

Ips acuminatus (Gyllenhal) in the Czech Republic: Flight dynamics and adult population structure

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Abstract

Ips acuminatus is a bark beetle species that is becoming increasingly important in Central Europe, yet its phenology and reproductive patterns remain insufficiently described. Understanding its life cycle and sex ratio dynamics is essential for effective monitoring and forest protection. The study was conducted over two consecutive seasons (2021–2022) in pine (*Pinus sylvestris*) stands in the Czech Republic using Theysohn® pheromone traps baited with various attractants (including ACP and PH). Flight activity, sex ratio and mating success were recorded and analysed throughout the seasons. A univoltine life cycle was observed, with a sharp, synchronized emergence in spring, occurring in late May and June. No second generation developed, although a minor emergence in mid-summer suggested limited partial brood. Sex ratios varied seasonally, with males predominating in early spring and shifting toward female bias later in the season. Baits containing cis-verbenol and α -pinene attracted significantly more females, indicating a possible trap bias. More than 90% of females were mated, despite a lower presence of males. These results suggest that *I. acuminatus* maintains a univoltine life cycle in Central Europe. However, changing climatic conditions may lead to shifts in phenology, flight activity and sex ratio. Cautious observation is therefore recommended.

KEYWORDS

Ips acuminatus, phenology, pheromone lures, population dynamics, pseudogamy, sex ratio, voltinism

INTRODUCTION

Intrasexual competition, reflected in the ratio of males to females, is a key factor influencing the population dynamics of sexually reproducing species—from fertilization and hatching to adulthood (Girondot & Pieau, 1993; McKellar et al., 2009). According to Fisher's principle, the reproductive investment of females should be equal for male and female offspring, resulting in an approximately equal sex ratio within the population (Fisher, 1930). While variation can occur due to factors such as ploidy and sibling mating (Hamilton, 1967), a sex ratio of ~1:1 is generally expected in diploid species (James et al., 2016). However, in some cases, male production may be reduced to maximize the

reproductive output of the population over a short period of time (Hamilton, 1967). A skewed sex ratio is most commonly observed in extinct insect species (James et al., 2016). In outbreak situations, the sex ratio can temporarily shift and later return to equilibrium. In *Ips typographus* (Linnaeus, 1758), for example, the ratio of males to females can increase to 1:2.6 during outbreaks and then subsequently return to 1:1 during endemic phases (Lobinger, 1996).

The life cycle and reproduction of *Ips acuminatus* (Gyllenhal, 1827) are consistent with the general biology of polygynous bark beetles. In late spring, when temperatures exceed 14°C, the males emerge from their hibernation (Bakke, 1968; Colombari et al., 2012). A further rise in temperature above 18°C triggers swarming behaviour, causing

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males to fly in search of suitable host trees (Alonso et al., 2007; Bakke, 1968; Lekander et al., 1977). Once they have found a host – typically the upper trunk or crown of pine trees (*Pinus* sp., Linnaeus, 1753) – the males bore a nuptial chamber (NC) to attract 1–7 females, occasionally up to 12 (Bakke, 1968; Colombari et al., 2012; Kirkendall, 1990; Kohnle et al., 1988; Loyning et al., 1996). After copulation, each female excavates a radial system of maternal galleries (MGs) extending from the NC (Hamilton, 1967), where she lays between 4 and 16 eggs in niches along both sides of the gallery (Colombari et al., 2012). The resulting offspring typically have a sex ratio of approximately 1:2 (males: females) (Hamilton, 1967). In northern Europe, populations of *I. acuminatus* are typically univoltine (Bakke, 1968), while in southern Europe, they can be bivoltine under favourable climatic conditions (Colombari et al., 2012; Hernández et al., 2004), often without the formation of sister broods (Pérez & Sierra, 2006). However, up to four sister broods have been reported in previous studies (Vallet, 1981). The presence of pseudogamous females with triploid genotypes significantly increases the sex ratio in *Ips acuminatus* populations up to 1:37.6 (M:F) (Bakke, 1968) – due to the higher survival rate of asexually produced offspring – mother clones. Like sexual females, pseudogamous strains also require sperm to trigger egg maturation (Bakke, 1968). Since males generally prefer to mate with sexual females, pseudogamous females must persuade males to accept them as mates (Kirkendall, 1990; Loyning et al., 1996). This often happens with young, inexperienced males, that become sexually mature shortly before mating and offer clonal females the opportunity to “trick” the male into copulation. The probability of fertilization increases with the density of females (Loyning et al., 1996). However, the limited availability of males in highly female-biased populations restricts the number of females capable of fertilization. Therefore, the proportion of mated females in such populations is generally low, ranging from 10% to 20% (Kirkendall, 1990). At the end of the season, the adult beetles search for hibernation sites, with about 90% hibernating under the bark and 10% in the forest litter (Colombari et al., 2012; Francke-Grosman, 1963; Lekander et al., 1977). Although hibernation typically occurs in the adult stage, recent observations have also reported hibernation of larvae and pupae, despite their sensitivity to frost (Meshkova et al., 2021). The tertiary sex ratio and the occurrence of pseudogamous females in populations of *Ips acuminatus* have been thoroughly studied in northern Europe (Bakke, 1968). However, data on central European populations remain scarce. With the recent increase in the local abundance of *I. acuminatus* (Foit & Čermák, 2014; Liška et al., 2021; Švestka, 2001), insights into the reproductive capacity and phenology of the species could improve predictive models for population dynamics and increase the effectiveness of monitoring and management strategies. In addition, the proportion of pseudogamous females within a population could serve as a useful indicator of population growth in newly colonized areas. The aim of the present study was therefore: (1) to evaluate the seasonal phenology under Central European conditions; (2) to analyse sex ratio in

populations of *I. acuminatus*; (3) to assess the potential rate of pseudogamous females; (4) to evaluate the effectiveness of different pheromone lures as suitable monitoring methods for *Ips acuminatus* in the Czech Republic.

MATERIALS AND METHODS

Study sites, phenology and seasonal dynamics

Changes in the sex ratio and the occurrence of pseudogamous females during the growing season were investigated at three locations in the Czech Republic in 2021 and 2022: Brandýs nad Labem–Stará Boleslav (L1) in Central Bohemia, GPS: 50.2109 N, 14.7128 E, altitude: 190 m a.s.l.; Bzenec (L2) in South Moravia, GPS: 48.9498 N, 17.2159 E, altitude: 230 m a.s.l.; Šemíkovice (L3) in the Jevíšovická Highlands, South Moravia, GPS: 49.0487 N, 16.0878 E, altitude: 410 m a.s.l. At each site, 12 Theysohn traps were set and baited with three specific pheromone baits—Acumiprotect (ACP), Acuwit (AW), Pheagr IAC (PH)—alongside one additional trap containing non-specific bait, Sexowit (SX) (Table 1). Each bait type was replicated three times. Samples were collected weekly from April to September and transported to the laboratory for sex determination. The sex ratio was then calculated as the ratio of males to females ($\delta\delta:\varphi\varphi = 1:x$) based on the total number of adults recorded in each sample (Figure 1).

The temperature data were collected using data loggers that were present at the site during the period of the experiment. The loggers recorded temperature at 30-min intervals, allowing the calculation of daily maximum ($T_{\max}$), minimum ($T_{\min}$) and average (T_{avg}) values. The precipitation data were taken from the METEOBLUE (2006–2023) (Figures 2 and 3).

The thermal sum for the emergence flight corresponds to an accumulation of degree days (DD), calculated according to the following equation: $\left(\frac{T_{\min}+T_{\max}}{2}\right) - T_{\text{baseline}}$. $T_{\min}$ refers to the daily minimum temperature, $T_{\max}$ to the daily maximum temperature and T_{baseline} to the lower emergence temperature in spring (Bessin & Villanueva, 2019) which was estimated at 6°C for *I. acuminatus* (Colombari et al., 2012).

Mating success

To investigate the ratio of mated and non-mated females in the MGs, all *I. acuminatus* females present were obtained from nine unbaited trap trees present at all study sites. The trap trees at L2 were non-baited with *Ips acuminatus* and were therefore not included in the results. The trap trees were placed 6–7 m from the forest edge at the sites in the clear-cut area at the beginning of the growing season (April 2021 and 2022). In the second half of July, when the trap trees contained advanced gallery systems of *I. acuminatus*, the trap trees were cut into one-meter-long sections and brought to the laboratory. A total of 139 sections were debarked, of which 22 sections

TABLE 1 An overview of synthetic pheromone baits used at selected sites during the growing season in both study years.

Product name	Acumiprotect	Acuwit	Pheagr IAC	Sexowit
Manufacturer	SEDQ s.l., Barcelona, Spain	Witasek-Pflanzenschutz GmbH, Feldkirchen, Austria	Scitech s.r.o., Prague, the Czech Republic	Witasek-Pflanzenschutz GmbH, Feldkirchen, Austria
Composition	Ipsenol, ipsdienol, cis-verbenol	Ipsenol, ipsdienol	Ipsdienol, ipsenol, cis-verbenol	2 phenylethanol, ipsdienol, α -pinene
Targeted species	<i>Ips acuminatus</i>	<i>Ips acuminatus</i>	<i>Ips acuminatus</i>	<i>Ips sexdentatus</i>

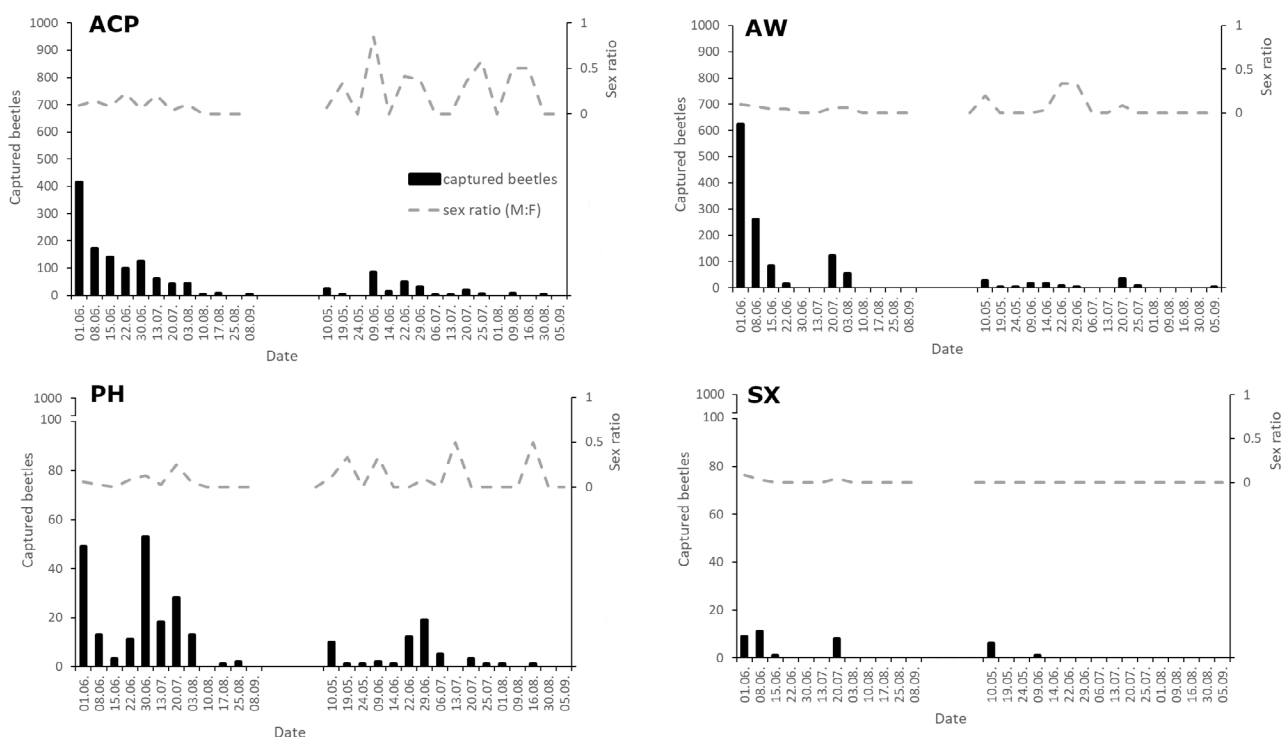


FIGURE 1 A number of *Ips acuminatus* beetles caught with different pheromone baits: ACP (Acumiprotect), AW (Acuwit), PH (Pheagr IAC), SX (Sexowit) using Theysohn traps ($N = 72$). The X-axis shows the date of sampling in 2 consecutive years (2021, 2022). The left Y-axis shows the number of beetles caught and the right Y-axis shows the sex ratio (male: Female).

showed signs of *I. acuminatus* infestation. From these sections, individual harems with all adult beetles present (parent, sister and offspring generations) were collected and placed into individually labelled microtubes and stored in a freezer until dissection. The number of NCs, MGs, eggs and larval galleries in each section was recorded.

Anatomy of the spermatheca (SPQ)

The spermatheca (SPQ) of *I. acuminatus* is a sclerotized C-shaped organ at the base of the female reproductive system (RS) (Figure 4). The vas deferens (SD) connects the SPQ to the RS at approximately the point where the genital chamber opens into the common oviduct (OC). The external opening of the accessory gland (AG) is also located at this point (Figure 4). At the tip of the SPQ is the sperm gland (SGL),

a collection of cells specialized in secretion whose function is unclear (Davey, 1985; Román-Ruiz et al., 2017).

Spermathecae staining

All *Ips acuminatus* females (including parent, sister and offspring generations) found in tree trunks at sites L1 and L3 in 2021 were collected for spermathecae staining. Ovaries with spermathecal pumps (SPs) were dissected in Ringer's solution under a Leica S6D microscope (Leica AG, Wetzlar, Germany), placed on microscope slides and stained to visualize spermatozoa using the May-Grünwald-Giemsa method, which has previously been applied to carabids, mosquitoes and occasionally to Scolytinae (Helinski & Knols, 2009; Román-Ruiz et al., 2017; Takami, 2002). Staining of the slides was performed as follows: After air-drying for 20 min, the samples were fixed in 100%

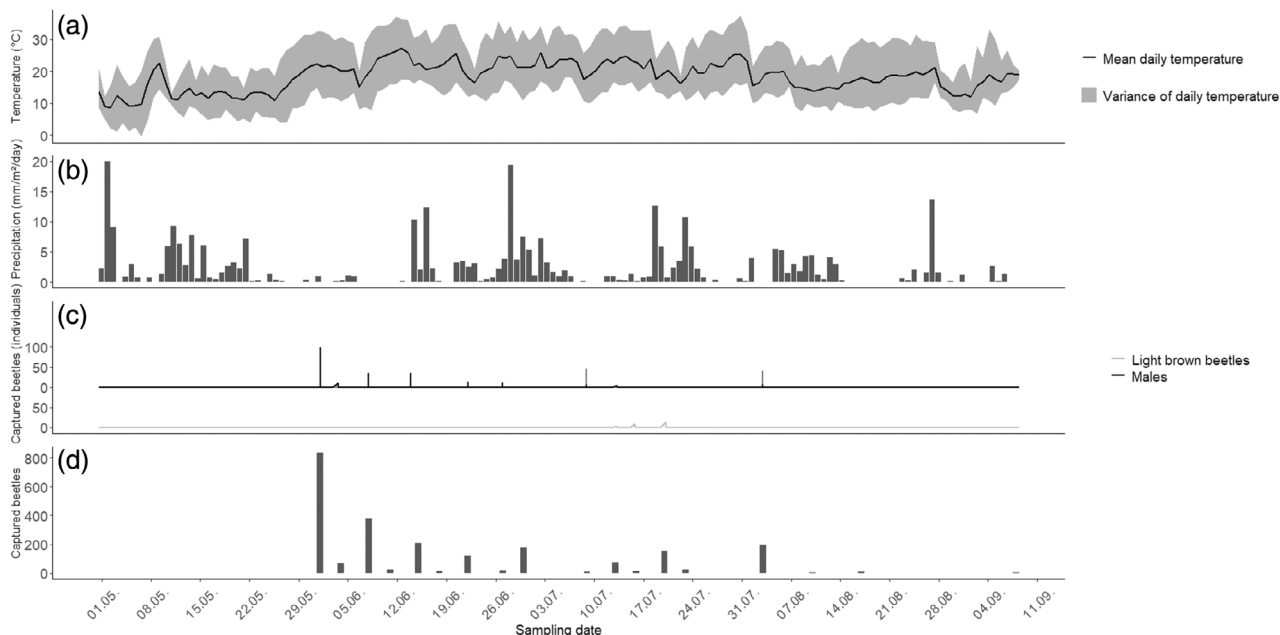


FIGURE 2 Flight activity of *Ips acuminatus* in 2021 (d) as a function of daily temperature (°C) (a) and precipitation ($\text{mm m}^{-2}.\text{day}^{-1}$) (b). The occurrence of males and light brown beetles throughout the season is also shown (c).

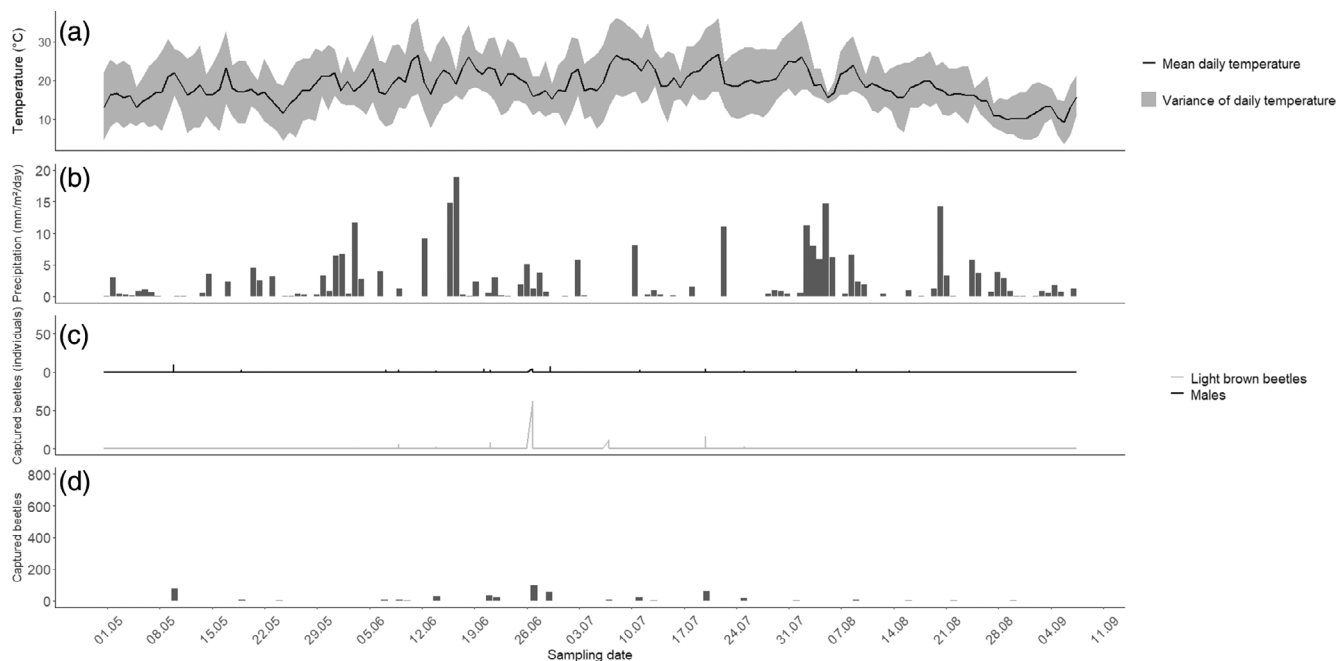


FIGURE 3 Flight activity of *Ips acuminatus* in 2021 (d) as a function of daily temperature (°C) (a) and precipitation ($\text{mm m}^{-2}.\text{day}^{-1}$) (b). The occurrence of males and light brown beetles throughout the season is also shown (c).

methanol for 30 min. This was followed by a two-step staining process- first with May-Grünwald solution at pH 6.8 for 8 min and then with Giemsa solution for 10 min. The stained samples were thoroughly rinsed with Sörensen buffer (twice for 1 min and once for 5 min), followed by a rinse in distilled water (once for 2 min and once for 5 min). After 30 min of drying, the slides were sealed with DePex mounting medium (Serva GmbH, Heidelberg, Germany). To facilitate

visualization of the spermatozoa, the SPs were repositioned immediately after application of DePex by gently pressing the coverslip. The embedding medium was cured overnight, and the contents of each SPQ were examined under an Olympus BX51 bright-field microscope (Olympus Inc., Tokyo, Japan) using immersion oil (type F for fluorescence/general microscopy, $n_e = 1.518$, $n_g = 1.41$; 23°C, Olympus Inc., Tokyo, Japan). Observations were performed at 400 $\times$ and 1000 $\times$

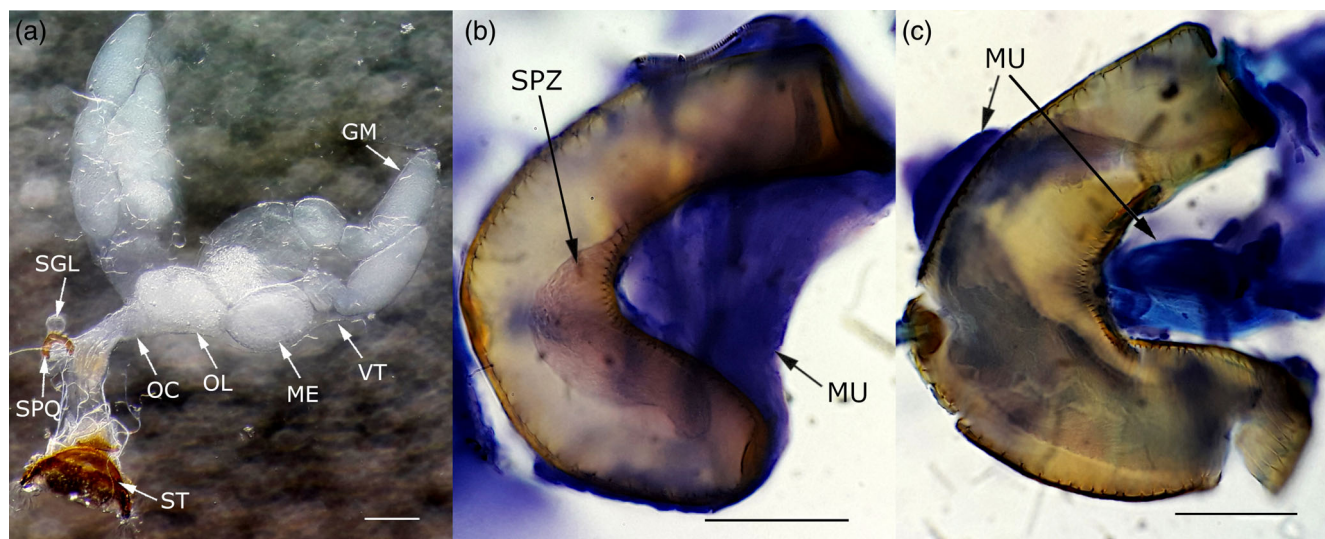


FIGURE 4 Reproductive system (a) and spermathecal pumps (SP) after May-Grünwald-Giemsa staining (b, c) of *Ips acuminatus* females (b, SP with spermatozoa; c, an empty SP); GM, germarium; VT, vitellarium; OL, lateral oviduct; OC, common oviduct; ME, mature egg; SPQ, spermatheca; SGL, sperm gland; ST, sternite; MU, spermathecal muscles; SPZ, spermatozoa. Scale bar: 20 µm.

magnification, and images were captured using the Olympus DP74 camera (Olympus Inc., Tokyo, Japan). Based on the observed number of spermatozoa, SPs were placed into three categories: empty, with few spermatozoa and full. All procedures were performed at room temperature.

Statistics

All statistical analyses were performed in R (version 4.3.3; R Core Team, 2024) on Windows 11 × 64 (build 26,100). Before a test was performed, the normality of the data was estimated with the omnibus normality test by D'Agostino and Pearson using the package moments (version 0.14.1; Komsta & Novomestky, 2022).

Pheromone lure attractiveness and the influence of location and year were tested by fitting generalized linear mixed models for Poisson distributed data using the package lme4 (version 1.1.35.2; Bates et al., 2015) and Matrix (version 1.6.5; Bates et al., 2024). The inclusion of our locations (L1, L2, L3) and trap location as a random effect (1|location:trap location) in the model served to account for a nested design. We included season and the bait as fixed-effects variables. Maximum likelihood (ML) estimation and BOBYQA were also used to optimize the model. We compared our model with simplified models that included locality as the only covariate to assess the significance of the treatment. Subsequent post hoc comparisons were also performed to determine the comparative effectiveness of baits for parametric models, with rudimentary adjustment of *p*-values (stepwise method) facilitated by the 'glht' function from the R package multcomp (version 1.4–25, Hothorn et al., 2008). Other statistical packages were used to estimate the results: magrittr (version 2.0.3; Bache & Wickham, 2022), DHARMa (version 0.4.7; Hartig, 2024), report (version 0.6.1; Makowski et al., 2023), GLMMadaptive (version

0.9.7; Rizopoulos, 2025), MASS (version 7.3.60.0.1; Venables & Ripley, 2002) and ggplot2 (version 3.5.1; Wickham, 2016).

Data visualization was performed with the packages lubridate (version 1.9.3; Grolemund & Wickham, 2011), report (version 0.6.1; Makowski et al., 2023), tibble (version 3.2.1; Müller & Wickham, 2023), patchwork (version 1.3.0; Pedersen, 2024), ggplot2 (version 3.5.1; Wickham, 2016), forcats (version 1.0.0; Wickham, 2023a), stringr (version 1.5.1; Wickham, 2023b), tidyverse (version 2.0.0; Wickham et al., 2019), dplyr (version 1.1.4; Wickham et al., 2023), purrr (version 1.0.2; Wickham & Henry, 2023), readr (version 2.1.5; Wickham, Hester, & Bryan, 2024) and tidyr (version 1.3.1; Wickham, Vaughan, & Girlich, 2024).

RESULTS

Attractiveness of pheromone lures

The number of *Ips acuminatus* beetles caught per bait type differed significantly ($df = 23$, $\chi^2 = 348.1$, $p < 0.001$) (Figure 5) depending on the bait used. Compared to the baseline (ACP), which was given as a model intercept (Estimate = 3687.55, SE = 40.01, $z = 92.17$, $p < 0.001$), all lures showed a significant decrease in attractiveness: AW (Estimate = −0.567, SE = 0.042, $z = -13.40$, $p < 0.001$), PH (Estimate = −1.586, SE = 0.062, $z = -25.66$, $p < 0.001$) and SX (Estimate = −3.577, SE = 0.154, $z = -23.15$, $p < 0.001$). Pairwise tests revealed significant differences between all bait types ($p < 0.0001$). In addition, the model revealed a significant seasonal effect (Estimate = −1.824, SE = 0.02, $z = -92.12$, $p < 0.001$).

The random effects showed no significant variability between locations and trap positions (variance = 0.885, SD = 0.94).

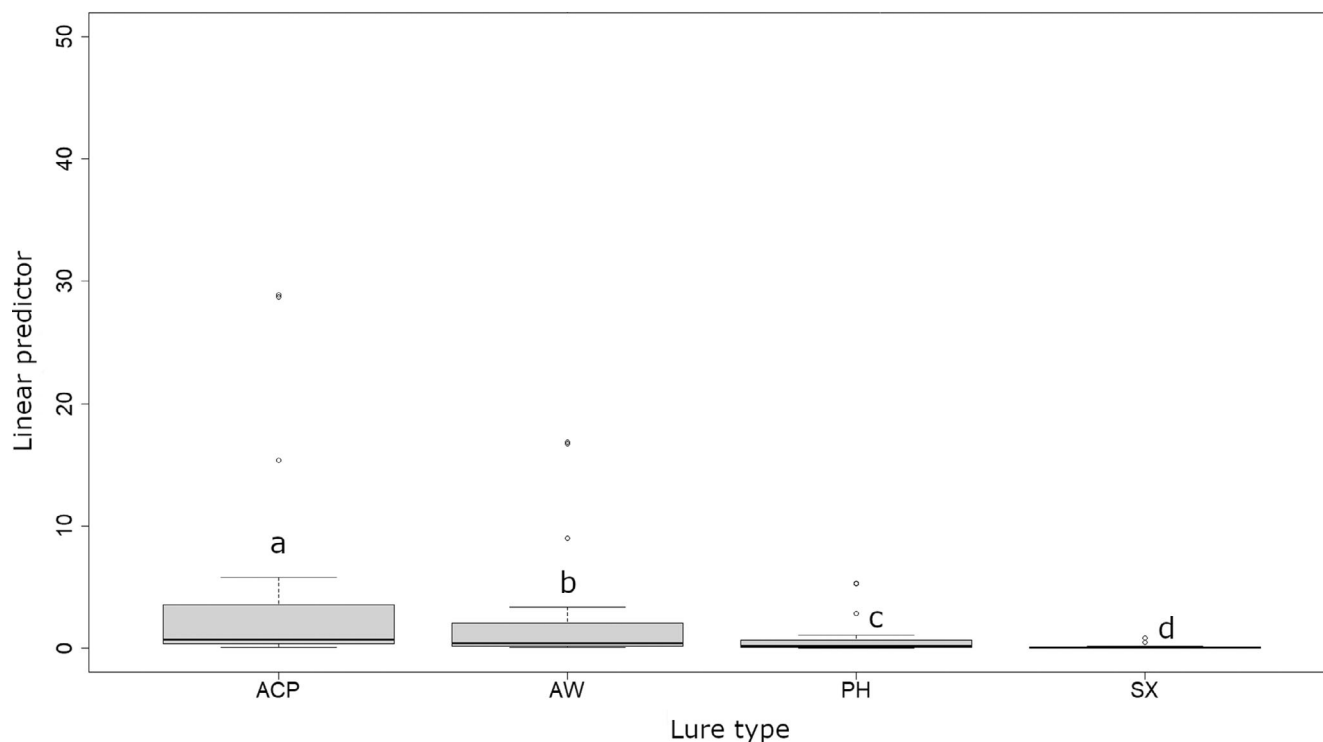


FIGURE 5 Effectiveness of the pheromone lure of *Ips acuminatus* during trapping. Different letters above the boxplots indicate statistically significant differences ($p < 0.05$). The X-axis shows the type of bait used: ACP (Acumiprotect), AW (Acuwit), PH (Pheagr IAC) and SX (Sexowit). The Y-axis shows a linear predictor related to a combination of factors considered in the model (location, season, sex, trap position).

Phenology, abundance and sex ratio

In the two growing seasons 2021 and 2022, a total of 2728 adult *I. acuminatus* were caught at our sites. In 2021, 2258 beetles were caught, but in 2022, the catch rate decreased significantly ($Z = 13.876$, $p < 0.01$), namely by a factor of 4.8, so that only 470 beetles were caught. The sex ratio of the beetles caught was 1:8.29 ($\delta\delta$: $\varphi\varphi$) in 2021 and 1:7.87 ($\delta\delta$: $\varphi\varphi$) in 2022. The catches and the sex ratio (range: 10.76–11.28% $\delta\delta$, 88.72–89.24% $\varphi\varphi$) differed between the years but also between the sites ($\chi^2 = 32.946$, $df = 2$, $p < 0.001$; range: 123–1926 individuals).

In 2021, the number of adult bark beetles caught showed a multimodal pattern (Figure 2). The first and most pronounced peak occurred between May 28 and June 2 (pre-flight thermal sum – 346.3 ± 3.15 DD), with the highest number of individuals recorded on May 29, when more than 800 beetles were captured in a single sampling event. This peak coincided with a period of increased daily temperatures, with minimums exceeding 10°C and maximums reaching 25 – 30°C with less temperature variability. Several precipitation events were recorded during this period, with daily precipitation reaching up to 10 mm m^{-2} . Male beetles were first observed between May 28 and 30, and light brown beetles appeared around July 14. After this initial peak, smaller increases in catch numbers were recorded around June 24, July 10 and

August 2. These dates coincided with periods of sustained warm weather, with daily highs above 20°C . Rainfall events occurred around June 26 and again on July 17, with daily totals occasionally exceeding 10 mm m^{-2} . Male beetles were detected again on July 10 and around August 3, coinciding with the secondary and tertiary increase in catches. Offspring were observed between July 10 and July 20, about 6–8 weeks after the initial flight peak. After early August, total catches gradually declined, becoming sporadic in mid-August and ceasing altogether in mid-September.

In 2022, adult bark beetle catches were low and irregular, with no clear peak in emergence (Figure 3). The emergence flight took place when the thermal sum exceeded 220.2 ± 21.1 DD. The highest number of beetles was recorded on May 8, when almost 250 individuals were captured. Smaller numbers were also observed between June 15 and 26 and again on July 20. The first captures coincided with an early rise in daytime temperatures at the end of April and the beginning of May, where maximum temperatures were above 20°C and minimum temperatures remained above 10°C . This early activity also followed a period of low but continuous rainfall. The first male beetles were detected from May 7, with the maximum around June 26. After the initial activity in May, further catches remained low and sporadic throughout the season. A second increase in catches between late June and early July coincided with stable warm temperatures, with daily highs around 25°C and moderate rainfall (up to

10–15 mm m⁻² day⁻¹). During this period, male beetles were discovered again from the beginning of August. Light brown beetles were recorded from June 26 to July 25, about 7–11 weeks after the first emergence in early May. From August onwards, overall catch numbers were very low and activity ceased in mid-September.

Study of MGs

Signs of *Ips acuminatus* infestation were documented on trap trees at sites L1 (in both years) and L3 (in 2021). At both sites, the mean infestation density reached 0.32 ± 0.27 NCs per dm², with a total of 284 NCs recorded. At site L1, the NCs were located exclusively in the trunk sections, while at L3, they were distributed over different parts of the trees: 22.4% in the trunk, 50% in the crown and 27.6% in the branches. The mean number of females per harem was 2.87 ± 1.35 (range: 1–14), with greater variability at L3 (SD = 2.51) than at L1 (SD = 0.18).

A total of 815 MGs were found on all trap trees. Of these, only 57 (7.0%) were occupied by adult beetles. On L1, 44 inhabited MGs were found, of which 39 (88.6%) were male-free and 35 (79.5%) were single-armed. The average egg deposition was 16.6 ± 3.30 eggs per gallery, and the average hatching success was $24.08 \pm 16.44\%$. Males were present only sporadically in the galleries: five individuals (7.6% of all beetles), all dark brown. Four of these males bored their NCs, and one was part of a harem. In contrast, females made up 90.2% of the beetles present, of which 96.15% were dark-coloured and 3.85% were light-coloured. Pupae were rare and accounted for about 2.2% of the individuals found in the galleries. Other developmental stages were not present.

Spermatheca and mating status

A total of 87 females of *I. acuminatus* were collected from MGs at sites L1 (54 individuals) and L3 (25 individuals). However, the mating status and condition of the spermathecal pump could only be examined in 40 females due to the relatively high presence of parasitic wasps (25.6%), entomopathogenic fungi (3.7%) and dead individuals (14.8%). At the time of dissection, each female contained an average of 2.37 ± 3.16 eggs (mean $\pm$ SD; range: 0–8), with 0.61 ± 0.79 eggs per oviduct (mean $\pm$ SD; range: 0–3). After isolation and staining of the spermathecae (Figure 4), spermatozoa were observed in 39 SPQ (90.7%). Of these, 28 SPQ (65.1%) were full, 11 SPQ (25.6%) contained a small number of spermatozoa and 4 SPQ (9.3%) were empty.

DISCUSSION

Although southern European populations of *Ips acuminatus* are known to emerge as early as April (Colombiari et al., 2012), the populations studied exhibited a consistent pattern across both 2021 and 2022. Their flight activity resembled the univoltine pattern typically observed

in northern or cooler regions (Bakke, 1968). Spring swarming started relatively late, in May and June, and was concentrated in a single, sharp and synchronized flight event. The late onset can be attributed to a later termination of hibernation, probably caused by suboptimal weather conditions in spring (Gehrken, 1985), in our case the unstable spring temperatures. A comparable trend has been observed in Norwegian populations at the northern edge of the species' range distribution (Bakke, 1968); this region has a more continental climate—characterized by lower humidity and higher temperatures—and where seasonal activity tends to occur later (Bakke, 1968). In both years, males were the dominant sex recorded during the first emergence, while juvenile beetles emerged mainly in June, indicating the formation of a partial brood, but with limited emergency, as this did not result in a secondary flight. Although the similarities in phenology point to northern rather than southern populations (Bakke, 1968; Colombiari et al., 2012), these traces of the formation of a new brood suggest a high flexibility in the voltinism of *I. acuminatus* and a likelihood of additional generations in the Czech Republic in the future, due to changing climatic conditions.

According to the observations of Bakke's (1968), the northern populations of *Ips acuminatus* exhibit a strongly female-biased sex ratio among the emerging beetles. In contrast, the sex ratio in our study fluctuated around 0.5 (0.2–0.7), with females marginally outnumbering males throughout the season—with the exception of spring emergence, when males predominated. This seasonal dynamic indicates a balanced sex ratio (Fisher, 1930), and compared to *I. sexdentatus* and *I. cembrae*, the observed sex ratio values are very similar (0.3–1) (Ettebest et al., 2013; Špoula & Kula, 2023). In contrast, the sex ratio is almost 1.5 times lower than that of *I. typographus* (Faccoli & Buffo, 2004). However, an increased proportion of males during first emergence in spring is characteristic of all species mentioned (Faccoli & Buffo, 2004; Ettebest et al., 2013; Špoula & Kula, 2023). This is not surprising, as *Ips* males typically act as pioneer beetles and initiate colonization of the host substrate in spring (Faccoli & Buffo, 2004; Gara, 1964; Kirkendall, 1983). Compared to other studies (Colombiari et al., 2012; Guérard et al., 2000), the relatively low infestation density of *I. acuminatus* observed at our sites indicates an endemic population status (Botterweg, 1982; Lobinger, 1996; Netherer & Pennerstorfer, 2001; Wermelinger, 2004). Several factors may contribute to the lower proportion of males and thus the overall sex ratio—such as pre-imaginal mortality of males due to greater sensitivity to environmental stressors (Ayres et al., 2000; Bentz & Mullins, 1999; James et al., 2016; Lachowsky & Reid, 2014; Régnière & Bentz, 2007; Reid & Purcell, 2011; Safranyik et al., 1999) and a reduction in males during the process of host colonization (Botterweg, 1982; Faccoli & Buffo, 2004). Considering the limited number of males observed, it appears that Central European populations may experience pre-imaginal male mortality, similar to southern populations (Colombiari et al., 2012). Coinciding with ongoing climatic changes, this trend could shift the sex ratio in favor of females in the future, as has been documented in *D. ponderosae* (Safranyik et al., 2010). Despite the low proportion of males in our populations, high mating success (>90%) among females suggests that sperm limitation was unlikely in this population (Kirkendall, 1990). Finally, the observed sex ratio cannot be attributed to a lack of food, as

the Scots pine stands at our study sites were sufficiently dense (Bakke, 1968).

Similar to other Scolytinae (e.g., *Ips tridentis* Mannerheim, 1852; *Ips borealis* Swaine, 1911; *Ips perturbatus* Eichhoff, 1869; *Ips pilifrons* Swaine, 1912, and *Pityophthorus puberulus* LeConte, 1868) (Deyrup & Kirkendall, 1983; Hopping, 1964; Kirkendall et al., 2015; Lanier & Oliver, 1966), a skewed sex ratio can also be influenced by the presence of sperm-dependent parthenogenetic females (Kirkendall, 1993). However, the detection of pseudogamy in *I. acuminatus* is difficult due to the monomorphic nature of the females (Bakke, 1968). The presence of pseudogamous females at our sites may be interfered with by a modest increase in female captures approximately 4–6 weeks following the spring flight, potentially reflecting a re-emergence to establish a sister brood – mirroring the pattern documented in *Ips confusus* (LeConte, 1876) and *I. typographus* (Cameron & Borden, 1967; Davidková & Doležal, 2017). However, our results, especially the observed presence of males during this period, are consistent with previous studies (Chinellato et al., 2014; Colombari et al., 2012; Pérez & Sierra, 2006), which could not confirm such events. This suggests that the differences in reproductive success are probably not due to local weather conditions or altitude (difference range: 500–1600 m a.s.l.) (Chinellato et al., 2014; Colombari et al., 2012; Pérez & Sierra, 2006). On the other hand, weather conditions may explain the variation in the onset of spring flight and the duration of development per generation, which lasted 6–8 weeks in 2021 but increased to 7–11 weeks in 2022. A similar trend was observed in southern populations of *I. acuminatus* and *I. typographus*, where suboptimal spring temperatures significantly prolonged development time (Chinellato et al., 2014; Colombari et al., 2012; Faccoli, 2009). Alternatively, the favourable thermal conditions in the first year of the study may have had a negative effect on the population in the following year (Chinellato et al., 2014). From our results, it can be concluded that the populations of *Ips acuminatus* in the Czech Republic have a univoltine life cycle with the possibility of a second generation.

The limitation of this work lies in the type of traps used. Although the Theysohn® type traps used in our study mimic the host substrate well and elicit landing behaviour (Faccoli & Buffo, 2004), the effect could be biased due to sex-specific preferences (Faccoli & Buffo, 2004). Certain components found in pheromone lures, such as cis-verbenol and α -pinene, could influence the sex ratio as observed in *Ips typographus* (Schlyter et al., 1987). Such an effect of cis-verbenol on the sex ratio of captured beetles could account for the significantly higher proportion of females caught in traps baited with ACP and PH. Ipsenol and ipsdienol could also have some influence on the sex ratio bias, as their main purpose is to attract females into a NC during the initial phase of the attack (Francke et al., 1986). However, the effect on males is not yet known, so further experiments should be carried out.

CONCLUSIONS

The results of the present study indicate that *Ips acuminatus* has a univoltine life cycle, with flight activity beginning in May, peaking in mid-

June and ending in August. No signs of a distinct second flight were observed in the populations monitored. Although small and scattered captures of first-generation adults occurred in June, these did not lead to a second emergence. The sex ratio was generally male-biased at the beginning of spring and showed a slight prevalence in favor of females as the season progressed, which differed slightly depending on the year and pheromone lure. Although the fertilization rate in our populations was more than 90%, we were unfortunately unable to identify the clonal and sexual females. Among the lures tested, ACP proved to be the most attractive, while both ACP and PH showed moderate differences in sex ratio. These results suggest that a combination of ACP and PH lures could be an effective tool for monitoring the flight dynamics of *I. acuminatus*.

AUTHOR CONTRIBUTIONS

Conceptualization, methodology, validation: Petr Doležal. *Formal analysis:* Daniela Hlávková. *Investigation:* Petr Doležal, Markéta Davidková, Jana Koudelková, and Daniela Hlávková. *Resources:* Petr Doležal. *Data curation:* Daniela Hlávková. *Writing—original draft preparation:* Daniela Hlávková. *Writing—review and editing:* Petr Doležal and Daniela Hlávková. *Visualization:* Daniela Hlávková. *Supervision, project administration, funding acquisition:* Petr Doležal.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in [Zenodo]: Hlávková et al. (2025) at <https://doi.org/10.5281/zenodo.16325731>.

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REFERENCES

- Alonso, R.H., Pérez, V., Sánchez, G., Castella, J., Palencia, J., Gil, J.M. et al. (2007) Ensayos de trapeo de escolítidos perforadores subcorticales

- en pinas mediante el uso de feromonas 2002–2005. *Ecología*, 21, 43–56.
- Ayres, M.P., Wilkens, R.T., Ruel, J.J., Lombardero, M.J. & Vallery, E. (2000) Nitrogen budgets of phloem-feeding bark beetles with and without symbiotic fungi. *Ecology*, 81(8), 2198–2210. Available from: [https://doi.org/10.1890/0012-9658\(2000\)0812198:NBOPF](https://doi.org/10.1890/0012-9658(2000)0812198:NBOPF)
- Bache, S. & Wickham, H. (2022) magrittr: a forward-pipe operator for R. R package version 2.0.3. Available from: <https://CRAN.R-project.org/package=magrittr>
- Bakke, A. (1968) Field and laboratory studies on sex ratio in *Ips acuminatus* (Coleoptera: Scolytidae) in Norway. *Canadian Entomologist*, 100, 640–648. Available from: <https://doi.org/10.4039/Ent1006406>
- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. Available from: <https://doi.org/10.18637/jss.v067.i01>
- Bates, D., Maechler, M. & Jagan, M. (2024) Matrix: sparse and dense matrix classes and methods. R package version 1.6–5. Available from: <https://CRAN.R-project.org/package=Matrix>
- Bentz, B.J. & Mullins, D.E. (1999) Ecology of mountain pine beetle (Coleoptera: Scolytidae) cold hardening in the intermountain west. *Environmental Entomology*, 28(4), 577–587. Available from: <https://doi.org/10.1093/ee/28.4.577>
- Bessin, R. & Villanueva, R. (2019) *Predicting insect development using insect degree days*. Cooperative extension service. Lexington, KY: University of Kentucky College of Agriculture, Food and Environment. Available from: <https://entomology.ca.uky.edu/ef123> [Accessed 3st February, 2023].
- Botterweg, P.F. (1982) Dispersal and flight behaviour of the spruce bark beetle *Ips typographus* in relation to sex, size and fat content. *Zeitschrift für Angewandte Entomologie*, 94(1–5), 466–489. Available from: <https://doi.org/10.1111/j.1439-0418.1982.tb02594.x>
- Cameron, E.A. & Borden, J.H. (1967) Emergence patterns of *Ips confusus* (Coleoptera: Scolytidae) from ponderosa pine. *Canadian Entomology*, 99(3), 236–244. Available from: <https://doi.org/10.4039/ent99.236-3>
- Chinellato, F., Battisti, A., Finozzi, V. & Faccoli, M. (2014) Better today but worse tomorrow: how warm summers affect breeding performance of a scots pine pest. *Agrochimica*, 58, 133–145.
- Colombiari, F., Battisti, A., Schroeder, L.M. & Faccoli, M. (2012) Life-history traits promoting outbreaks of the pine bark beetle *Ips acuminatus* (Coleoptera: Curculionidae, Scolytinae) in the south-eastern Alps. *European Journal of Forest Research*, 131(3), 553–561. Available from: <https://doi.org/10.1007/s10342-011-0528-y>
- Davey, K.G. (1985) The female reproductive tract. In: Kerkut, G.A. & Gilbert, L.I. (Eds.) *Comprehensive insect physiology, biochemistry and pharmacology*. Oxford: Pergamon Press, pp. 15–36.
- Davidková, M. & Doležal, P. (2017) Sister broods in the spruce bark beetle, *Ips typographus* (L.). *Forest Ecology and Management*, 405, 13–21. Available from: <https://doi.org/10.1016/j.foreco.2017.08.040>
- Deyrup, M. & Kirkendall, L.R. (1983) Apparent parthenogenesis in *Pityophthorus puberulus* (Coleoptera: Scolytidae). *Annals of the Entomological Society of America*, 76(3), 400–402. Available from: <https://doi.org/10.1093/aesa/76.3.400>
- Etchebeste, I., Lencina, J.L. & Pajares, J. (2013) Saproxylic community, guild and species responses to varying pheromone components of a pine bark beetle. *Bulletin of Entomological Research*, 103(5), 497–510. Available from: <https://doi.org/10.1017/S0007485312000879>
- Faccoli, M. (2009) Effect of weather on *Ips typographus* (Coleoptera Curculionidae) phenology, voltinism, and associated spruce mortality in the southeastern Alps. *Environmental Entomology*, 38(2), 307–316. Available from: <https://doi.org/10.1603/022.038.0202>
- Faccoli, M. & Buffo, E. (2004) Seasonal variability of sex-ratio in *Ips typographus* (L.) pheromone traps in a multivoltine population in the southern Alps. *Journal of Pest Science*, 77(3), 123–129. Available from: <https://doi.org/10.1007/s10340-003-0038-x>
- Fisher, R.A. (1930) *The genetical theory of natural selection*. Oxford: Clarendon Press. Available from: <https://doi.org/10.5962/bhl.title.27468>
- Foit, J. & Čermák, V. (2014) Colonization of disturbed scots pine trees by bark- and wood-boring beetles. *Agricultural and Forest Entomology*, 16(2), 184–195. Available from: <https://doi.org/10.1111/afe.12048>
- Francke, W., Pan, M.-L., Bartels, J., König, W.A., Vité, J.P., Krawielitzki, S. et al. (1986) The odour bouquet of three pine engraver beetles (*Ips* spp.). *Journal of Applied Entomology*, 101(1–5), 453–461. Available from: <https://doi.org/10.1111/j.1439-0418.1986.tb00879.x>
- Francke-Grosman, H. (1963) Die Übertragung der Pilzflora bei dem Borkenkäfer *Ips acuminatus* Gyll.: Ein Beitrag zur Kenntnis der Ipiden-Symbiosen. *Zeitschrift für Angewandte Entomologie*, 52, 355–361. Available from: <https://doi.org/10.1111/j.1439-0418.1963.tb02046.x>
- Gara, R.I. (1964) Studies on the flight behaviour of *Ips confusus* (Lec.) (Coleoptera: Scolytidae) in response to attractants [Ph.D. thesis]. Oregon State University, Corvallis, OR, United States. Available from: https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/7w62fc462?locale=en [Accessed: 10th July 2025].
- Gehrken, U. (1985) Physiology of diapause in the adult bark beetle, *Ips acuminatus* Gyll., studied in relation to cold hardiness. *Journal of Insect Physiology*, 31(12), 909–916. Available from: [https://doi.org/10.1016/0022-1910\(85\)90024-1](https://doi.org/10.1016/0022-1910(85)90024-1)
- Girondot, M. & Pieau, C. (1993) Effects of sexual differences of age at maturity and survival on population sex ratio. *Evolutionary Ecology*, 7(6), 645–650. Available from: <https://doi.org/10.1007/bf01237827>
- Grolemund, G. & Wickham, H. (2011) Dates and times made easy with lubridate. *Journal of Statistical Software*, 40(3), 1–25. Available from: <https://www.jstatsoft.org/v40/i03/>.
- Guérard, N., Dreyer, E. & Lieutier, F. (2000) Interactions between scots pine, *Ips acuminatus* (Gyll.) and *Ophiostoma brunneo-ciliatum* (math.): estimation of the critical thresholds of attack and inoculation densities and effects on hydraulic properties in the stem. *Annals of Forest Science*, 57(7), 681–690. Available from: <https://doi.org/10.1051/forest:2000149>
- Hamilton, W.D. (1967) Extraordinary sex ratios. *Science*, 156(3774), 477–488. Available from: <https://doi.org/10.1126/science.156.3774.477>
- Hartig, F. (2024) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.7. Available from: <https://CRAN.R-project.org/package=DHARMa>
- Helinski, M.E.H. & Knols, B.G.J. (2009) Sperm quantity and size variation in un-irradiated and irradiated males of the malaria mosquito *Anopheles arabiensis* Patton. *Acta Tropica*, 109(1), 64–69. Available from: <https://doi.org/10.1016/j.actatropica.2008.10.002>
- Hernández, R., Pérez, V., Sanchez, G., Castella, J. & Palencia, J. (2004) Ensayos de atracción captura de *Ips acuminatus* (Coleoptera: Scolytidae). *Ecología*, 18, 35–52.
- Hlávková, D., Koudelková, J., Davidková, M. & Doležal, P. (2025) *Ips acuminatus* (Gyllenhal) in The Czech Republic (version v1). Zenodo. <https://doi.org/10.5281/zenodo.16325731>
- Hopping, G.R. (1964) The breeding evidence indicating two genetic types of females of *Ips tridens* Mannerheim (Coleoptera: Scolytidae). *The Canadian Entomologist*, 96(1–2), 117–118. Available from: <https://doi.org/10.4039/ent96117-1>
- Hothorn, T., Bretz, F. & Westfall, P. (2008) multcomp: simultaneous inference in general parametric models. R package version 1.4–25. Available from: <https://CRAN.R-project.org/package=multcomp>
- James, P.M.A., Janes, J.K., Roe, A.D. & Cooke, B.J. (2016) Modeling landscape-level spatial variation in sex ratio skew in the mountain pine beetle (Coleoptera: Curculionidae). *Environmental Entomology*, 45(4), 790–801. Available from: <https://doi.org/10.1093/ee/nvw048>
- Kirkendall, L.R. (1983) The evolution of mating system in bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae). *Zoological*

- Journal of the Linnean Society, 77, 293–352. Available from: <https://doi.org/10.1111/j.1096-3642.1983.tb00858.x>
- Kirkendall, L.R. (1990) Sperm is a limiting resource in the pseudogamous bark beetle *Ips acuminatus* (Scolytidae). *Oikos*, 57(1), 80. Available from: <https://doi.org/10.2307/3565740>
- Kirkendall, L.R. (1993) Ecology and evolution of biased sex ratios in bark and ambrosia beetles. In: Wrensch, D.L. & Ebbert, M.A. (Eds.) *Evolution and diversity of sex ratio in insects and mites*. London: Chapman and Hall Inc, pp. 235–345. Available from: https://doi.org/10.1007/978-1-4684-1402-8_8
- Kirkendall, L.R., Biedermann, P.H.W. & Jordal, B.H. (2015) Evolution and diversity of bark and ambrosia beetles. In: Vega, F.E. & Hofstetter, R.-W. (Eds.) *Bark beetles: biology and ecology of native and invasive species*. Oxford, UK: Academic Press, Elsevier Inc, pp. 85–156. Available from: <https://doi.org/10.1016/b978-0-12-417156-5.00003-4>
- Kohnle, U., Vité, J.P., Erbacher, C., Bartels, J. & Francke, W. (1988) Aggregation response of European engraver beetles of the genus *Ips* mediated by terpenoid pheromones. *Entomologia Experimentalis et Applicata*, 49(1–2), 43–53. Available from: <https://doi.org/10.1111/j.1570-7458.1988.tb02475.x>
- Komsta, L. & Novomestky, F. (2022) Moment, cumulants, skewness, kurtosis and related tests. R package version 0.14.1. Available from: <https://CRAN.R-project.org/package=moments>
- Lachowsky, L.E. & Reid, M.L. (2014) Developmental mortality increases sex-ratio bias of a size-dimorphic bark beetle. *Ecological Entomology*, 39(3), 300–308. Available from: <https://doi.org/10.1111/een.12108>
- Lanier, G.N. & Oliver, J.H. (1966) “Sex-ratio” condition: unusual mechanisms in bark beetles. *Science*, 153(3732), 208–209. Available from: <https://doi.org/10.1126/science.153.3732.208>
- Lekander, B., Bejer-Petersen, B., Kangas, E. & Bakke, A. (1977) The distribution of bark beetles in the Nordic countries. *Acta Entomologica Fennica*, 32, 1–36.
- Liška, J., Knížek, M. & Vélé, A. (2021) Evaluation of insect pest occurrence in areas of calamitous mortality of scots pine. *Central European Forestry Journal*, 67(2), 85–90. Available from: <https://doi.org/10.2478/forj-2021-0006>
- Lobinger, G. (1996) Variations in sex ratio during an outbreak of *Ips typographus* (Col., Scolytidae) in southern Bavaria. *Anzeiger Für Schädlingskunde, Pflanzen-Schutz, Umweltschutz*, 69(3), 51–53. Available from: <https://doi.org/10.1007/bf01906274>
- Loyning, M.K., Kirkendall, L.R. & Loyning, M.K. (1996) Mate discrimination in a pseudogamous bark beetle (Coleoptera: Scolytidae): male *Ips acuminatus* prefer sexual to clonal females. *Oikos*, 77(2), 336–344. Available from: <https://doi.org/10.2307/3546074>
- Makowski, D., Lüdecke, D., Patil, I., Thériault, R., Ben-Shachar, M. & Wiernik, B. (2023) Automated results reporting as a practical tool to improve reproducibility and methodological best practices adoption. R package. Available from: <https://easystats.github.io/report/>
- McKellar, A.E., Turcotte, M.M. & Hendry, A.P. (2009) Environmental factors influencing adult sex ratio in Trinidadian guppies. *Oecologia*, 159, 735–745. Available from: <https://doi.org/10.1007/s00442-008-1257-x>
- Meshkova, V., Kochetova, A., Zinchenko, O. & Skrylnik, Y. (2021) Biology of multivoltine bark beetles (Coleoptera:Scolytinae) in the north-eastern steppe of the Ukraine. *The Bulletin of Kharkiv National Agrarian University. Phytopathology and Entomology*, 2017(1–9), 1–2.
- METEORBLUE. (2006–2023) Pozorované historické údaje o klimatu a počasí. Available from: <https://www.meteorblue.com> (in Czech)
- Müller, K. & Wickham, H. (2023) tibble: Simple Data Frames. R package version 3.2.1. Available from: <https://CRAN.R-project.org/package=tibble>
- Netherer, S. & Pennerstorfer, J. (2001) Parameters relevant for modelling the potential development of *Ips typographus* (Coleoptera: Scolytidae). *Integrated Pest Management Reviews*, 6(3/4), 177–184. Available from: <https://doi.org/10.1023/a:1025719301446>
- Pedersen, T. (2024) patchwork: the composer of plots. R package version 1.3.0. Available from: <https://CRAN.R-project.org/package=patchwork>
- Pérez, G. & Sierra, J. (2006) Eficacia de cebos atrayentes y trapas en el control de *Ips acuminatus* (Coleoptera: Scolytidae). *Boletín de Sanidad Vegetal Plagas*, 32, 259–266.
- R Core Team. (2024) R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available from: <https://www.R-project.org/>
- Régnière, J. & Bentz, B. (2007) Modeling cold tolerance in the mountain pine beetle, *Dendroctonus ponderosae*. *Journal of Insect Physiology*, 53(6), 559–572. Available from: <https://doi.org/10.1016/j.jinsphys.2007.02.007>
- Reid, M.L. & Purcell, J.R.C. (2011) Condition-dependent tolerance of monoterpenes in an insect herbivore. *Arthropod-Plant Interactions*, 5(4), 331–337. Available from: <https://doi.org/10.1007/s11829-011-9137-4>
- Rizopoulos, D. (2025) GLMMadaptive: generalized linear mixed models using adaptive Gaussian quadrature. R package version 0.9–7. Available from: <https://CRAN.R-project.org/package=GLMMadaptive>
- Román-Ruiz, A.K., Michel, B., Dufour, B.P., Rojas, J.C., Cruz-López, L. & Barrera, J.F. (2017) Description of the sperm and spermatheca of *Hypothenemus hampei* (Coleoptera: Curculionidae: Scolytinae) for the differentiation of mated and unmated females. *Annals of the Entomological Society of America*, 110(4), 353–359. Available from: <https://doi.org/10.1093/aesa/sax033>
- Safranyik, L., Barclay, H., Thomson, A. & Riel, W.G. (1999) A population dynamics model for the Mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae). Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre. Information Report BC-X-386. Canada, Victoria, BC, 41 pp.
- Safranyik, L., Carroll, A.L., Régnière, J., Langor, D.W., Riel, W.G., Shore, T.L. et al. (2010) Potential for range expansion of mountain pine beetle into the boreal forest of North America. *The Canadian Entomologist*, 142(5), 415–442. Available from: <https://doi.org/10.4039/n08-cpa01>
- Schlyter F., Byers, J.A., & Löfqvist, J. (1987) Attraction to pheromone sources of different quantity, quality, and spacing: Density-regulation mechanisms in bark beetle *Ips typographus*. *J Chem Ecol* 13, 1503–1523. Available from: <https://doi.org/10.1007/BF01012294>
- Špoula, J. & Kula, E. (2023) Evaluating the effectiveness of installations for monitoring and control of *Ips cembrae* (Heer). *Sylvan*, 167(4), 233–244. Available from: <https://doi.org/10.26202/sylvan.2023029>
- Švestka, M. (2001) Development and use of pheromone dispenser in forest protection against *Ips acuminatus*. *Thayensia*, 4, 153–159. [in Czech].
- Takami, Y. (2002) Mating behavior, insemination and sperm transfer in the ground beetle *Carabus insulicola*. *Zoological Science*, 19(9), 1067–1073. Available from: <https://doi.org/10.2108/zsj.19.1067>
- Vallet, E. (1981) Study of the decline of Scotch pine in the Centre region and of the principal associated scolytid pests: *Tomicus piniperda*, *Ips sexdentatus* and *Ips acuminatus* (Col. Scolytidae). Doctoral Thesis. Orleans, France: Université d'Orléans. 4(143), 31 pp.
- Venables, W.N. & Ripley, B.D. (2002) *Modern applied statistics with S*, Fourth edition. New York: Springer. Available from: <https://www.stats.ox.ac.uk/pub/MASS4/>
- Wermelinger, B. (2004) Ecology and management of the spruce bark beetle *Ips typographus* review of recent research. *Forest Ecology and Management*, 202(1–3), 67–82. Available from: <https://doi.org/10.1016/j.foreco.2004.07.018>
- Wickham, H. (2016) *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag. Available from: <https://ggplot2.tidyverse.org>
- Wickham, H. (2023a) forcats: tools for working with categorical variables (factors). R package version 1.0.0. Available from: <https://CRAN.R-project.org/package=forcats>

- Wickham, H. (2023b) stringr: simple, consistent wrappers for common string operations. R package version 1.5.1. Available from: <https://CRAN.R-project.org/package=stringr>
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R. et al. (2019) Welcome to the tidyverse. *Journal of Open Source Software*, 4(43), 1686. Available from: <https://doi.org/10.21105/joss.01686>
- Wickham, H., François, R., Henry, L., Müller, K. & Vaughan, D. (2023) dplyr: a grammar of data manipulation. R package version 1.1.4. Available from: <https://CRAN.R-project.org/package=dplyr>
- Wickham, H. & Henry, L. (2023) purrr: functional programming tools. R package version 1.0.2. Available from: <https://CRAN.R-project.org/package=purrr>
- Wickham, H., Hester, J. & Bryan, J. (2024) readr: read rectangular text data. R package version 2.1.5. Available from: <https://CRAN.R-project.org/package=readr>.

- Wickham, H., Vaughan, D. & Girlich, M. (2024) tidyr: Tidy messy data. R package version 1.3.1. Available from: <https://CRAN.R-project.org/package=tidyr>

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