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SHORT COMMUNICATION

The life cycle of the emerald ash borer *Agrilus planipennis* in European Russia and comparisons with its life cycles in Asia and North America

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Abstract

1 *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), native to Asia, is a destructive invasive pest of ash *Fraxinus* spp. in U.S.A., Canada and European Russia. It is spreading quickly and will probably soon be detected in other European countries.

2 Information about the life cycle of the pest is needed for detection and survey efforts, development of control options and predicting the potential range in Europe. The life cycle has been studied in North America and Asia, although it has not previously been studied in European Russia.

3 The number of larval instars and the duration of development of *A. planipennis* in European Russia were determined. Distributions of width of epistome and length of urogomphi indicated four larval instars. The number of excretory ducts and the presence of ledges did not provide a clear differentiation between instars. Development in most of the specimens took 2 years.

4 Generation time is flexible. In warmer regions (Tianjin), most individuals finish development in 1 year, whereas, in colder regions (Moscow, Changchun, Harbin), it takes 2 years. In intermediate climatic regions (Michigan), the ratio of 1 : 2-year life cycles depends on additional factors. The flexibility of the life cycle allows *A. planipennis* to establish in regions with different climates.

Keywords *Agrilus planipennis*, Buprestidae, Coleoptera, EAB, emerald ash borer, Europe, *Fraxinus*, life cycle, pest.

Introduction

Emerald ash borer *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) is one of the most destructive forest pests in the world (Herms & McCullough, 2014). In Europe, it is a quarantine pest included in the NAPPO Alert List, the EPPO A2 list of pests recommended for regulation and the EU Annex II/A1 (EPPO, 2014). This pest of ash *Fraxinus* spp. originating from East Asia was first detected in North America (U.S.A.) in 2002 (Haack *et al.*, 2002) and in Europe (Russia) in 2003 (Mozolevskaya & Izhevskiy, 2007). Subsequently, it has spread quickly in both continents (Cappaert *et al.*, 2005; Orlova-Bienkowskaja, 2014). The epicentre of invasion in European Russia is Moscow (Orlova-Bienkowskaja, 2013). Damage by *A. planipennis* has facilitated the outbreak of some other xylophagous beetles: *Hylesinus varius* Fabricius (Coleoptera: Curculionidae: Scolytinae), *Tetrops starkii* Chevrolat (Coleoptera: Cerambycidae) and *Agrilus convexicollis* Redtenbacher (Coleoptera: Buprestidae) (Orlova-Bienkowskaja & Volkovitsh, 2014; Orlova-Bienkowskaja, 2015). There is little doubt that *A. planipennis* will cross the border of Russia and soon also be found in other countries (Straw *et al.*, 2013). Native European species of ash *Fraxinus excelsior* L. is highly susceptible to the pest (Majorov *et al.*, 2012). The ecological and economic consequences of the establishment of *A. planipennis* could be significant because ash trees are common and play an important role in the biodiversity of European forests (FRAXIGEN, 2005).

Efforts to contain the spread of *A. planipennis* and to manage populations in infested areas will require a broad understanding of its biology, including its life history. First, basic information on phenological events (adult activity, generation time and

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overwintering behaviour) is needed for detection and survey efforts and the development of control options. Second, generation time strongly influences *A. planipennis* population dynamics and the rate of spread. Third, knowledge of the life cycle provides the basis for studying interactions with natural enemies, such as the recently discovered parasitoid *Spathius polonicus* Niezabitowski (Hymenoptera: Braconidae: Doryctinae) native to Europe (Orlova-Bienkowskaja & Belokobylskij, 2014). In addition, understanding the life cycle should help to clarify the key evolutionary adaptations that allow *A. planipennis* to become established in regions where the climate differs significantly from the climate in its native range.

The life cycle of *A. planipennis* in the U.S.A. and China is well-known (Cappaert *et al.*, 2005; Wang *et al.*, 2005, 2010; Liu *et al.*, 2007; Wei *et al.*, 2007; Duan *et al.*, 2010, 2014). Adults feed on ash leaves to reach sexual maturity and then mate in the canopy. Eggs are laid on the bark surface and the larvae penetrate to the interface between the xylem and phloem, where they then develop. The larvae overwinter once (as prepupae in self-constructed pupal cells in the xylem) or twice (first as younger-instar larvae, second as prepupae). The life cycle of *A. planipennis* in European Russia has not been studied previously. It is known that adults begin to emerge in late May or early June, peak flight occurs between 5 and 15 June, and some full-grown larvae overwinter in pupal cells (Mozolevskaya & Izhevskiy, 2007). The duration of development and the number of instars in species of Buprestidae can differ between regions (Beer, 1949). The present study aimed to determine the number of instars and the duration of development of *A. planipennis* in European Russia.

The life cycle of *A. planipennis* has been examined previously in southeastern Michigan (U.S.A.) (Cappaert *et al.*, 2005; Duan *et al.*, 2010, 2014), as well as in Tianjin, Benxi, Harbin and Changchun (China) (Wang *et al.*, 2005, 2010; Liu *et al.*, 2007; Wei *et al.*, 2007). In the present study, the life cycles in different regions are compared and summarized in a series of phenological diagrams. This summary suggests that the duration of the life cycle is flexible. Usually, in one part of a cohort (i.e. the generation of specimens hatched from eggs in the same year), the life cycle is 1 year, whereas it is 2 years for the other part of the same cohort. In warmer regions (in particular, in Tianjin), most specimens complete development in 1 year, whereas, in colder regions (Harbin and Changchun), this takes 2 years. In intermediate climatic regions (Michigan), the ratio between 1- and 2-year life cycles depends on additional factors. In particular, generation time is shorter in weakened trees (e.g. by girdling) compared with healthy trees (Tluczek *et al.*, 2011).

Materials and methods

For determination of the period of adult activity, approximately 100 *Fraxinus pennsylvanica* Marsh. trees were surveyed for adults twice a week from 15 May 2014 to 19 July 2014. Sweep nets and sticky bands were used, although the most effective method was to collect adults from leaves by hand. The last specimen was detected on 9 July. Adults were also collected in July 2011 and in June and July 2013. Immature stages of *A. planipennis* were collected each month from the beginning of August 2013 until the end of July 2014 (i.e. the whole year from the hatching of one cohort of larvae to the hatching of another cohort). Larvae were collected from approximately 100 infested *F. pennsylvanica* in Moscow. The trees were 10–30 years old and grew near the street. Their diameter at breast height was 20–50 cm. All trees were alive, lightly infested and had their foliage density reduced. We were able to find only one to four larvae in each tree, and so severe competition between larvae was unlikely. It was not possible to fell the trees and so we collected larvae from under the bark of the lower part of the main stems (up to 1.5 m). Accordingly, the lower 1.5 m of trunks of standing trees was debarked using a chisel and hammer.

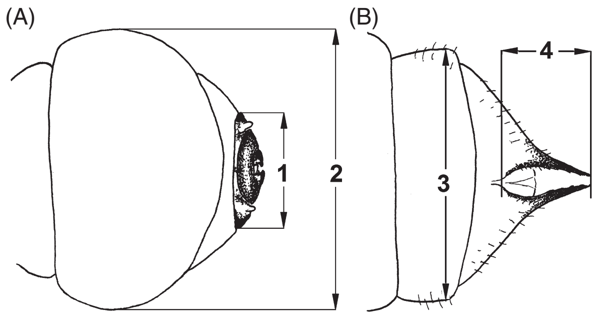

Figure 1 Measurements used for distinguishing between larval instars of *Agrilis planipennis*. (A) Anterior part of the body. (B) Posterior part of the body. 1, width of epistome; 2, width of prothorax; 3, width of last abdominal segment; 4, length of urogomphi.

Two hundred and eight larvae and prepupae were collected from the cambial region and outer sapwood. The methods of collection, duration of collection and the number of collected larvae correspond to studies made by other researchers in U.S.A. and China, and so the results are comparable (200 larvae were collected during the study of the life cycle in 2004 in Michigan, U.S.A.: Cappaert *et al.*, 2005; 700 larvae were collected from August 2003 to August 2004 in Tianjin: Wang *et al.*, 2005).

Six characters were used for distinguishing larval instars: (i) width of the epistome (i.e. exposed sclerotized portion of the head capsule, sometimes erroneously referred to as the peristome) (Wang *et al.*, 2005); (ii) width of the prothorax; (iii) length of the urogomphi (i.e. paired terminal processes); (iv) width of the last abdominal segment (Fig. 1); (v) number of excretory ducts on the urogomphi; and (vi) the presence or absence of ledges (i.e. numerous secondary subdivisions of excretory ducts). These characters have been used previously for determining the number of instars of *A. planipennis* in the U.S.A. (Cappaert *et al.*, 2005; Chamorro *et al.*, 2012) and China (Wang *et al.*, 2005). The duration of the life cycle was determined based on seasonal presence of different life stages inside trees in the same way as previously carried out for the duration of the life cycle of *A. planipennis* in North America (Cappaert *et al.*, 2005) and China (Wang *et al.*, 2005).

Results and Discussion

Larval instars

The distribution of measurements of the sclerotized parts (width of the epistome and length of the urogomphi) indicated that there are four distinct size classes (Fig. 2). The measurements of the

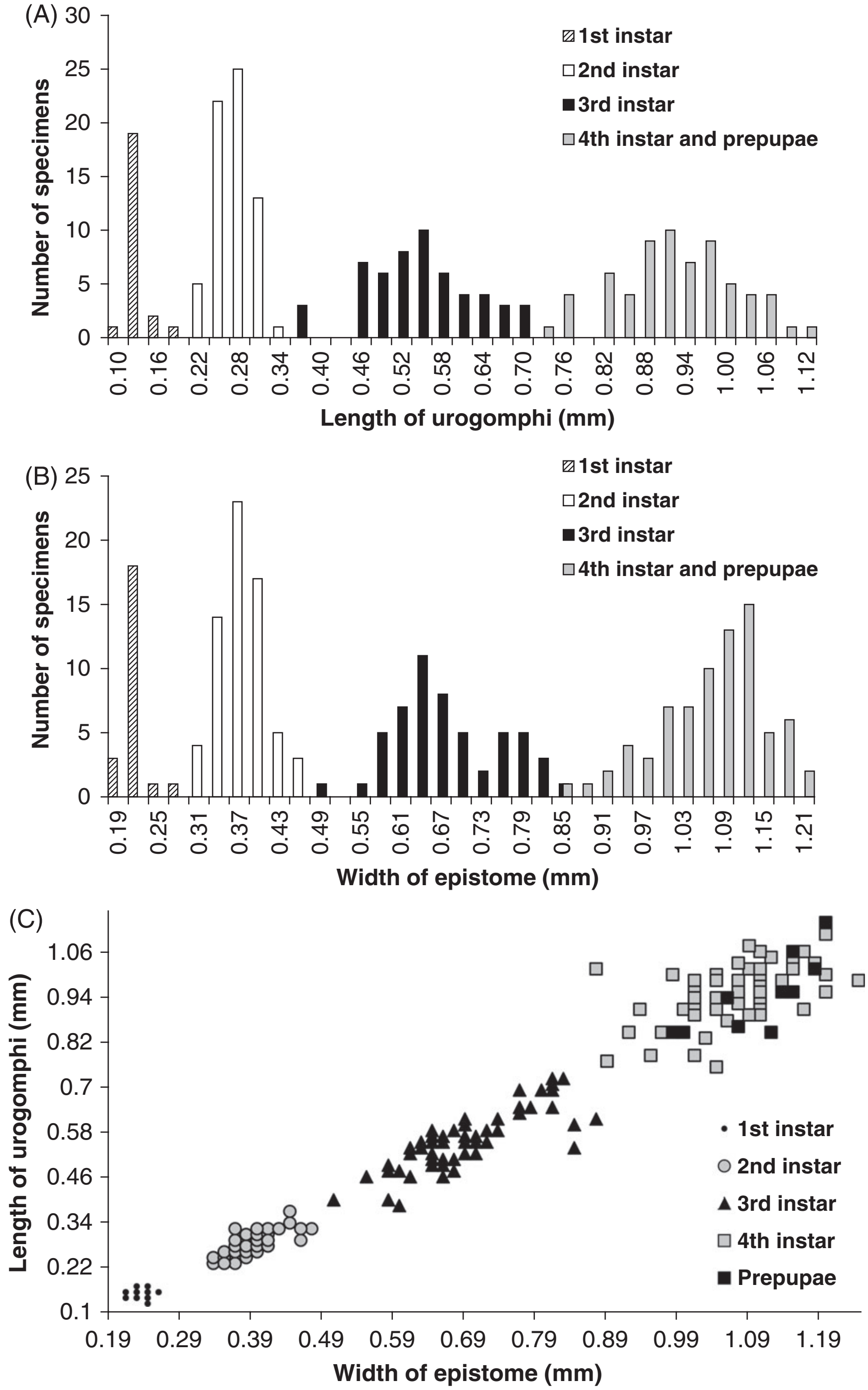

Figure 2 (A–C) Distribution of measurements of sclerotized parts of larvae of *Agrilus planipennis*.

smallest larvae correspond to those of first instars reared in the laboratory (Cappaert *et al.*, 2005; N. W. Siegert, unpublished data). Measurements of the largest larvae correspond to those of prepupae (i.e. nonfeeding terminal phase of the fourth instar lying in a pupal cell). Therefore, we have confirmed that there are four larval instars.

Widths of the prothorax and the last abdominal segment were shown not to be appropriate characters for distinguishing instars because they did not effectively separate larvae into distinct size classes (Table 1). Furthermore, these soft parts of the larvae gradually increase as it grows and develops over time.

Chamorro *et al.* (2012) suggest that the developmental stages can be distinguished by the number of excretory ducts making up the terminal processes (two in first instar and three in the second, third and fourth instars and prepupa) and the presence (third and fourth instars and prepupa) or absence (first and

Table 1 Measurements of the immature stages (for each metric character, the interval between the minimal and maximal value and the mean value with confidence interval 95% are indicated)

Stage	Width of epistome (mm)	Length of urogomphi (mm)	Width of last segment (mm)	Width of prothorax (mm)	Number of excretory ducts	Ratio of specimens with ledges (%)
First instar	0.22–0.29	0.12–0.20	0.23–0.40	0.52–0.8	1–2	0
	0.24 ± 0.01	0.15 ± 0.01	0.28 ± 0.02	0.64 ± 0.03		
Second instar	0.34–0.48	0.23–0.37	0.38–0.71	0.62–1.38	1–3	0
	0.39 ± 0.01	0.29 ± 0.01	0.57 ± 0.02	1 ± 0.04		
Third instar	0.51–0.88	0.38–0.72	0.68–1.65	1.03–2.29	2–3	24
	0.69 ± 0.02	0.56 ± 0.02	1.19 ± 0.05	1.65 ± 0.08		
Fourth instar	0.88–1.25	0.75–1.10	1.63–2.77	1.97–3.38	3	78
	1.07 ± 0.02	0.94 ± 0.02	2.08 ± 0.05	2.52 ± 0.09		
Prepupa	0.98–1.20	0.85–1.14	1.86–2.49	2.26–3.54	3	90
	1.11 ± 0.02	0.95 ± 0.02	2.21 ± 0.05	2.94 ± 0.09		

second instars) of ledges. Our data indicated that these characters are variable and do not provide a clear differentiation between instars (Table 1). In particular, some specimens of the second and third instars had two excretory ducts, and the large portion of specimens of third and fourth instars and prepupae had no ledges.

Life history

The flying period of *A. planipennis* adults was shown to start in early June in Moscow. Adult beetles were captured from 8 June to 5 July in 2013 and from 2 June to 9 July in 2014. Adults were found feeding on ash foliage and ovipositing in bark crevices of stems. In early June, there were many third and fourth instars present under the bark (Fig. 3). These larvae could not belong to the cohort of beetles that emerge as adults the same year because no prepupae were found until August. They also cannot belong to the cohort that hatched from eggs during the current year because they were present before oviposition took place or during the very beginning of the oviposition period. Therefore, they belonged to a separate cohort, indicating that the life cycle lasts more than 1 year for most individuals. Most larvae developed to the fourth instar by the end of July. In August, some excavated pupal cells and became prepupae. The new cohort of current-year first instars was also present at this time.

From late August to early May, the distribution of larval instars did not change considerably. Many larvae remained in the first instar from autumn to the beginning of May. Larvae did not grow much if at all in this cold period. Larvae of all instars were present in winter.

The potential for *A. planipennis* development in Moscow to last for ≥3 years remains a possibility. A delay in development occurs in some Buprestidae (Beer, 1949) and no direct laboratory or field observations on the duration of development of *A. planipennis* in Moscow have occurred to date. It appears that all larvae collected in June and July belonged to the same cohort. In early June, approximately half of them were third instars and the other half were fourth instars. By the end of July, almost all the larvae reached the fourth instar. Our sample size was limited, and so it is possible that some individuals may complete their development in 1 year. The development time of larvae developing in the upper part of ash trees was not investigated and may be different from the larval development occurring in the lower part of the trees. There are, however, no data supporting possible differences in other regions where development time has been studied (Cappaert *et al.*, 2005; Wang *et al.*, 2005). Nevertheless, it is possible that the 2-year life cycle might be related to host condition and/or larval population density because the trees sampled were relatively healthy and contained low numbers of larvae.

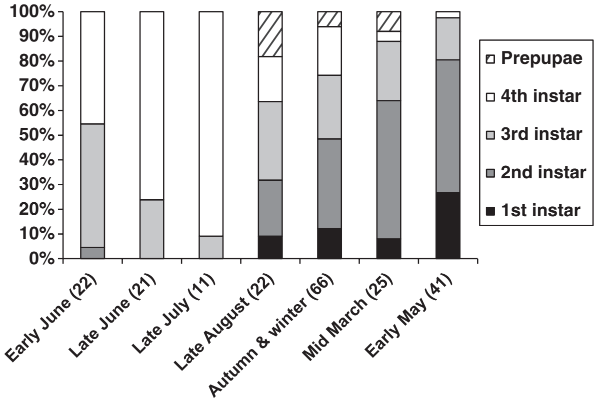

Figure 3 Ratio of different development stages of *Agrilus planipennis* in different seasons. The number of examined specimens is indicated in parentheses.

Comparison of life cycle in different regions

Comparison of the life cycle of *A. planipennis* in Moscow with data on its life cycle in southeastern Michigan (U.S.A.) (Cappaert *et al.*, 2005), as well as in Tianjin, Harbin and Changchun (China) (Wang *et al.*, 2005, 2010; Liu *et al.*, 2007; Wei *et al.*, 2007), confirmed that there are four larval instars in all these locations, although the duration of development varies (Table 2). The adult flight period is also different in different regions. In Moscow, adults occur from early June to early July (our data); in Tianjin, from early May to late June (Wang *et al.*, 2010); and, in Michigan, from mid May to early September (Cappaert *et al.*, 2005).

In the southern part of the native range in Tianjin and Benxi, the life cycle is 1 year in almost all specimens and larvae overwinter once as prepupae in pupal cells (Wang *et al.*, 2005; Liu *et al.*,

Table 2 Life cycle of *Agrilus planipennis* in different parts of its range: China (Wang *et al.*, 2005; Liu *et al.*, 2007; Wei *et al.*, 2007), U.S.A. (Cappaert *et al.*, 2005) and European Russia (original data)

Region	Mean temperature of July (°C)	Number of months with mean temperature above 10 °C	Duration of life cycle (year)	First year												Second year												Third year			Host plant
				May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	
Tianjin, China (38°55′N, 117°31′E)	27	7	1	◇	◇	◇	◇	◇	◇	◇																					*Fraxinus velutina*
						■	■	■	■	■	■	■	■	■	■																
																•	•	•													
Michigan, U.S.A. (42°22′N, 83°11′W)	22	6	1			◇	◇	◇	◇	◇																					*Fraxinus pennsylvanica*
									■	■	■	■	■	■	■																
																•	•	•	•												
			2				◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇										*Fraxinus pennsylvanica*
																					■	■	■	■	■	■	■				
																												•	•	•	
Harbin, China (45°43′N, 126°37′E)	23	5	2		◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇												*Fraxinus mandshurica*
																			■	■	■	■	■	■	■	■	■	■			
																												•	•	•	
Changchun, China (42°46′N, 125°27′E)	24	5	2			◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇											*Fraxinus pennsylvanica*
																					■	■	■	■	■	■	■	■	■		
																													•	•	
			2		◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇													*Fraxinus mandshurica*
																		■	■	■	■	■	■	■	■	■	■	■			
																											•	•	•		
Moscow, Russia (55°59′N, 37°10′E)	18	5	2				◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇	◇													*Fraxinus pennsylvanica*
																			■	■	■	■	■	■	■	■	■	■			
																													•	•	

◇, larvae; ■, prepupae; •, adults. The period of active feeding of larvae is shaded grey. Egg and pupa stages are not shown. The duration of life cycle was determined based on the seasonal presence of different life stages inside trees. Climatic data are from Hijmans *et al.* (2005).

2007). Few larvae of younger instars (<1%) overwinter in their galleries and continue development the next year, taking 2 years to complete development (Wang *et al.*, 2010). In Harbin, which is located much further north, the life cycle is 2 years and larvae overwinter twice: the first time in larval galleries and the second time in the pupal cells (Wei *et al.*, 2007). It was suggested that, in Changchun, which is north of Tianjin but south of Harbin, the life cycle of *A. planipennis* is 1 year and unsynchronized with overwintering at any larval stage (Liu *et al.*, 2007). The seasonal distribution of larval stages in Changchun, however, indicates that the life cycle in most specimens is 2 years (Liu *et al.*, 2007; Wei *et al.*, 2007). Development is synchronized because all pupae appear from overwintered prepupae. Adults emerge in June and early July, although there are third and fourth instars at the same time, which cannot belong to the same cohort as the adults. In Michigan, one part of the population has a 1-year life cycle, although another part exhibits a 2-year cycle (Cappaert *et al.*, 2005). Some larvae hatch in the summer, reach the prepupal stage in autumn of the same year and become adults next spring. When larvae fail to reach the fourth instar before winter, pupation appeared to be delayed until the second autumn. Delayed development also appears to be more common in low-density *A. planipennis* populations. In stressed trees, larvae develop faster than in healthy trees (Tluczek *et al.*, 2011). In Moscow, the life cycle of *A. planipennis* was found to be 2 years.

The duration of the life cycle could be different in different host plants. The studies in Changchun carried out on *F. pennsylvanica* (Liu *et al.*, 2007) and *Fraxinus mandshurica* Rupr. (Wei *et al.*, 2007), however, have not revealed significant differences in the life cycle. The life cycle in Moscow and Michigan, however, appears to differ, despite larvae developing on *F. pennsylvanica* in both regions.

The speed of larval development may be predominantly determined by climate, primarily the duration of the warm period and the amount of heat that larvae receive in one season. The number of months with mean temperature above 10 °C is seven in Tianjin; six in Michigan; and five in Moscow, Harbin and Changchun (Hijmans *et al.*, 2005). The mean temperature in summer in Moscow is approximately 4 °C lower than in Michigan and 5–9 °C lower than in Harbin, Changchun and Tianjin (Table 2). In many insect species that survive in both warm and cold regions or habitats, such as the xylophagous beetle *Dendroctonus rufipennis* Kirby (Scolytidae), the duration of the life cycle varies according to conditions; larval development lasts for an additional year or more at lower temperatures (Danks, 1992). If the life cycle is 2 years, the population consists of two cohorts, which reach maturity in subsequent years. In this case, the cohorts are not isolated from each other because a small portion of the each cohort finishes development faster or slower than the main part. This phenomenon is termed cohort-splitting (Danks, 1992). Flexibility in the duration of the life cycle is typical for some buprestid beetles. For example, the development of *Agrilus anxius* Gory native to North America varies with latitude and host condition. In the north part of the range, larvae require at least 2 years to develop and, in the south, development lasts 1 or 2 years depending on host vigor (Beer, 1949). Climate-related differences in the duration of life cycle, as well as in fecundity of females (Marshall *et al.*, 2013), may result in differences in *A. planipennis* population dynamics at different latitudes.

Conclusions

Although *A. planipennis* has four larval instars in all regions where larvae have been studied, the duration of development varies from 1 to 2 years according to climatic conditions. In regions with a warmer climate, most individuals overwinter once as prepupae; in regions with a colder climate, most individuals overwinter twice: the first time as larvae and the second time as prepupae. In regions with an intermediate climate, a part of the population has a 1-year life cycle and another part has a 2-year life cycle. The flexibility of the life cycle allows *A. planipennis* to establish in regions with different climates.

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