# Reproductive performance and natural antagonists of univoltine population of *Ips typographus* (Coleoptera, Curculionidae, Scolytinae) at epidemic level: a study from Šumava Mountains, Central Europe

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**Abstract:** Lukášová K., Holuša J., Grucmanová Š. 2012: Reproductive performance of univoltine population of *Ips typographus* (Coleoptera, Curculionidae) at epidemic level in Central Europe: case study of small-scale and short-term bark beetles outbreak in the Šumava Mts. – *Beskydy*, 5 (2): 153–162

Population of *I. typographus* was studied in one locality with small-scale and short-term outbreak distant from large-scale and long-term outbreak area by several hundred meters. In total, ten spruce trees infested by the spruce bark beetle were examined. Always four stripes of bark (sample area) with the length equal to half the circumference of the trunk and the width of approximately 0.5 m were analyzed. The local spruce bark beetle population was characterized by high population density (1.5±1.2 entry holes per dm$^2$), low number of eggs per female, and short maternal galleries. Relatively low reproductive success (0.8 female offspring per one mother beetle, percentage of surviving individuals varies between 1 and 18 % was documented. The parasitism rate of living developmental stages of spruce bark beetle by larval parasitoids averaged 14 %. The level of infestation by pathogens and endoparasitoids in maternal beetles from their galleries was low. Highly likely, it is a result of short-term outbreak during which response of parasitoids was delayed in time.

**Keywords:** spruce bark beetle, *Ips typographus*, natural enemies, intraspecific competition, epidemic level of population

## Introduction

Over the past century, outbreaks of *Ips typographus* (Linnaeus, 1758) occurred in many places across Europe (Grégoire, Evans 2004). Since 1950, 2–9 million m³ of wood have been damaged annually by bark beetles, and predominantly by *I. typographus* (Schelhaas et al. 2003). In the 1990s, outbreaks of the beetle were also documented in places where they had not occurred previously (Grégoire, Evans 2004). Although the forests of the Šumava Mountains had been significantly altered by economic activities over the past centuries, today they are dominated by artificially established forests. During the 1990s, the large-scale outbreak of *I. typographus* was documented in the central part of the Šumava

Mountains, leading to disintegration of spruce stands. On the Czech side of the border with Germany, two main management approaches were applied during the outbreak. Part of the stands was left without any anthropogenic intervention, and in the remaining area the bands of clear cuts were created near the so-called intervention-free zone (Mánek, Ešnerová 2007). In January 2007, according to to estimates by the admistration of Šumava National Park, the wind storm Kyrill damaged approximately 15,000 m³ of wood in areas of those second zones around the so-called "Calamity Skidway" area. This represents about 20–40 ha of strongly damaged forest (Svoboda 2007). One year after the wind event, there was a remarkable increase in the

volume of trees infested by bark beetles. In 2011, more than 235,000 m³ of infested wood was recorded, which is a slight decrease in comparison to 2009 and 2010. In the Šumava Mountains, the outbreak of *I. typographus* outbreak lasted over 15 years. In cases of such long-term outbreaks, with high population densities of *I. typographus* retained high above average over many years and absence of management by forestry practices, a significant increase of mortality and parasitism in the beetle is often presumed (Weslien, Schroeder 1999).

The spruce bark beetle *Ips typographus* is one of the economically most serious pest species of Norway spruce in Eurasia (Christiansen, Bakke 1988). For successful colonization of living trees, a high density of attacking individuals is needed to overcome the defensive system of the trees (Mulock, Christiansen 1986, Christiansen et al. 1987). Reproductive success of the beetles depends on three main conditions: temperature, natural enemies, and inter- as well as intraspecific competition (Faccoli, Bernardinelli 2011). In early stages of the development of the offspring generation significant mortality is caused by predators, i. e. flies of the *Medetera* genus (Dipútera) with frequency of 0.2–0.26 % (Herard, Mercadier 1996). Also *Thanasimus formicarius* (Linnaeus, 1758) (Coleoptera) is able to reduce the offspring generation *of I. typographus* by as much as 18 % (Mills 1985). In the final larval stages and in the pupal stage, parasitoids predominate (Krüger, Mills 1990, Feicht 2004). It is highly likely that at the endemic level predation effectively reduces the beetle density and its population growth. The questions as to whether predation also effectively reduces the epidemic population of the beetle remains open (Kausrud et al. 2012).

In Europe, nine species of pathogens are described as attacking *I. typographus* (Wegensteiner 2004, Holuša et al. 2009). Although their distribution has been monitored by many authors (survey see Wegensteiner 2004, Takov et al. 2010, Lukášová, Holuša 2012), their influence on population dynamics of the beele is still unknown. When considering parasitism by nematodes, we presume its influence on the rate of development, fertility, survival and flight activity of the beetles (Nickle 1963, Lieutier 1981, Kaya 1984 Tenkáčová, Mituch 1986). Although an influence of nematodes on flight activity of the beetle has not yet been proven (Forsse 1987), fertility may decrease as documented by 20 % reduction of the size of the oocytes in infected females (Thong, Webster 1975).

There are no works evaluating reproductive success in univoltine population of *I. typographus* in mountain conditions in Central Europe at an epidemic level, except for the studies of parasitism from the Bavarian side of the Šumava Mountains (Kalina 2000, Feicht 2004). There also are no studies dealing with the levels of parasitism, pathogen infections and nematode parasitism among maternal beetles and/or on parasitism of the offspring generation of the beetle.

The purpose of the study was to record the levels of pathogen infection of maternal beetles, parasitism of the offspring, number of predators, and reproductive success of the univoltine generation of *I. typographus* in small-scale and short-term outbreak with high population density in an area in epidemic level.

## Materials and Methods

### Study site

To evaluate parasitism in the population of *I. typographus* a special study was carried out at the following three study sites in the locality "Na Ztraceném": Ptačí potok (PP) I–III (48° 59′ 23.617″ N, 13° 30′ 40.858″ E; 48° 59′ 11.240″ N, 13° 30′ 5.403″ E; and 48° 59′ 28.669″ N, 13° 29′ 31.022″ E, at elevation 1150 m a.s.l.) on 23 August 2011. The locality is situated in the area with the epidemic level of *I. typographus* and the forest stand is characterized by 80 % alochtonous trees. The forest is representing by *Piceetum* acid stands (spruce on acid substrates), i.e. firm, not waterlogged with the presence of small-reed (*Calamagrostis* spp.) or blueberry (*Vaccinium myrtillus*). The forest mostly consists of Norway spruce *Picea abies* (Linnaeus) Karsten, rowan *Sorbus aucuparia* Linnaeus, and also dwarf pine *Pinus mugo* Turra on peat-bogs. Most spruce stands inthe locality are 60–80 years old and the original spruce stand was approximately 160 years old. During the period 1991–2007, the area (286 ha) was in the intervention regime (man-affected, managed forest), later it was on intervention-free regime. Above-average precipitation (1,224 mm per year) and average annual temperature between 5 and 6 °C is characteristic for this area. First trees infested by *I. typographus* were found in 2010. The locality with the short-term outbreak of the beetle is distant from long-term (>10 years) outbreak area approximately 700 meters.

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### Analysed trees

At the edges of the sites, there were groups of trees or places with trees infested or already left by bark beetles. Spruce trees infested by bark beetles (presence of entry holes, boring dust, resin on the bark) were selected and felled (2, 2, and 6 infested trees at each study sites). Diameter of felled trees ($d_{1.3}$) was 29 cm - median (range 17–33 cm). After the branches removed four distinct sample areas (I–IV) were examined for the presence of *I. typographus* and its natural enemies on each tree trunk. The sample areas were represented by debarked bands with length equal to the half the tree circumference and the width of approximately 0.5 m. Sample area I was situated 0.5 m from the tree base, sample area II in the middle between the base and the bottom of the tree's crown, sample area III at the beginning of the crown, and sample area IV in the centre of the crown. Height/length of the trunk, trunk diameter and thickness of the bast and bark in particular samples/sections, and the dimensions of each sample/section were recorded for each tree examined.

### Material sampling and data recording

In each sample area, 10 maternal galleries of *I. typographus* were studied if this was possible, and the number of nuptial chambers (entry holes) was recorded, as was the number of eggs laid by the females, the length of maternal galleries, the number of individuals of the different development stages (larvae of the 1st–3rd instars, pupae, callow beetles), number of emergence holes, maternal beetles remaining in the gallery. Also the presence of other bark beetle species was recorded.

The average number of eggs per female (±SD) and average length of maternal galleries (±SD) were calculated. The main response variables - colonization density, reproductive success and production of *I. typographus* were summarized using mean values per dm² of the bark (± SD). Reproductive success was defined as the average number of offspring per mother beetle, calculated as [number of beetles produced· 0.5]/ [number of egg galleries] (Hedgren, Schroeder 2004). Sex ratio was defined as a number of maternal galleries per one nuptial chamber.

The presence and number of larvae and adults of predators of *I. typographus* were recorded, especially those among Raphidioptera and *Medetera* (Diptera) and *Thanasimus* spp. (Coleoptera).

Maternal beetles were collected from each trunk sample area and held under cold conditions (4 °C) in Eppendorf plastic vials. In the laboratory, the beetles were dissected two days after collection, and the native dissections of their visceral organs (especially the digestive system, Malphigian tubules, gonads, fat body) were observed under a light microscope (magnification 100x to 400x, Arsenal LPE 5013i-T) and the presence of viruses, microsporidia, protozoa, nematodes and parasitoids was recorded.

The rate of parasitism of *I. typographus* by parasitoids (especially by representatives of Hymenoptera: Braconidae, Pteromalidae) was determined by visual examination in the field. The numbers of their larvae, pupae and cocoons of the given groups of Hymenoptera were recorded. The surviving individuals represent the sum of all living stages of bark beetles, and from these the larvae infected by parasitoids were subtracted. The rate of parasitism by parasitoids was calculated as the ratio of the total number of parasitoids (parasitoids larvae on the bark beetle larvae as well as outside bark beetle larvae, cocoons and pupae of the parasitoids in the beetles galleries) to the sum of parasitoids and all the living development stages of the bark beetles.

### Data analysis

Differences in number of parasitoids among trees and percentage of parasitism on tree sample areas (I–IV) were tested using the nonparametric Kruskal-Wallis test. Relationship between the number of entry holes of *I. typographus* and percentage of parasitism in infested trees was explored by regression analyses. The data were statistically evaluated using Statistica 9.

## Results

The volume of harvested wood infested by bark beetles it the locality "Na Ztraceném" was increasing steadily from 30th June until 15th August 2011, when 9,748 m³ of wood infested by bark beetles (5–72 % rate, depending on the individual segments) was reported in the area of 286 ha. In this second year of outbreak, *I. typographus* was documented on all infested trees. In average, a total of 34 m³/ha was infested by bark beetles. The species was present in 87.5 % of all samples. Exceptionally (in two samples), *Polygraphus poligraphus* (Linnaeus, 1758) was detected. Places not infested by *I. typographus* were either too dry or covered by the resin, or they were suitable for the beetle (fresh bast) but were not colonized.

The average number of nuptial chambers (entry holes) of *I. typographus* was 1.5±1.2 per dm² (0–2.8 holes per dm²). The length of maternal

galleries was 61.1±11.4 mm. The average number of eggs per female was 23.1±4.4. The population of *I. typographus* consisted of larvae (L3), pupae and callow beetles. The number of living specimens in various stages (larvae without parasitoids, pupae, callow beetles) was 6.7±5.4 individuals per dm². No emergence holes were observed. The proportion of maternal beetles remaining in the gallery was 11%. Reproductive success was 0.8 daughters (female offspring) per one mother beetle, percentage of surviving individuals varied between 1 and 18%. Sex ratio was 1.4±0.6.

The average number of predatory larvae of *Medetera* spp. was 0.2±0.2 per dm². The number of larvae of *Thanasimus* spp. averaged 0.03±0.06 per dm². Snakefly larvae (Raphidioptera) averaged 0.009±0.030 per dm².

From the 10 trees, a total of 228 live maternal beetles were dissected. The entomopoxvirus *ItEPV* was detected in the middle intestine of only 3.9% of those individuals. The microsporidium *Chytridiopsis typographi* [(Weiser, 1954) Weiser, 1970] was observed only once, in the form of thin-walled cysts within the stomodeum. The neogregarine *Mattessia schwenkei* (Purrini, 1977) was identified in the fat body in 34.2% of maternal beetles examined. In the samples, the presence of intestinal (12.4%) and extraintestinal nematodes (10.8%) was determined by dissection. In most cases, these were invasive larvae which were very difficult to identify. In 6.5% of the samples, the species *Contortylenchus diplogaster* (von Linstow, 1890) Rühm, 1956 was detected.

Only one dead maternal beetle was found in a maternal gallery upon which the hyphal filaments of a fungus from the genus *Beauveria* were evident.

The eggs of endoparasitoids were detected in 0.4% of adults of *I. typographus*. *Tomicobia seitneri* (Ruschka 1924) in the first larval instar in 1% of the beetles examined. Not closely specified endoparasitoids were detected in 14.7% of adults.

Larvae of ectoparasitoids were detected on the larvae of the third instar and pupae of *I. typographus*, the pupae of Chalcidoids (chalcid flies) from the Pteromalidae family or the cocoons of Braconidae were found only rarely. Adults were observed in two cases only. The average number of ectoparasitoids was 0.9±1.2 individuals per dm², and the average parasitism was 14.3±18.3%. The average number of parasitoids did not statistically differ among the studied trees (Kruskal-Wallis test: H=11.5, p>0.1). Percentage of parasitism did not differ among particular tree sample areas (Kruskal-Wallis test: H=6.5, p>0.5; Fig. 1).

No statistically significant correlation was found between the number of entry holes and the percentage of parasitism (y=8.2591+2.8691*x, r=0.17, p>0.5; R²=0.0289).

## Discussion

The volume of wood infested by *I. typographus* and other bark beetle species in the locality "Na Ztraceném" was increasing from the beginning of 2011, growing more than eight times from May to August. In this second year of outbreak, in average 34 m³/ha was infested by bark beetles. The number of maternal galleries in the studied trees was around 0.4 per dm² (number of entry holes*sex ratio). This conforms to published data (Komonen et al. 2010) about the large number of maternal galleries in standing trees. In fallen trees the densities of the chambers were 1.24±0.72/dm² and 1.62±1.26/dm², while in standing trees it was 4.46±2.07/dm². As in our data, no significant dependence on tree height (i.e. tree sample area) had been detected earlier by Komonen et al. (2010).

High population densities are also evidenced by the length of the maternal galleries and number of eggs laid. Various authors (e.g. Pfeffer 1952, Martínek 1961, Zumr 1985) have stated different numbers of eggs per female, but the averages range around 60 eggs. Low number of eggs per female (on average 23.1±4.4) at studied site can be explained by intraspecific competition which increases with growing population density. This is also confirmed by the results of other studies. For example, Anderbrant (1990), Weslien (1994), Grodzki (2004) likewise state that high density leads to a decrease in maternal gallery length and a reduction in the number of eggs laid.

In view of the number of eggs laid and the proportion of stadia living during the study and not parasitized (we are presuming there will no longer be high mortality), the portion of surviving individuals of *I. typographus* in particular tree sample areas is apparently small (1–18%). These numbers are, however, completely within the range of the known data. Of the original number of eggs laid, only 7–22% were surviving to become beetles, according to Thalenhorst (in Klimetzek, Vité 1989). Karpinski (1935) documented the mortality of *I. typographus* in a range of 96.3 and 98.8% and affected by various factors during development. Niemeyer (1987) studying the mortality of pre-imaginal stages in situations with 30,000–40,000 larvae per a tree determined the mortality to be approximately 50–75%. Such high larvae mortality in the larvae
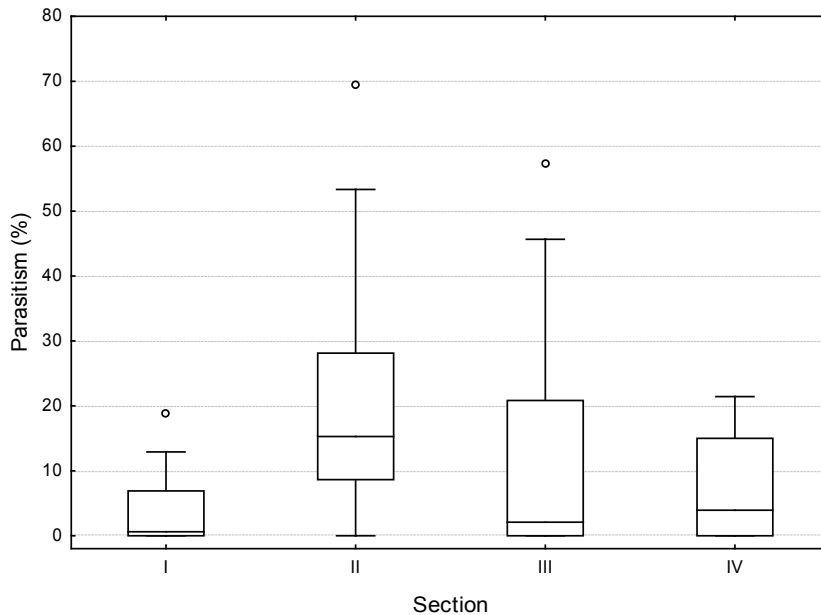
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*Fig. 1: Percentage of parasitism in I. typographus between tree sample areas I-IV. Box plots show median plus upper and lower quartiles for all three study sites in the Šumava Mts. in 2011. Minimum and maximum values are shown by the upper and lower whiskers (1.5 × interquartile range). Circles indicate outlying values. Sample area I was situated 0.5 m from the tree base, sample area II at middle distance between the base and the bottom of the tree's crown sample area III at the beginning of the crown, and sample area IV at the center of the crown.*

of *I. typographus* is most probably due to spatial competition. With high population densities, the competition among larvae increases. Fewer offspring then accrue to any individual female (Anderbrant 1990). Although the larvae tend to avoid one another in the galleries (De Jong et al. 1986), in cases of accidental crossing of their galleries cannibalism has been observed (Doležal, Sehnal 2007).

With the approximately determined number of 4 females per dm² and 6.7 surviving stadia per dm², the reproductive success is 1.6 stadia per female. This corresponds to the published data. Egg gallery density correlated negatively with reproductive success (Komonen et al. 2010, Faccoli, Bernardinelli 2011, Kausrud et al. 2012). At the density of 0.5 females per 1 dm², more than 20 offspring accrue to the average female; at the density of 31 females per dm², it is only 0.6 (Anderbrant et al. 1985, Anderbrant, Schlyter 1989). The reproductive success, as measured by number of offspring per female, was greater for down trees (8±7.5) than standing trees (1.82±1.18), and this can be explained by higher densities of galleries in the standing trees (Komonen et al. 2010).

At high densities, the duration of development of *I. typographus* decreases, but pupation always occurs only after ingesting a minimal quantity of food, and thus reaching the minimal weight of the larva. De Jong et al. (1986) state that the minimal length of the larval gallery was 20 mm, at which point the pupae weighed 1.6 mg. From this, the influence of the density of maternal and larval galleries per unit of area on the quality of the population can be indirectly inferred (De Jong et al. 1986). Competition resulting from high population densities is therefore considered to be the main factor influencing mortality and fertility of the beetle (De Jong et al. 1986, Anderbrant 1988, 1990, Wermelinger 2004, Faccoli, Bernardinelli 2011).

Due to high elevation and cool climate, there is only one generation of *I. typographus* documented regularly in the study area (Kalina 2000, Wermelinger 2004). Over the study period, therefore, overwintering maternal beetles as well as their offspring in the stages of higher instar larvae, pupae and callow beetles occurred in low numbers in the galleries during maturation feeding. No emergence holes were observed. This means that the beetles leave the bark and dig into the surrounding area (e.g. forest floor, where they overwinter) only after maturation of their gonads.

The members of the genus *Thanasimus* and flies of the genus *Medetera* are the most common predators of *I. typographus*, as are parasitic wasps from the families Pteromalidae and Braconidae (Eck 1990, Schopf, Kohler 1995, Weslien, Schroeder 1999, Hulcr 2001, Wermelinger 2002, Zelený 2007). The rate of occurrence of natural enemies in general, depends on a host tree species and even varies by a individual tree, as the bark texture is especially important (Lawson et al. 1997). The quantities of predators, pathogens and parasitoids correspond to the beetles' population density, but their response can be delayed by weeks or even as much as a year (Kausrud et al. 2012).

In this small-scale and short-term outbreak with high population density of *I. typographus* in an area in epidemic level the pathogenic infections of the maternal beetles are not high. For example, a common microsporidium *C. typographi* (Wegensteiner 2004, Takov et al. 2010) was determined only in one case, and *ItEPV* infection was also not high (3.9% of analysed individuals), even though Šumava locations have been among the places with very high infection (Weiser et al. 2000, Weiser 2002). A higher level of infection was displayed by the neogregarine *M. schwenkei* (34.2% of maternal beetles). This data can be overestimated. However, as it concerns beetles which remained in the galleries and never left them; such beetles could be affected by *M. schwenkei* infection occurring in the fat body in the form of scaphoid spores. All this, theoretically, may influence the tendency of beetles to emerge. It is presumed that only newly infected individuals leave the galleries, and therefore the pathogen occurs at higher rates towards the end of the vegetation season (Weiser 2002). The obtained data about pathogenic organisms (percentages) correspond with and/or are almost identical to the previous findings from the Šumava Mountains (Weiser et al. 2000).

The absence of the eugregarinida *Gregarina typographi* (*Fuchs,* 1915) is very surprising, as it is one of the most common pathogens of bark beetles (Wegensteiner 2004, Takov et. al. 2010) which is very intensively transferred in nuptial chambers of the beetle (Lukášová, Holuša 2011). Such absence, documented also in the populations with high densities of the beetle, is caused by the absence of those infections in the initial populations, Parasitism by entomophagous nematodes was greater than expected. For example, Tenkáčová, Mituch (1986, 1987, 1991) report from various locations (e.g. the Tatra National Park), report the presence of nematodes in bark beetles in the range of 4.3–5.1% of individuals examined. In the case of *I. typographus* in the Šumava National Park, higher values of parasitism by nematodes might be explained by the high density of the beetle population easily accessible to nematodes. In the case of *Contortylenchus diplogaster*, the given studies report its occurrence in about 9% of *I. typographus* individuals in the spring generation and slightly under 1% in the summer generation. The obtained data on the parasitism by this nematode species in the study area confirm to the known findings.

When evaluating the total rate of parasitism, it is necessary to observe how its values change on within individual trees, as even at relatively high levels of parasitism such rate only occurs in a small percentage of samples while the rest samples show very low parasitism (Hougardy, Grégoire 2001). Eck (1990) reported, for example, that if while infestation ranged between 0% and 70% more than half of the wood samples showed mortality of *I. typographus* below 5%. In the study area this was similar. *T. seitneri* responds to the *I. typographus* aggregation pheromone (Faccoli 2000). It is a common endoparasitoid in the adults (Eck 1990), but the rate of parasitism is low, i.e. 0–9.5% (Feicht 2004). The data in this instance fall entirely within the expected range, even though it concerns only larvae of the first instar, where the species affiliation is clear. In some cases, the total parasitism can reach 20–50% (Faccoli 2000). Other endoparasitoid larvae cannot be identified precisely. We can presume the samples to include the presence of another common species of endoparasitoid *Ropalophorus clavicornis* (*Wesmael*, 1835) (Faccoli 2001, Wermelinger 2002, Zelený 2007).

Most parasitoids of the Scolytinae are among the ectoparasitoids of larvae and attack their hosts through the bark (Kenis et al. 2004). Within the same tree, the representatives of Pteromalidae and Braconidae are predominate on the upper part of the trunk (with lower tree diameter), where the bark is thinner and smoother (Wermelinger 2002). In our study percentage of parasitism did not differ among trees section. This is probably the result of comparable bast and bark thickness of the trees, which did not vary much in the particular sections.

The parasitism rate most often varies in the range of 5–55% (Mills 1986, Eck 1990, Wermelinger 2002, Feicht 2004), but it can be even higher (Weslien 1992, Markovic, Stojanovic 2003). Parasitism rate in this study is near the lower limit of the published data outbreak

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## Acknowledgments

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