

Is *Ips amitinus* (Coleoptera: Curculionidae) Abundant in Wide Range of Altitudes?

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Abstract: The distribution of bark beetle *Ips amitinus* was determined in Czech Republic and Poland, and within individual host trees (spruce). It was detected in more than half of the studied localities, from the lowland through medium upland locations to the highest localities in Tatra Mts. region. A similar pattern of *I. amitinus* occurrence from lowlands to mountains can be expected throughout Central Europe, wherever its major host (spruce) is grown. *I. amitinus* was commonly found in the middle parts of the spruce crown. When *I. typographus* abundance was high, *I. amitinus* abundance was low. The development pattern of *I. amitinus* could be very similar to that of *I. typographus*. *I. amitinus* has one generation per year in mountainous areas of Central Europe but might have two generations per year below 600 m a.s.l.

Key words: occurrence, distribution on tree, generation, Central Europe

Introduction

The bark beetle *Ips amitinus* (Eichhoff, 1872) belongs to a group of secondary insect pests of *Picea abies* (L., 1753) Karsten, 1881 that includes the bark beetles *Ips typographus* (L., 1758) and *Pityogenes chalcographus* (L., 1761) (PFEFFER, SKUHRAVÝ, 1995; GRODZKI 1997, GRODZKI 2004, MAZUR *et al.* 2006).

I. amitinus is widespread throughout Europe where *P. abies* and *P. sylvestris* occur, but it is mostly absent in the Nordic countries (EPPO/CABI, 1997). *I. amitinus* is known from Austria, Belgium, Bulgaria, Croatia, Czech Republic, Western France, Germany, Hungary, Northern Italy, Lithuania, Latvia, FYRMacedonia, the Netherlands, Poland, Romania, Kaliningrad region, Slovakia, Slovenia, Spain (although not recently), Switzerland, Southwestern Ukraine, and Former Yugoslavia (PAVLOVSKIJ 1955,

PFEFFER 1955, JURC, BOJOVIĆ 2004, VOOLMA *et al.* 2004). This species has expanded northward into the eastern part of Fennoscandia (MANDELSHTAM 1999, KOPONEN 1975, ANNILA, NUORTEVA 1977, BIERMANN, THALENHORST, 1977, HELIÖVAARA *et al.* 1991, JAKOVLEV, SIITONEN 2005). Recently, *I. amitinus* was recorded at Murmansk, north of the Arctic Circle (VOOLMA *et al.* 2004).

Occurrence of *I. amitinus* have been recorded on *P. abies*, *Pinus cembra* (L., 1753) (HELLRIGL 1985, STAUFFER, ZUBER 1998), *Pinus mugo* (Turra, 1764), *Abies alba* (Miller, 1768), *Larix decidua* (Miller, 1768) (EPPO/CABI, 1997), *Pinus sylvestris* (L., 1753), and other species of *Pinus* (KNÍŽEK, TRÝZNA 2002, DOMINIK 2003). *I. amitinus* is also an important component of the fauna of blue spruce (*Picea*

pungens (Engelmann, 1879) in Central Europe (KULA *et al.* 2009, 2011, KULA, ZĄBECKI 2010, POP *et al.*, 2010)).

It often remains undetected because it is confused with other, more common species of bark beetles with which it often co-occurs (KNÍŽEK, 2001). Therefore, the occurrence and abundance of this species is not sufficiently recognized. Quality data have been provided by only a few papers, and these papers focused mainly on other species of bark beetles (ZUMR 1984, KNÍŽEK 2001, MIHALCIUC *et al.* 2001, NOVOTNÝ *et al.* 2002, JURC, BOJOVIĆ 2004, KUŚ, KUŚ 2004, GRODZKI *et al.* 2006, KULA *et al.* 2007, ØKLAND, SKARPAAS 2008, GRODZKI 2009).

Compared with *I. typographus*, which has the same hosts as *I. amitinus* (EPPO/CABI, 1997) but is recognized as a major pest, *I. amitinus* is scarcely mentioned in the scientific literature. While the biology and ecology of *I. typographus* have been described and modelled (LIEUTIER 2002, GRÉGOIRE, EVANS 2004, WERMELINGER 2004), only sporadic information is available regarding the basic ecological characteristics of *I. amitinus* (ZUMR 1982, ZUBER 1992, COELN *et al.* 1996).

The objective of this work was to determine the distribution of *I. amitinus* in an area ranging in elevation from 250-1300 m a.s.l.

Materials and Methods

Characteristics of study areas

Research was conducted in Czech Republic (one study region) and in Poland (three study regions). The research in Czech Republic was conducted in three biogeographically different areas in the eastern part of the country. The terrain of the lowest altitudes has a flat, upland character with a typical elevation of 220-300 m a.s.l. The climate is moderately warm and provides abundant precipitation (700-900 mm/y). The area has low forest cover (9%, about 30% of which is represented by spruce), with isolated forest complexes in an agricultural landscape. The terrain in the middle altitudes consists of plateaux cut by a network of deep valleys. The elevation ranges from 300 to 700 m. The climate is cold, with rainfall at 600-800 mm/y. Forest cover is 40%, of which 67% is represented by spruce. The terrain of the highest localities in Western Carpathians is characterized by mountains with elevations of 500-1200 m. The cli-

mate is mostly cold and provides abundant rainfall. Forest cover exceeds 70%, of which spruce represents more than 70% (CULEK 1996). In Poland, the research was done in three main Carpathian regions with relatively cold climates: Bieszczady Mts. study region (800-850 m, rainfall 1000-1200 mm), Gorce Mts. study region (1000-1200 m, rainfall 1000 mm), and Tatra Mts. study region (1100 m, rainfall 1100-2000 mm). In Bieszczady Mts., spruce stands consist of small islands of Norway spruce that are surrounded by beech and fir stands. Forest stands in Gorce and Tatra Mts. are dominated by spruce.

Study of trap trees for detection of *I. amitinus* at Havířov, Libavá, and Smrk Mt. in Czech Republic)

Trap trees were used in three study areas in Czech Republic: Havířov (three large forest sites: 49°49'N 18°22'E; 49°48'N 18°24'E; 49°50'N 18°22'E; indicated by small stars in Fig. 1), the area surrounding the town of Libavá (at three sites: 49°40'N 17°38'E; 49°38'N 17°30'E; 49°44'N 17°37'E; indicated by medium stars in Fig. 1), and Smrk Mt. (at one site: 49°30'N 18°22'E; indicated by the large star in Fig. 1). At each study area, spruce trees 25-35 cm in diameter (at breast height, DBH) and without beetle infestation were cut at the edge of mature forest stands (older than 80 years). The number of trap trees used at each area and in each year are indicated in Table 1. To assess bark beetle abundance, bark beetle entry holes were counted on four sections of the stem (sections were identified but the tree was left intact, i.e., it was not cut into sections). The first section (the bottom) extended from the bottom of the cut tree to 0.5 m higher on the trunk. The second section (the stem) was midway between the bottom and the beginning of the crown. The third section (the middle) was at the beginning of the crown, and the fourth section (the crown) was in the centre of the crown. On each section, one rectangular strip on the stem surface was designated; the length of the strip was equal to half of the section's circumference, and the width was 0.5-1.0 m. The circumference of each section and the strip dimensions were measured and recorded in the field.

The trap trees were debarked 6 to 7 weeks after they had been cut; this was estimated to be the time when III instar larvae and pupae of the first generation would be present. Entry holes made by bark beetles were enumerated in each strip, and the

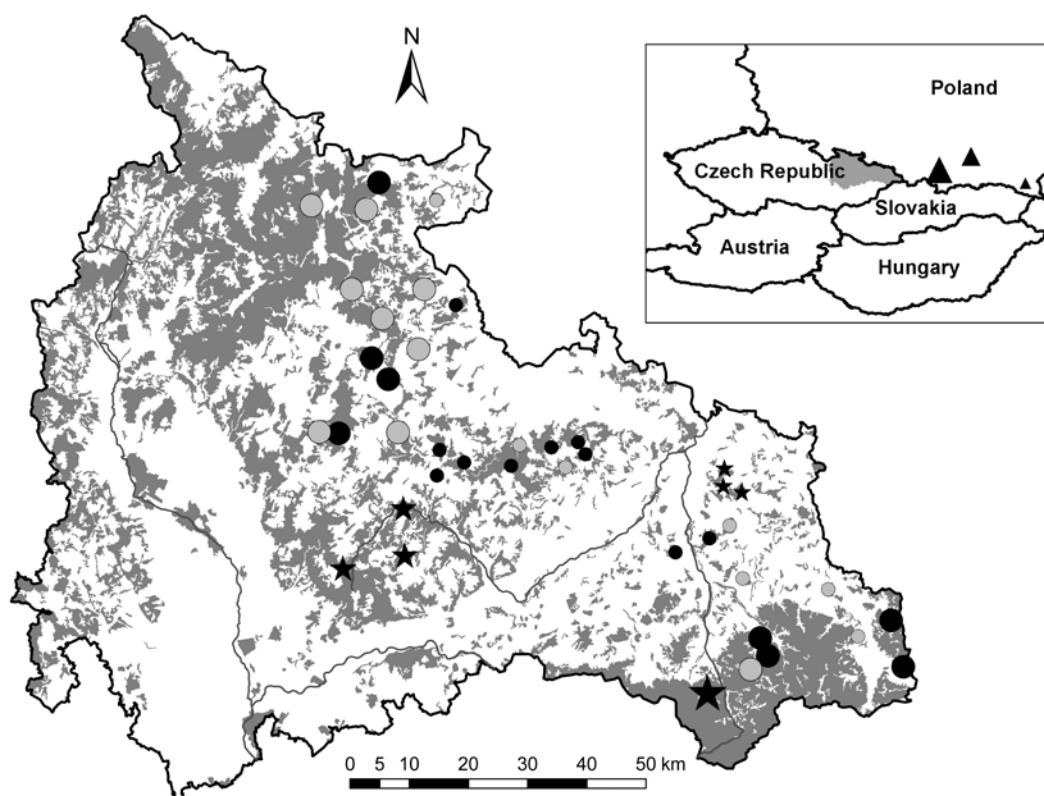


Fig. 1. Locations surveyed for occurrence of *Ips amitinus* in Czech Republic and Poland. Occurrence (presence = black symbols and absence = grey symbols) was studied using trap trees (stars), sanitary felled trees (circles), and infested trees (triangles). Small, medium, and large stars indicate Havířov, Libavá, and the Smrk Mt. (all in Czech study region), respectively. Small and large circles indicate localities lower than 500 m or higher than 500 m, respectively. The large, medium, and small triangle indicate Tatra Mts., Gorce Mts., and Bieszczady Mts. study region.

Table 1. Number of trap trees (felled in spring/summer) used at three study areas (with seven sites in total) in Czech Republic ^a. The seven sites with trap trees are indicated by stars in Fig. 1.

Study area	Altitude (m a.s.l.)	Year					
		2005	2006	2007	2008	2009	2010
Havířov	265-295	45/0	40/0	30/0	0/0	0/0	0/0
Libavá	550-655	0/0	0/0	0/0	60/52	30/16	20/20
Smrk Mt.	1180-1200	0/0	0/0	0/0	0/0	11/16	5/5

^a Each trap tree was laid on the soil surface close to where it was cut.

species and developmental stage of the beetle(s) in the gallery associated with each entry hole were determined. The beetles were identified by examining the galleries and beetles in the field, or, if necessary, by examining the beetles after they had been taken to the laboratory.

At the study area of Havířov, trap trees were prepared in the same time period (from 15 February to 20 April) of every year (2005-2007). Entry holes were counted and bark beetles were studied on 10 June 2005, 2 June 2006, and 5 June 2007.

Traps trees were used at three sites in the area surrounding the town of Libavá and were prepared

every year (2008-2010) in the same time period from 5 April to 5 May for detection of parental beetles and from 15 June to 15 July for detection of filial beetles. Entry holes were counted and bark beetles were studied on 5-8 June 2008, 15-17 August 2008, 5 June 2009, 23 July 2009, 27 June 2010, and 1 August 2010.

Trap trees were used at one site in Smrk Mt. study area and were prepared in early May and late August in 2009 and in late June and late August in 2010. Entry holes were counted and bark beetles were studied on 18 June 2009, 24 July 2009, 7 July 2010, and 20 September 2010.

Study of sanitary felled trees at 37 localities in Eastern Czech Republic

From 2006–2009, logged spruce trees were studied at 34 localities in the eastern part of Czech Republic (from 50°14' N, 17°26' E to 49°31' N, 18°48' E at elevations of 300–450 and 500–700 m; Table 2). Studied trees were between 60 and 120 years old and had been logged because they were suffering from drought, attack by *Armillaria* sp., and recent invasion by large numbers of bark beetles. The localities were visited twice yearly (May–June and August–September), and more than 10 trees were studied on each visit to each locality. If more than one beetle entry hole per dm² was found on a tree in at least one of its parts (base, centre of trunk, or crown), it was considered to have been invaded by large numbers of beetles. The density of entry holes was determined for three 1-m by 10-cm areas, one area for each part of the trunk. Logged trees that were dry were not studied.

Study of infested trees in Poland

Standing, infested trees in three regions in Poland (Bieszczady Mts., Gorce Mts., and Tatra Mts.) were felled, and bark beetle entry holes were counted on four areas of the stem using the same methods that has been already described. Trees were examined twice yearly (June/July and August/September/October).

The study site in Bieszczady Mts. was at 49°02'01"N, 22°51'46"E (see small triangle in Fig. 1). The trees at this site were examined twice yearly (June/July and August/September/October) in 1998–2000. A total of 47 trees were studied.

The study site in Gorce Mts. was at 49°33'00"N; 20°15'24"E (see medium triangle in Fig. 1). The trees at this site were examined twice yearly in 1999–2002 (June/July and August/September/October). A total of 35 trees were studied.

The study site in Tatra Mts. was at 49°14'40"N; 20°05'30"E (see large triangle in Fig.1). The trees at this site were examined twice yearly in 2003, 2004 and 2006 (June/July and August/September/October). At total of 45 trees were studied.

Statistical analysis

Because the data were not normally distributed, nonparametric tests (Kruskal-Wallis and Mann-Whitney) were used. STATISTICA 8.0 was used for all statistical analyses.

Results

Study of trap trees at Havířov, Libavá, and Smrk Mt.

I. amitinus was detected on trap trees in all seven study sites at these three areas though not in every season (Table 3). At the lowest elevation in the study area Havířov, it was always found in June (Table 3). In middle altitudes in Libavá, *I. amitinus* was found in June 2009, June 2010, and August 2010. *I. amitinus* was most abundant in Smrk Mt. (Table 2).

At Havířov, the number of entry holes were highest in the crown section and declined toward the bottom of the tree; the numbers of entry holes per dm² differed between crown and bottom sections (Kruskal-Wallis test: $z=4.97$; $p<0.00001$), stem and crown sections (Kruskal-Wallis test: $z=4.66$; $p<0.0001$), and middle and crown sections (Kruskal-Wallis test: $z=3.98$; $p<0.001$). At Libavá, the number of entry holes per dm² did not significantly differ between the trap areas (Kruskal-Wallis test: $H(3, N=760) = 1.20$; $p>0.05$). At Smrk Mt., the number of entry holes per dm² differed among trap areas (Kruskal-Wallis test: $H(3, N=145) = 14.52$; $p<0.01$), and multiple comparisons confirmed that entry holes were less abundant in bottom sections than in middle (Kruskal-Wallis test: $z=2.88145$; $p<0.05$) and crown sections (Kruskal-Wallis test: $z=2.93$; $p<0.05$).

I. typographus was found in all trap trees at all three study areas. The abundances of *I. typographus* and *I. amitinus* were not correlated in 2010 at Havířov ($r=0.02$; $p>0.10$) or in June 2010 at Smrk Mt. ($r=-0.40$; $p>0.05$). The abundances of these two species were negatively correlated at Libavá in June 2009 ($r=-0.19$; $p<0.05$) and at Smrk Mt. in June 2009 ($r=-0.61$; $p<0.00001$).

Study of sanitary felled trees at 34 localities in Eastern Czech Republic

At 300–450 m, standing trees that were weak and infested by *I. amitinus* were found in all studied periods during 2006–2010, with the exception of May–June 2009 (Table 4). *I. amitinus* was found at almost 67% of the 15 localities at this elevation (small circles in Fig. 1), and the percentage of infested trees was highest in May–June 2007 (Table 4).

At 500–700 m (large circles in Fig. 1), trees infested by *I. amitinus* were detected in July and August during 2007–2009 at more than 40% of the

Table 2. Localities in Eastern Czech Republic used for study of sanitary felled trees. The 34 localities are indicated by circles in Fig. 1.

Study localities	Altitude (m a.s.l.)	Coordinates
Dolní Datyně	290	49°45'40.227"N, 18°23'39.935"E
Paskov	290	49°42'48.828"N, 18°16'23.595"E
Pazderná	300	49°40'58.12"N, 18°26'6.79"E
Václavovice	310	49°44'21.485"N, 18°20'58.906"E
Třinec	320	49°40'36.701"N, 18°38'12.827"E
Pustá Polom	350-420	49°52'3.452"N, 18°0'22.929"E
Bystřice nad Olší	390	49°36'34.239"N, 18°42'55.427"E
Slezské Rudoltice	390	50°12'49.539"N, 17°38'16.085"E
Cvilín	400	50°3'29.363"N, 17°42'26.204"E
Jánské koupele	400	49°50'11.691"N, 17°42'2.393"E
Kajlovec	400	49°51'18.456"N, 17°53'11.738"E
Dubová	450	49°49'16.328"N, 17°45'38.756"E
Jakubčovice	450	49°49'40.062"N, 17°59'57.209"E
Kyjovice	450	49°51'0.985"N, 18°2'32.887"E
Lesní Albrechtice	450-500	49°49'21.41"N, 17°52'17.111"E
Hlubočec	450-520	49°51'21.727"N, 17°57'42.44"E
Čermná	490	49°47'51.069"N, 17°41'59.768"E
Janov	500	50°13'58.133"N, 17°29'55.015"E
Bílčice	550	49°51'27.132"N, 17°35'57.913"E
Brantice	550	50°4'39.579"N, 17°37'44.326"E
Dlouhá Stráň	550	49°57'58.327"N, 17°31'16.94"E
Horní Benešov	550	49°59'10.034"N, 17°37'44.421"E
Nové Heřminovy	550	50°1'39.082"N, 17°32'15.149"E
Široká Niva	550	50°4'1.984"N, 17°27'31.291"E
Nýdek	600	49°38'15.716"N, 18°47'22.112"E
Písek	600	49°34'8.004"N, 18°49'35.106"E
Pražmo	600	49°35'42.035"N, 18°29'15.825"E
Razová	600	49°56'11.003"N, 17°33'53.499"E
Dlouhá Voda	650	50°11'25.044"N, 17°28'29.543"E
Drakov	700	50°11'17.167"N, 17°20'40.27"E
Spálené	700	50°10'4.682"N, 17°26'54.237"E
Dětrichov	750	49°50'47.596"N, 17°24'54.72"E
Krásná	900	49°34'8.493"N, 18°30'32.821"E
Ostravice	1000	49°32'45.527"N, 18°28'17.045"E

localities; the percentage of trees infested by *I. amitinus* ranged from 0 to 28% in 2007, from 0 to 9% in 2008, and from 0 to 38% in 2009. *I. typographus* was found at all localities (Table 4).

Study of infested trees in Poland

I. amitinus was found on standing infested trees in all three regions studied in Poland from June to August in all years. It was occasionally found in October. The density of entry holes ranged from 0 to 1.2 per dm² (Table 5).

At the site in Bieszczady Mts., the median numbers of entry holes per dm² differed among sections of infested trees (Kruskal-Wallis test: $H(3, N=188) = 20.20; p > 0.001$). Multiple comparison confirmed that entry holes were less abundant in bottom sections than in stem sections (Mann-Whitney test, $z = -3.59; p < 0.001$), middle sections (Mann-Whitney test: $z = -2.83, p < 0.01$), and crown sections (Mann-Whitney test: $z = -3.10; p < 0.01$).

The median number of entry holes per dm² also differed among sections of infested trees at the site

Table 3. Number of *Ips amitinus* entry holes/dm² on trap trees in study areas in Eastern Czech Republic (mean±SD).

Year	Period	Study areas (Altitudes)		
		Haviřov (265-295 m a.s.l.)	Libavá (520-655 m a.s.l.)	the Smrk Mt. (1260 m a.s.l.)
2005	June	0.03±0.12	–	–
2005	August	–	–	–
2006	June	0.04±0.17	–	–
2006	August	–	–	–
2007	June	0.08±0.26	–	–
2007	August	–	–	–
2008	June	–	0	–
2008	August	–	0	–
2009	June	–	0.25±0.61	1.22±1.14
2009	August	–	0	0
2010	June	–	0.01±0.02	0.22±0.17
2010	August	–	0.03±0.07	0

Table 4. Percentage of incidentally felled trees infested by *Ips amitinus* in an amount more than one enter hole per dm² in Eastern Czech Republic (mean±SD).

Year	Period	Elevation (m a.s.l.)	
		300-450	500-700
2006	May-June	1.42±3.07	–
2006	July-August	23.02±3.07	–
2007	May-June	–	–
2007	July-August	1.42±1.37	5.00±4.46
2008	May-June	–	–
2008	July-August	0.89±2.67	2.88±4.46
2009	May-June	0±2.66	–
2009	July-August	5.68±3.07	8.77±3.15

in Tatry Mts. (Kruskal-Wallis test: H (3, N=356) = 36.63; p<0.0001). Entry holes were more abundant in crown sections than in bottom sections (Mann-Whitney test: z=-3.11; p<0.01) or in stem sections (Mann-Whitney test: z=-2.63; p<0.01).

At the site in Gorce Mts., Kruskal-Wallis test indicated significant differences in median numbers of entry holes per dm² among sections of trees (H (3, N=136) = 15.38; p<0.01), but these differences were not confirmed by the Mann-Whitney test. No entry holes were found in bottom and stem sections, and very few were found in middle and crown sections.

I. typographus was found on all trees at all three sites in Poland. The abundances of *I. typographus*

and *I. amitinus* were negatively correlated at Tatry Mts. (r=-0.19; p<0.05). Although the relationships were not statistically significant, abundances of *I. typographus* and *I. amitinus* tended to be negatively correlated at Gorce Mts. (r=-0.51; p>0.05) and the Bieszczady Mts. (r=-0.21, p>0.05).

Discussion

The presented results demonstrate that *I. amitinus* is a common species in the studied area, which is the centre of the range for this species. It was detected in more than half of the studied localities, from the lowest location through medium upland locations to the highest study sites in Tatra and Gorce Mts. regions. A similar pattern of its occurrence from lowlands to mountains can be expected wherever spruce (the major host of *I. amitinus*) is grown in Central Europe. In the present study, the number of entry holes per dm² of on a trap tree usually did not exceed 0.1 at lower elevations (300–450 m) and ranged from 0 to 0.2 at middle elevations (500–700 m). At high elevations of Carpathians (1000 m), which are connected to Smrk Mt. area, the number of entry holes was greater than 1 per dm². This high number of enter holes is the result of a local outbreak of *I. typographus* and *I. amitinus* that occurred on about 10 ha in 2007 in Smrk Natural Reserve (unpublished data). *I. amitinus* frequently appeared together with *I. typographus* in all areas. Both species reproduce at the same time (JURC, BOJOVIĆ 2004, ØKLAND, SKARPAAS 2008). On standing trees, *I. amitinus* was less abundant in the Polish study areas than in the areas in Czech Republic. Although ZUMR (1984) reported that *I. amitinus* is the most abundant bark beetle in spruce mountain forests, the proportion of bark beetles represented by *I. amitinus* vs. *I. typographus* was highly variable in the current study. When *I. typographus* abundance was high, *I. amitinus* abundance was low in the present study and in previous studies (GRODZKI 1997, KULA, ZĄBECKI 2002). In the lower elevations, *I. duplicatus* (Sahlberg, 1836) is very abundant (HOLUŠA *et al.* 2010) and may also compete with *I. amitinus*. *I. amitinus* is probably a common and abundant species in this region of lower altitudes because the fitness of the spruce trees in this region has been reduced by drought and *Armillaria* sp. (HOLUŠA, LIŠKA 2002).

I. amitinus was found on both standing trees and felled trees (see also KUŠ, KUŠ 2004, GRODZKI *et*

Table 5. Abundance of *Ips amitinus* enter holes/dm² on standing infested trees in Poland (mean±SD).

Year	Period	Region (Altitudes)		
		Bieszczady (800-850 m a.s.l.)	Tatras (1100 m a.s.l.)	Gorce (1000-1200 m a.s.l.)
1998	July	0,26±0,48	–	–
1998	August	0,12±0,19	–	–
1999	June	0,35±0,55	–	0,002±0,008
1999	September	0,29±0,37	–	0,03±0,14
2000	June	0,27±0,51	–	0,07±0,22
2000	September	0	–	0
2001	June	–	–	0,02±0,08
2001	September	–	–	–
2002	June	–	–	0,04±0,16
2002	September	–	–	0
2003	June	–	0,024±0,073	–
2003	August	–	–	–
2004	June	–	0,022±0,074	–
2004	August	–	0,019±0,089	–
2006	June	–	0,014±0,079	–
2006	October	–	0,014±0,079	–

al. 2006, KULA *et al.* 2007, WITRYLAK, 2008). Felled trees are attractive to most pest species in the genus *Ips*, including *I. typographus* (PFEIL 1827), *I. cembrae* (Heer, 1836) (GRODZKI 2010), *I. acuminatus* (Gyllenhal, 1827) (ZASEV 1952), and *I. sexdentatus* (Börner, 1776) (BESCELI, EKICI 1969) but not *I. duplicatus* (SIERPIŃSKI 1958). Like most other *Ips* species, *I. amitinus* most often reproduces in dying or weakened trees, but it can also contribute to tree death, especially in the case of young trees and trees in plantations (KNÍŽEK 2001, MIHALCIUC *et al.* 2001, NOVOTNÝ *et al.* 2002, ØKLAND, SKARPAAS 2008, GRODZKI, 2009).

At all localities in the current study, *I. amitinus* entry holes were more abundant in crown sections than in other sections. In contrast to *I. typographus*, *I. amitinus* prefers to breed in tree parts with relatively small dimensions (ZUMR 1984, EPPO/CABI 1997). Galleries of *I. amitinus* are most often found on younger trees (GRODZKI 2009), in the upper part of weakened trees, or in large-diameter weakened trees where the galleries of *I. amitinus* overlap those of *I. typographus* (JURC, BOJOVIĆ 2004). Therefore, we conclude that *I. amitinus* prefers the middle parts of the crown from the boundaries of the green branches for reproduction. This finding is consistent with previous reports (ZUMR 1984, GRODZKI 1997, JAKUŠ 1998, KULA, ZĄBECKI 2001, PLAŠIL, CUDLÍN 2005).

On standing, infested trees at elevations up to 400 m, *I. amitinus* was abundant during two periods of the year (June–July and August–October). During both periods, we found larvae, pupae, and callow beetles in the galleries, which indicates that the beetle completes two generations per year. Unfortunately, we could not confirm this with data from trap trees because only the parental generation of bark beetles was studied on trap trees at lower elevations (Table 1). If *I. amitinus* has two generations per year at lower elevations, its development pattern would be very similar to that of *I. typographus* (WERMELINGER 2004) and *I. duplicatus* (HOLUŠA *et al.* 2003).

Although traps trees were felled in spring and summer at medium elevations of 500–600 m, the occurrence of multiple generations per year at these elevations is unclear because there were few temporal replicates within the same site and year. The data from medium elevations are consistent with the occurrence of only one generation per year, except perhaps in Libavá in 2010, when *I. amitinus* was found in trap sections in both June and August; the abundances, however, were low.

At high elevations, a peak in detection of *I. amitinus* occurred only in June. The present study therefore confirms that *I. amitinus* completes one generation per year in the mountains. In Czech Republic, trap trees prepared in July were not infested in 2009

or 2010, although callow beetles of the first generation were found on trap trees in June and July; the data therefore indicate that the failure to detect a second generation did not result from a lack of first-generation beetles. Results from Poland also failed to indicate the development of a second generation at higher elevations (above 800 m). Although galleries of *I. amitinus* were found in August in Poland, these beetles were probably of the first and only generation. The time interval after examinations in June was only 6 weeks, and galleries detected in August likely resulted from the development of some individuals whose eggs were laid later. In September and October, galleries of *I. amitinus* were found only in a few cases. These could have been galleries produced by beetles emerging later or by sister brood. Compared with data from trap trees (which were known to be free of beetles when they were cut), data from standing trees do not provide clear information concerning time of infestation.

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