.6	3.4	7.8

Table 4 Mean monthly maximum temperatures from May to November at Central Park, New York City (U.S.A.), Chicago O'Hare airport (U.S.A.), Burlington International airport (Vermont, U.S.A.) and East Malling Research Station (U.K.): 30-year mean maximum surface air temperatures, 1981–2010

	Mean monthly maximum temperature (°C)			
Month	New York	Chicago	Vermont	East Malling
May	22.0	21.1	19.6	16.3
June	26.7	26.5	24.6	19.6
July	29.4	28.9	27.2	22.2
August	28.6	27.7	26.1	22.3
September	24.4	23.8	21.4	19.0
October	18.1	16.8	14.0	15.1
November	12.6	9.0	7.5	10.9

of individuals that were taking either 2 or 3 years to complete their development but with most individuals taking 3 years, particularly in cooler years.

Note that a life cycle completed within 3-years at Paddock Wood is spread over four calendar years (i.e. adults emerging in 2012 would have started out as eggs laid in the autumn of 2009) (Fig. 4; life cycle 3). Under a 2-year life cycle, the eggs would have been laid in the autumn of 2010 (Fig. 4; life cycle 2c).

Implications for management

The eradication programme implemented at Paddock Wood required that all trees that were infested with *A. glabripennis*, and any other trees within 100 m that could have acted as a host for the pest, were felled and destroyed before any adult beetles emerged (EPPO, 2013a; Straw *et al.*, 2015). The last infested tree was felled and destroyed on 9 July 2012 and all other host trees within the infestation area were destroyed by 3 August 2012 (Straw *et al.*, 2015). The present analysis indicates that no *A. glabripennis* adults were likely to have emerged before mid-August and therefore the eradication programme was successful in removing the infested trees before the pest had a chance to disperse and lay eggs.

Small numbers of *A. glabripennis* larvae, in the early phases of colonizing a new host tree, are notoriously difficult to detect and it is possible, even after all of the host trees within the infested area have been felled, that some infested trees remain undetected in the surrounding area. Consequently, the standard procedure is to continue to survey trees around the site of an *A. glabripennis* outbreak for a minimum of 4 years, or a period of not less than twice the length of the pest's life cycle (EPPO, 2013a). At Paddock Wood, because the life cycle appears to be predominantly of 3 years in duration, annual surveys will have to be carried out until at least 2018 and only then, if no further infestation has been found, will it be possible to declare the outbreak to have been eradicated.

Surveys and monitoring are a major component of eradication programmes against *A. glabripennis* and the extended period over which surveys will need to be continued at Paddock Wood will add significantly to the total cost of the control programme compared, for example, with situations in central and southern Europe, where the life cycle is completed in 1 or 2 years. On the other hand, a longer life cycle is likely to be associated with a slower rate of population increase, a reduced capacity for the population to spread and a lower probability of new populations becoming established, either by spread from an established infestation or after a new introduction. The prospects for containing and eradicating an outbreak of *A. glabripennis* in the U.K. are probably higher, therefore, and the ultimate costs of eradication may be lower, than in areas where the climate is more favourable for the pest and where its populations have the potential to increase and spread much more rapidly.

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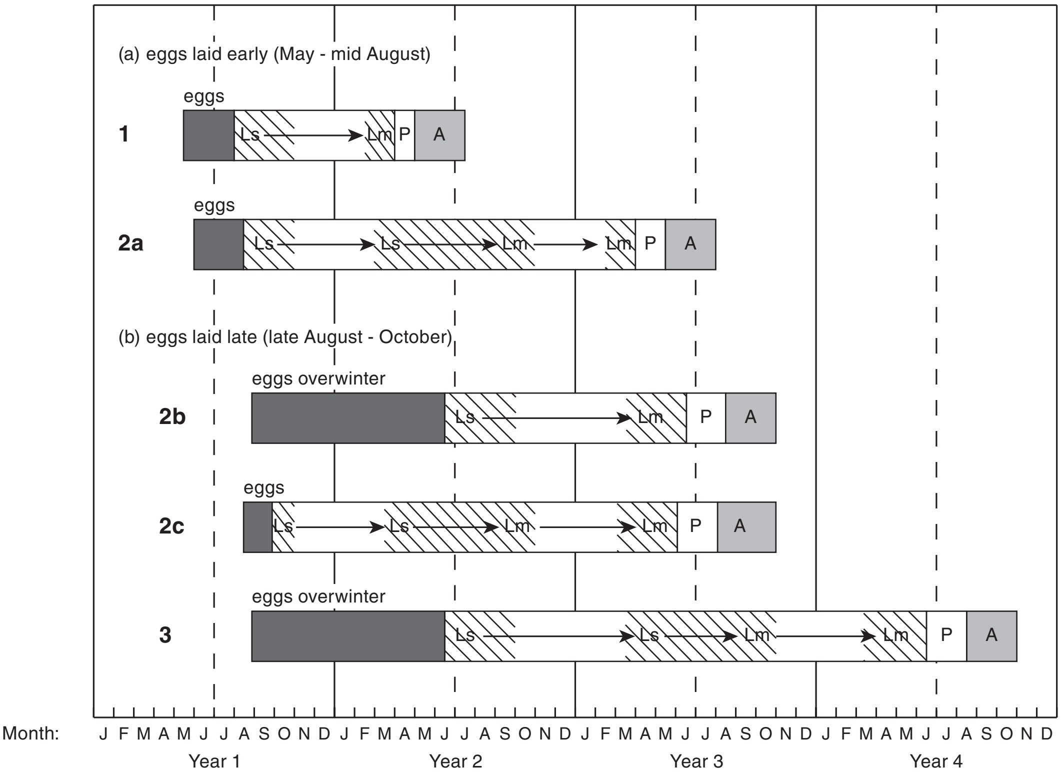

Figure 4 Diagrammatic representation of life-cycle variation in *Anoplophora glabripennis*. In warmer climates, adult beetles emerge early in the year and eggs are laid in spring and summer, and complete development usually takes 1–2 years (life cycles 1 and 2a). In cooler climates, adult beetles emerge in late summer and autumn and, although some eggs may hatch in the autumn (life cycle 2c), most overwinter and hatch in the following spring and complete development takes 2–3 years (life cycles 2b and 3). Ls, small larvae; Lm, large larvae; P, pupae; A, adult (period of peak adult activity). Hatched areas indicate when larvae are active and feeding; white areas within the larval sections of the life cycles indicate over-wintering.

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