



Contribution to bionomy of *Hylesinus fraxini* (Coleoptera: Curculionidae: Scolytinae) and its monogamy in the Czech Republic

Príspevek k bionomii *Hylesinus fraxini* (Coleoptera: Curculionidae: Scolytinae) a jeho monogamii v Českej republike

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Abstract

This study focused on bionomics of the ash bark beetle *Hylesinus fraxini* (Panzer 1779). The study area was at Jilové u Prahy in the Central Bohemian Region of the Czech Republic. In February 2014, three common ash (*Fraxinus excelsior*) trees were felled and *Hylesinus fraxini* infestation was subsequently observed from March. Beetles were collected from 20 debarked logs and dissected under stereomicroscope, and their sex was determined. Five logs with bark beetles were placed into photoelectors. Beetles that emerged were collected and put into the second photoelector with fresh ash wood to determine whether they would establish the second generation. The analysis showed that each gallery system with a pair of bark beetles contained one male with only one female. If one adult of *H. fraxini* was found in the gallery system, it was usually female. Therefore, possible polygamy of *Hylesinus fraxini* was not confirmed in Central Bohemia. Maternal gallery length significantly correlated with the number of eggs laid per female. Offspring beetles did not establish the second generation, as only maturation feeding occurred in fresh wood.

Keywords: common ash bark beetle; bionomics; polygamy; voltinism; Central Bohemia

Abstrakt

Výzkum byl zaměřen na bionomii lýkohuba jasanového *Hylesinus fraxini* (Panzer, 1779). Studijní plocha se nacházela v obci Jilové u Prahy ve Středočeském kraji. V únoru 2014 byly pokáceny 3 stromy jasanu ztepilého (*Fraxinus excelsior*) a následně byl od března pozorován nálet *Hylesinus fraxini*. Špalky byly odkorněny a z nich získaní dospělci byli za pomoci stereomikroskopu vypitváni a bylo určeno jejich pohlaví. Pět nalétnutých špalků bylo ponecháno ve fotoelektru. Vylétnutí jedinci byli odebráni a umístěni do fotoelektru s čerstvým jasanovým dřívím pro zjištění možnosti založení druhé generace. Analýza dospělců ukázala, že v každém požerku, kde byl nalezen pár, se nacházela vždy samice se samcem. Pokud se v požerku vyskytoval pouze jeden dospělec, jednalo se většinou o samici. Nebyla tedy potvrzena možná polygamie u *Hylesinus fraxini* ve Středních Čechách. Délka matečných chodeb statisticky významně korelovala s počtem vykladených vajíček jednou samicí. Nová generace nezaložila další pokolení, na čerstvém dříví proběhl pouze úživný říz.

Klíčová slova: lýkohub jasanový; bionomie; polygamie; voltinismus; střední Čechy

1. Introduction

The ash bark beetle *Hylesinus fraxini* (Panzer 1779) is the secondary pest on common ash (*Fraxinus excelsior* L.) trees suffering from crown dieback frequently caused by the tracheomycotic fungus *Chalara fraxinea* (Kowalski 2006) (Skovsgaard et al. 2010). Even though ash bark beetle infestation is only secondary, its increased abundance and negative impacts on trees can cause the death of individual trees (Knížek & Modlinger 2013).

H. fraxini occurs across a wide range of conditions covering the whole Europe and to the east reaching Asia as far as China. It also occurs in parts of northern Africa (Knížek & Modlinger 2013). Its increased occurrence is caused by suitable conditions where ash is used to improve stand quality. At higher population densities, it also infests healthy and newly planted trees (Pfister 2012). It prefers younger trees with weaker bark. It infests older trees in the crowns and branches and then spreads to the trunk (Křístek & Urban 2013).

The beetle can develop on several tree species (Pfeffer 1955; Marchant 1973; Arndt et al. 2007), but it occurs most frequently on *F. excelsior*. In the southern part of its range, it often develops on olive (*Olea europaea* L.) (Lozano & Campos 1992). Its regular outbreaks on host trees affect forest management (Teusdea et al. 2012). It sporadically occurs outside its range, if conditions are suitable for its development, and it is expected to spread further to new areas (Lieutier et al. 2004).

The scientific literature contains a number of conflicting opinions as to the bionomics of *H. fraxini*. Inconsistencies in the data mainly concern questions about the number of females in gallery systems (Loyning & Kirkendall 1999; Rudinsky & Vallo 2009; Modlinger & Knížek 2012) and the number of generations per season (Procházka 2009; Křístek & Urban 2013). Knowledge of these characteristics is important for forest managers to prepare timely and effective preventive and protective measures against this pest, and particularly to determine the number of trap tree series.

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The main objectives of this study were to determine whether *H. fraxini* is monogamous or bigamous by collecting adults and determining their sex and to detect any potential occurrence of the second generation in Central Bohemia.

2. Material and Methods

The study site was at Jílové u Prahy in the Central Bohemian Region of the Czech Republic (49°53'42"N, 14°29'49"E; 370 m a.s.l.). The area is classified in the fourth oak and third oak–beech altitudinal vegetation zones and is characterised by depleted mesophilic biota including acidophilic oak forests, flowering beech forests, and oak–hornbeam forests (Culek 1996). The area is dominated by ash–birch (*F. excelsior*–*Betula pendula* Roth.) stands with admixed oak (*Quercus robur* L., *Q. petraea* (Matt.) Liebl.) and hornbeam (*Carpinus betulus* L.). Ashes with symptoms of *H. fraxini* infestation commonly occur at the location. Bark calluses, gallery systems, and emergence holes had been observed on the bark of dry trees.

On 22 February 2014, three young ashes marked in advance were felled ca 500 m from the study area. The trees were cut into 50–70 cm long logs, from which 25 logs with diameters of ca 10 cm were selected. The logs were leant against a fence partially shaded by trees within the study area.

During May and June, 20 colonised logs were gradually processed. Prior to debarking, the logs were always measured for precise section length and diameter as well as phloem thickness. The bark above the entry holes was removed by knife in such a manner as not to damage *H. fraxini* individuals. This procedure was repeated until the bark was removed from all the maternal galleries, larval galleries, and pupal chambers of each gallery system. For each gallery system, the maternal gallery length was measured, the developmental stage (eggs, larvae, pupae) was determined, and the clutch

size in each maternal gallery branch was counted. All data were recorded in a table. Samples of *H. fraxini* adults were collected from each gallery system and inserted separately into marked microtubes (Eppendorf, 2.5 ml). The samples were stored separately for each trap tree, kept at 5°C, and then immediately processed. Laboratory dissection determined the sex of each individual according to the presence of male or female gonads.

Three photoelectors were installed in a room temperature at ca 22°C. Five colonised logs were placed into the photoelectors. Regularly collected individuals (every 3–5 days) were counted and placed into the second photoelector with fresh ash wood to allow potential establishment of the second generation. On 14 October 2014, this wood was debarked and its gallery systems were analysed.

Microsoft Excel 2010 was used to create an overview table and calculate basic statistics. Statistical analyses (tests of normality, paired t-tests, ANOVA and correlation calculations) were carried out and point and box plots were processed in STATISTICA 12.

3. Results

The first infestation of *H. fraxini* was observed on 22 April 2014 after 1 week with daily mean temperatures exceeding 10°C (source: Czech Hydrometeorological Institute). In the following days with higher temperatures, increasing numbers of beetles were observed. Females began creating entry holes immediately, and wood dust waste from the created galleries appeared in the study area.

During May and June, 357 entry holes were counted on 20 logs from the study area after debarking, which corresponds to 1.2 ± 0.5 entry holes per dm² of bark surface. The gallery systems were often densely clustered in the areas of uneven bark. Phloem thickness ranged around 1–2 mm. The

Table 1. Data from analysed traps used to capture *Hylesinus fraxini* at Jílové u Prahy in 2014.

| Trap tree | Date | Trap tree diameter [mm] | Population density per dm ² | Σ ♀♀ | Σ ♂♂ | Σ | Life stage | Maternal gallery length \pm SD | Number of eggs \pm SD |
|-----------|--------------|-------------------------|--|-------------|-------------|----------|------------|----------------------------------|-------------------------|
| 1 | 15 May 2014 | 69 | 1.76 | 17 | 11 | 28 | E–L | 40.7 \pm 7.7 | 46.4 \pm 10.2 |
| 2 | 30 May 2014 | 89 | 2.44 | 33 | 26 | 59 | E–L | 45.2 \pm 7.9 | 68.6 \pm 13.7 |
| 3 | 31 May 2014 | 88 | 0.82 | 12 | 2 | 14 | E–L | 43.7 \pm 6.4 | 61.2 \pm 9.5 |
| 4 | 5 June 2014 | 84 | 1.66 | 21 | 5 | 26 | E–L | 54.8 \pm 8.7 | 82.8 \pm 16.4 |
| 5 | 6 June 2014 | 97 | 2.08 | 30 | 5 | 35 | E–L | 50.0 \pm 10.5 | 83.6 \pm 17.8 |
| 6 | 7 June 2014 | 80 | 1.01 | 12 | 4 | 16 | E–L | 47.6 \pm 8.1 | 63.7 \pm 14.0 |
| 7 | 7 June 2014 | 95 | 1.42 | 22 | 6 | 28 | E–L | 40.7 \pm 6.9 | 58.8 \pm 11.0 |
| 8 | 8 June 2014 | 97 | 1.36 | 17 | 7 | 24 | E–L | 44.7 \pm 10.7 | 57.7 \pm 15.1 |
| 9 | 8 June 2014 | 85 | 1.08 | 13 | 3 | 16 | L | 45.6 \pm 7.5 | 61.6 \pm 10.4 |
| 10 | 10 June 2014 | 84 | 1.36 | 19 | 2 | 21 | L | 51.2 \pm 12.3 | 69.2 \pm 20.6 |
| 11 | 11 June 2014 | 76 | 1.09 | 14 | 0 | 14 | L–P | 43.7 \pm 8.8 | 53.0 \pm 11.6 |
| 12 | 11 June 2014 | 95 | 1.42 | 22 | 5 | 27 | L–P | 47.1 \pm 10.0 | 59.5 \pm 12.6 |
| 13 | 13 June 2014 | 104 | 1.19 | 21 | 0 | 21 | L–P | 47.6 \pm 11.4 | 55.4 \pm 13.7 |
| 14 | 14 June 2014 | 65 | 0.75 | 8 | 1 | 9 | L–P | 46.9 \pm 11.2 | 57.3 \pm 12.9 |
| 15 | 14 June 2014 | 129 | 0.89 | 23 | 4 | 27 | L–P | 53.0 \pm 9.1 | 74.2 \pm 16.4 |
| 16 | 16 June 2014 | 116 | 0.59 | 11 | 1 | 12 | L–P | 47.3 \pm 11.1 | 69.2 \pm 16.9 |
| 17 | 16 June 2014 | 92 | 0.94 | 13 | 1 | 14 | L–P | 46.6 \pm 9.3 | 64.9 \pm 13.8 |
| 18 | 18 June 2014 | 94 | 0.61 | 8 | 0 | 8 | L–P | 46.3 \pm 8.0 | 65.9 \pm 11.3 |
| 19 | 18 June 2014 | 86 | 1.08 | 14 | 0 | 14 | L–P | 41.6 \pm 8.9 | 59.1 \pm 13.9 |
| 20 | 20 June 2014 | 124 | 1.23 | 22 | 0 | 22 | L–P | 44.3 \pm 9.9 | 59.7 \pm 16.6 |

N – mean, ♀♀ – females, ♂♂ – males, Σ – sum, E – eggs, L – larvae, P – pupae, SD – standard deviation.

gallery systems found on trap trees with phloem thickness of <1 and those with 1–2 mm thick phloem had identical population densities (Shapiro-Wilk test of normality: $W = 0.93624$, $p > 0.05$; ANOVA: $F(1, 18) = 2.0167$, $p > 0.05$).

A total of 435 individuals were collected from the maternal galleries and nuptial chambers. The gallery systems from which the pairs of adults were collected always contained one female and one male. A total of 73 adult pairs were collected (Table 1). Among solitary individuals, there were 279 females and only 10 males. Males began emerging from gallery systems relatively early, and when the first pupae were emerging there were males only with a small number of females (Table 1).

The mean maternal gallery length was 46.4 ± 9.2 mm, and the mean clutch size was 63.6 ± 13.9 eggs. In mid-May, larvae began gradually appearing among egg clutches. Pupae were observed ca 1 month later, i.e. in mid-June (Table 1).

Fully developed beetles began emerging from ash wood in early July, and their emergence continued to mid-August (Fig. 1). A total of 1,493 *H. fraxini* adults emerged from the colonized trap trees. These individuals were transferred to five prepared photoelector trees with 200–300 adults each. Only maturation feeding of adults was observed in the newly colonised photoelector trees after debarking without any nuptial chambers or laid eggs. The galleries had irregular shapes and extended up to several centimetres. No evidence of the second generation was found.

Within the individual gallery systems, no significant differences in the length of branches in maternal gallery (Shapiro-Wilk test of normality: $W = 0.95548$, $p > 0.05$; t-test: $t = 1.046616$, $p > 0.05$) or in the number of laid eggs (Shapiro-Wilk test of normality: $W = 0.94316$, $p > 0.05$; t-test: $t = 1.555459$, $p > 0.05$) were revealed.

Neither the total maternal gallery length ($y = 46.2828 + 0.1261 \cdot x$; $r = 0.0160$; $p > 0.05$) nor the number of laid eggs

($y = 58.2886 + 4.2757 \cdot x$; $r = 0.2202$; $p > 0.05$) correlated with *H. fraxini* population density in trap trees. In contrast, significant linear correlation was found between the maternal gallery length and the number of laid eggs ($y = -0.2252 + 1.3923 \cdot x$; $r = 0.8469$; $p < 0.00001$; Fig. 2). Mean density of 1.3 ± 0.1 eggs per 1.0 mm maternal gallery was recorded.

4. Discussion

Under suitable conditions, adult beetles, lured by volatile substances from a weakened tree, infest the tree in large numbers over several hours or days (Lieutier et al. 2004). The adults' main flight activity lasts only several days with temperatures exceeding 16°C. Flight activity begins at 10:00–11:00 and reaches its peak at 13:00–15:00 (Pedrosa-Macedo 1977). The beginning of flight activity and infestation of prepared trap trees was observed in March after the first week with mean temperature of 12.2°C (i.e. during 16–22 March 2014). The beetles' flight activity was concentrated into the period in March with higher temperatures. Adults are active during the warmest times of day, around noon (Pedrosa-Macedo 1977). The observed infestation with population density of 1.2 per dm² was lower than in Ukraine, where the mean density reached 2.6 families per dm² (Novak et al. 2008). The difference in the population densities between the trap trees with phloem <1 mm thick and those with 1–2 mm thick phloem was not significant, showing that *H. fraxini* does not have a preference for a specific phloem thickness.

Multiple origins of mating systems, otherwise rare in insects-various forms of monogamy and harem polygyny, are an especially exciting feature of wood boring beetles (Kirkendall 1983). Host selection and gallery initiation are typically performed by females in monogamous species, and males in polygamous species, a distinction that holds at a genus level. In the case of monogamous species (e.g.

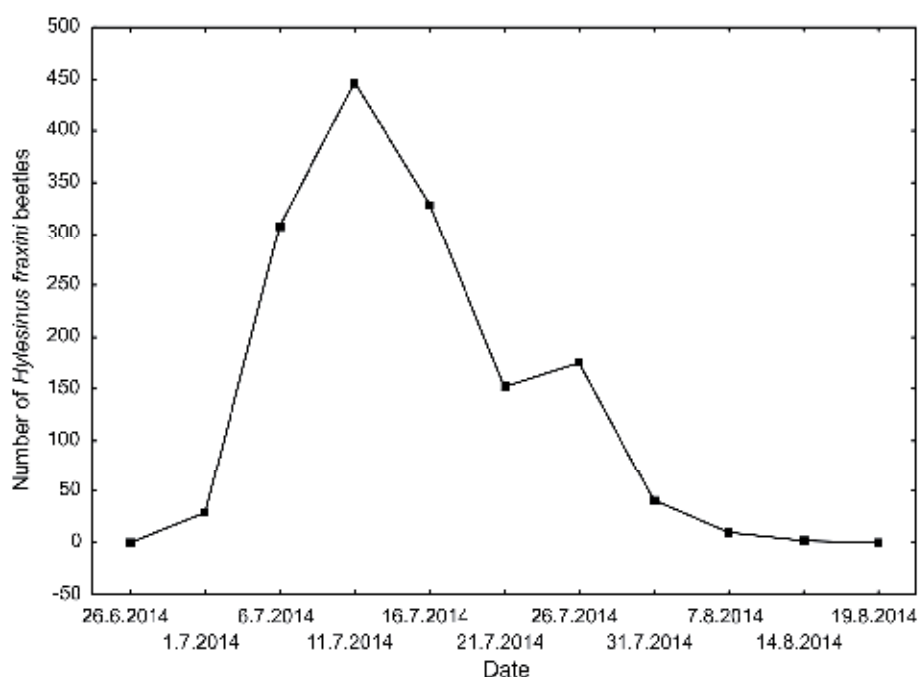


Fig. 1. Number of *Hylesinus fraxini* individuals leaving photoelectors in 2014.

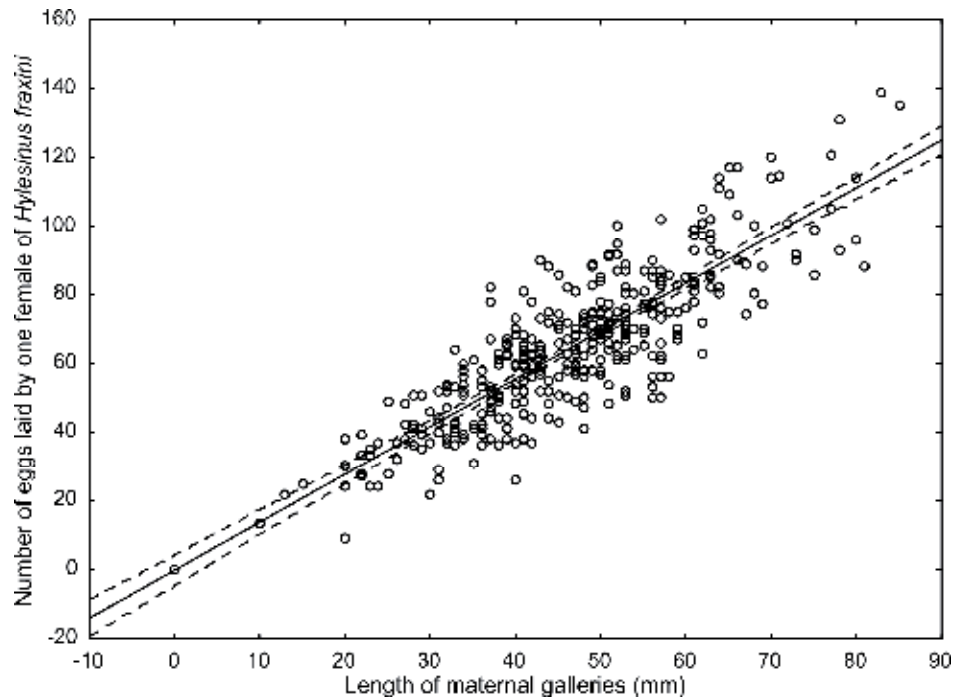


Fig. 2. Correlation between total maternal gallery length and number of eggs laid by *Hylesinus fraxini* females at Jílové u Prahy in 2014. Circles: maternal gallery length vs. the number of eggs laid in each gallery system, bands: 95% confidence interval.

Trypodendron spp., *Scolytus* spp.), females arrive at a tree, and initiate boring of galleries while realising pheromones (Ciesla 2011; Vega & Hofstetter 2015). Males arrive after and attempt to enter the gallery. In polygamous species, males usually initiate gallery construction in the form of a nuptial chamber. Among these species males control mate selection (e.g. *Ips* spp. and *Pityogenes* spp.) (Pfeffer 1995; Schlyter & Zhang 1996; Wermelinger 2004). Some polygamous species include pseudogynous females, that require mating, but reproduce parthenogenetically (e.g. *I. acuminatus*) (Loynning & Kirkendall 1996; Vega & Hofstetter 2015).

In the case of *H. fraxini*, suitable host trees are infested first by females, which immediately begin creating entry holes and a system of galleries for eggs (Loynning & Kirkendall 1999). To attract males, females produce primary attractants (Lieutier et al. 2004). While constructing maternal galleries, mating occurs on the bark or inside the gallery system (Loynning & Kirkendall 1999).

After boring a nuptial chamber, females progressively bore two galleries (Modlinger & Knízek 2012) transversely to the chamber and gradually lay eggs in them (Lieutier et al. 2004). This is apparently the reason why there were no pronounced differences in the lengths of the left and right gallery system branches and the numbers of eggs laid inside. Nor was the relationship between the adult population density and either total maternal gallery length or the number of eggs laid significant. Under suitable conditions, eggs are laid from March to April (Lozano & Campos 1992). First eggs are laid 5–12 days after the start of host material infestation (Pedrosa-Macedo 1977). They are gradually deposited along the entire length of both galleries leading out of the maternal chamber. Each transparent, oval egg is placed into a small hole (Lieutier et al. 2004).

There was a significant linear correlation between the number of laid eggs and the maternal gallery length. Longer galleries contained substantially larger numbers of eggs. The determined value of $r = 0.85$ is comparable with the value $r = 0.75$ stated by Lozano & Campos (1992). As expected, the mean maternal gallery length (46.4 mm) was within the most commonly stated interval of 2.5–10 cm, and the galleries were frequently densely clustered (Pfeffer 1955; Křístek & Urban 2013). The mean clutch size of 63.6 eggs per female was almost double the stated averages ranging around 35–38 eggs (Chapman 1958; Lozano & Campos 1992), but it falls within the range recorded in earlier studies (Russo 1932), which reported a higher number of eggs of around 60–80 eggs per female. This substantial difference could have been caused by the different infestation density on trap trees. Weaker infestation was also probably reflected in the absence of significant correlation between population density and maternal gallery length or clutch size. *H. fraxini* lays eggs in the range of 0.2–1.7 eggs/mm (Lozano & Campos 1992). The determined mean clutch density of 1.4 eggs per mm is within this range.

H. fraxini is generally monogamous, but gallery systems with two females have been found in Slovakia (Modlinger & Knízek 2012). Males most frequently mate with only one female. The analysis of collected individuals did not reveal the presence of multiple females in a single gallery system. The galleries and nuptial chambers contained 73 pairs, and solitary individuals, out of which 279 were females and 10 males. The finding of solitary females could indicate that males left females soon after copulation. The individuals found alone were always females previously fertilized. After a pair is formed, the male helps to create the galleries for a long time but leaves the galleries before the female. Gallery systems where two females have been found normally

contained more eggs than monogamous systems, although the males in these gallery systems did not double their reproductive success as determined for other bark beetle species. This has led to the hypothesis that these gallery systems are initially the work of a single female to which a male later lures the second female. Most of the males in the Slovak population had two females, although the polygamy of this species has not been found elsewhere. The species is stated as being monogamous in Germany, Spain, France, and England. In Norway, bigamy occurred only in rare cases (in 4 out of 114 gallery systems) (Loyning & Kirkendall 1999). Assuming that *H. fraxini* was a bigamous species, each female would inhabit one of the gallery system's two branches (Rudinsky & Vallo 2009). This would probably result in different lengths of the right and left galleries, and different egg numbers in each branch. This hypothesis was not confirmed as the difference between the branches was negligible.

Callow beetles emerge for maturation feeding gradually from June (Pfister 2012) until early July (Novák et al. 1974). The emergence peak for *H. fraxini* adults occurred around 11 July, and the number of captured individuals gradually decreased until the beginning of August (Fig. 2). In association with feeding, individuals created irregular galleries up to several cm long in which they frequently overwintered. *H. fraxini* did not establish a new generation in the photoelectors, thus confirming the hypothesis that the species is univoltine (i.e. having only one generation per year). It does, however, usually have a sister generation (Křístek & Urban 2013).

5. Conclusion

H. fraxini began infesting trap trees in the second half of March at temperatures above 10°C. Adults emerged from the infested photoelector trap trees from the end of June until the beginning of August with peak activity on 11 July. Maturation feeding subsequently took place on new trap trees. The entire development lasted about 3 months.

H. fraxini is a monogamous species. A presence of two or more females was not recorded in any of the 357 analysed gallery systems. The number of laid eggs correlated positively with the maternal gallery length. In Central Bohemia, *H. fraxini* had only a single generation, and after completing their development in infested trap trees only maturation feeding took place. No evidence of the second generation was found.

Acknowledgement

The research and the publication of the results were supported by Project No. QJ1330233 of the National Agency for Agricultural Research of the Ministry of the Agriculture of the Czech Republic.

References

- Arndt, E., Unterseher, M., Morawetz, W., Klotz, S., 2007: The canopy of a temperate floodplain forest. Leipzig, Department of Systematic Botany, Botanical Garden, and Herbarium Universitatis Lipsiensis, University of Leipzig, 16 p.
- Chapman, R. F., 1958: Notes on the biology of *Hylesinus fraxini* (PZ) (Col: Scolytidae). Entomologist's Monthly Magazine, 94:45–247.
- Ciesla, W. M., 2011: Forest Entomology: A Global Perspective. Oxford, Wiley-Blackwell, 400 p.
- Culek, M., 1996: Biogeografické členění České republiky. Prague, Enigma, s. r. o., 347 p.
- Kirkendall, R. L., 1983: The evolution of mating systems in bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae). Zoological Journal of the Linnean Society, 77:293–352.
- Knížek, M., Modlinger, R., 2013: Škodliví činitelé v lesích Česka 2012/2013. Sborník referátů z celostátního semináře s mezinárodní účastí. Průhonice, 11. 4. 2013. Zpravodaj ochrany lesa, 17:28–32.
- Křístek, J., Urban, J., 2013: Lesnická entomologie. Prague, Academia, 445 p.
- Lieutier, F., Day, K. R., Battisti, A., Grégoire, J.-C., Evans, H. F., 2004: Bark and wood boring insects in living trees in Europe, a synthesis. First edition 2004, reprinted 2007. Dordrecht, Springer, 569 p.
- Loyning, M., Kirkendall, L. K., 1996: Mate discrimination in a pseudogamous bark beetle (Coleoptera: Scolytidae): male *Ips acuminatus* prefer sexual to clonal females. Oikos, 77:336–344.
- Loyning, M. K., Kirkendall, L. K., 1999: Notes on the mating system of *Hylesinus varius* [F.] (Col., Scolytidae), a putatively bigynous bark beetle. Journal of Applied Entomology, 123:77–82.
- Lozano, C., Campos, M., 1992: Oviposición y fecundidad de *Leperisinus varius* (Fabricius, 1775) (Col.: Scolytidae), en un olivar de la provincia de Granada (España). Boletín de la Asociación española de Entomología, 16:105–112.
- Marchant, K. R., 1973: Worldwide introduction and establishment of bark and timber beetles (Coleoptera: Scolytidae and Platypodidae). Burnaby, B. C., Department of Biological Sciences, Simon Fraser University, 76 p.
- Modlinger, R., Knížek, M., 2012: Lýkohubi na jasanu. Lesní ochranná služba, Lesnická práce (Supplementum), 91:I–IV.
- Novák, V., Hrozinka, F., Starý, B., 1974: Atlas hmyzích škůdců lesních dřevin. První vydání. Prague, Státní zemědělské nakladatelství, 128 p.
- Novak, L. V., Meshkov, V. L., Gamayunova, S. G., 2008: Biological peculiarities of common ash bark beetle *Hylesinus varius* (F.) (*H. fraxini* Panz.) in Kharkov region. Agroforestry: Science Collection – Kharkov. Ukrainian Research Institute of Forestry and Forest Melioration, 112:255–260.
- Pedrosa-Macedo, J.-H., 1977: Zur Bionomie, Ökologie und Ethologie des Eschenbastkäfers, *Leperisinus varius* F. (Col., Scolytidae). Journal of Applied Entomology, 88:188–204.
- Pfeffer, A., 1955: Kůrovcoviti – Scolytoidea (řád brouci – Coleoptera). Fauna ČSR sv. 6. Prague, Nakladatelství československé akademie věd, 344 p.
- Pfeffer, A., 1995: Zentral- und westpalaearktische Borken- und Kernkäfer (Coleoptera: Scolytidae, Platypodidae). Pro Entomologia, c/o Naturhistorisches Museum, Basel, 310 p.
- Pfister, A., 2012: Aktuelle Schäden durch Eschenbastkäfer in der Steiermark. Forstschutz Aktuell, 54:22–25.

- Procházka, J., 2009: Vertikální stratifikace letové aktivity kůrovců a jádrohlodů (Coleoptera: Scolytinae, Platypodinae) v lužních lesích jižní Moravy. Bakalářská práce. Brno, Masarykova univerzita, Přírodovědecká fakulta, Ústav botaniky a zoologie, 41 p.
- Rudinsky, J. A., Vallo, V., 2009: The ash bark beetles *Leperisinus fraxini* and *Hylesinus oleiperda*: stridulatory organs, acoustic signals, and pheromone production. *Journal of Applied Entomology*, 87:417–429.
- Russo, G., 1932: Contributo alla conoscenza degli scolitidi. III. Ilesinini dell'olivo. *Bollettino del Laboratorio di Zoologia Generale e Agraria della R. Scuola Superiore d'Agricoltura, Portici*, 26:87–114.
- Schlyter, F., Zhang, Q.-H., 1996: Testing avian polygyny hypotheses in insects: harem size distribution and female egg gallery spacing in three *Ips* bark beetles. *Oikos*, 76:57–69.
- Skovsgaard, J. P., Thomsen, I. M., Skovsgaard, I. M., Martinussen, T., 2010: Associations among symptoms of dieback in even-aged stands of ash (*Fraxinus excelsior* L.). *Forest Pathology*, 40:7–18.
- Teusdea, A., Fodor, E., Haruta, O., Gabor, G., 2012: Pattern recognition applied to *Ips typographus* and *Hylesinus fraxini* (Coleoptera: Scolytidae) systems of galleries. *Journal of Environmental Protection and Ecology*, 13:331–337.
- Vega, F. E., Hofstetter, R. W., 2015: *Bark Beetles: Biology and Ecology of Native and Invasive Species*. San Diego, Academic Press, 620 p.
- Wermelinger, B., 2004: Ecology and management of the spruce bark beetle *Ips typographus*—a review of recent research. *Forest Ecology and Management*, 202:67–82.