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University of South Bohemia in České Budějovice
Faculty of Science

Neglected aspects of bark beetle (Coleoptera: Scolytinae) ecophysiology

Ph.D. Thesis

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České Budějovice 2019

This thesis should be cited as:

Davídková, M., 2019: Neglected aspects of bark beetle (Coleoptera: Scolytinae) ecophysiology. Ph.D. Thesis Series, No. 14. University of South Bohemia, Faculty of Science, School of Doctoral Studies in Biological Sciences, České Budějovice, Czech Republic, 59 pp.

Annotation

The thesis describes several unknown aspects of the spruce bark beetle, *Ips typographus* (L.), and the double-spined bark beetle, *Ips duplicatus* (Sahlberg.), life-cycles and ecophysiology. The first study focuses on *I. typographus* and its dispersal under epidemic conditions in the National park Šumava and introduces a novel method of fluorescent marking and detection of captured specimens. The second study is focused on ability of *I. typographus* to establish so-called sister-broods, i.e. re-emergence of females that are capable to continue egg laying without a need to mate again. The importance of sister-broods becomes apparent mainly in recent hot and dry vegetation seasons, which is demonstrated by a comparison of recent and historical data. The third study focuses on temperature-dependent development of *I. duplicatus* under laboratory conditions by the means of sandwich method. Altogether, the studies underline practical importance of ecophysiological studies on bark beetles as one of the tools for their effective management.

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

České Budějovice, 19.8.2019

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This thesis originated from a partnership of Faculty of Science, University of South Bohemia, and Institute of Entomology, Biology Centre of the Czech Academy of Sciences, supporting doctoral studies in the Physiology and Developmental Biology study programme.

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Financial support

The studies were financially supported by:

- Project in the framework of the Operation Programme "Cross-Border Cooperation Austria – Czech Republic" of the European Union's European Regional Development Fund.
- Project LH 12098 from the Ministry of Education, Youth and Sports.
- Project 08/2009 – 2015 Forests of the Czech Republic, state enterprises.
- Project 02/2014 – 2018 from the Forests of the Czech Republic, state enterprises.

Acknowledgements

First, I sincerely thank RNDr. Petr Doležal, Ph.D. who has been my supervisor since my bachelor’s studies, for his support, guidance, and for his patience. Without him the completion of this work would not have been possible. I thank to all people who helped me with field experiments, especially to Ing. Venuše Plchotová, Ing. Oldřich Vojtěch, Ph.D., and Ing. Jiří Groda. I thank Prof. Robert Van Saun, DVM, MS, PhD for English correction of the manuscripts and his valuable advices. Special thanks belong to my family, who supported me through those many years of my studies.

List of papers and author’s contribution

The thesis is based on the following papers (listed chronologically):

1. Doležal, P., Okrouhlík, J., **Davídková, M.** (2016). Fine fluorescent powder marking study of dispersal in the spruce bark beetle, *Ips typographus* (Coleoptera: Scolytidae). European Journal of Entomology, 113(1), 1–8. (IF = 0.965)
   https://doi.org/10.14411/eje.2016.001
   Markéta Davídková, carried out the field experiments and the laboratory work (sex and physiological status determination of captured marked adults) with PD and JO.

2. **Davídková, M**., Doležal, P. (2017). Sister broods in the spruce bark beetle, *Ips typographus* (L.). Forest Ecology and Management, 405, 13–21. (IF= 3.126) https://doi.org/10.1016/j.foreco.2017.08.040
   Markéta Davídková designed the study together with PD, carried out the field experiments and the laboratory work, analyzed the data and wrote the manuscript with PD.

3. **Davídková, M**., Doležal, P. (2019). Temperature-dependent development of the double-spined spruce bark beetle *Ips duplicatus* (Sahlberg, 1836) (Coleoptera; Curculionidae). Agricultural and Forest Entomology. Advance online publication. (IF = 1.815)
   https://doi.org/10.1111/afe.12345
   Markéta Davídková designed the study together with PD, carried out the laboratory work, analyzed the data and wrote the manuscript with PD.

Co-author agreement

RNDr. Petr Doležal, Ph.D., the supervisor of this thesis and co-author of all presented manuscripts, fully acknowledges the contribution of Markéta Davídková as the author and her contributions as stated above.

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Content

CHAPTER I.

General Introduction

1. Introduction

Natural disturbances by fire, wind, drought and insect outbreaks are part of forest ecosystem dynamics. They create heterogenity and diversity (Bouget a Duelli, 2004; Seidl et al., 2017). In recent years, disturbance regimes in many forest ecosystems have changed (Schelhaas et al., 2003). There has been an increase of forest fires, insect outbreaks and periods of drought, in which climate change and increased variability of climate play a key role (Schelhaas et al., 2003; Linder et al., 2010). Abiotic disturbances are considered a consequence of climate extremes and frequently precede insect outbreaks or forest fires. Most important climate driver that influences forest ecosystems is temperature, followed by water availability (Schelhaas et al., 2003). Climate scenarios predict that by 2100 the temperature in UK and Ireland will increase by 2 °C, in Central Europe by 3 °C and in northern Europe by 4-5°C. Long life-span of trees makes forest ecosystems very sensitive to climate change (Linder et al., 2010), thus in the future disturbance by fire, drought wind, pathogens and insect outbreaks are likely to increase. It is predicted that disturbance by fire can increase by 82 %, by drought by 74 % and by insect outbreaks by 78 % (Schelhaas et al., 2003). Significantly higher number of disturbances is predicted in conifer forests than in broadleaf and mixed stands (Seidl et al., 2017), which can be documented by an increasing number of forest fires, windthrow damage and bark beetles outbreaks in European forests Since 1960 to 2000 (Schelhaas et al., 2003).

The most important biotic disturbance agents in European forests are insects (Schelhaas et al. 2003). Since 1988 to 2007, 3,6 % of total forest area in Europe has been affected by biotic disturbances. Of this number, 1,8% is insect-induced tree damage, 0,9 % pathogens and diseases and 0,9 % wildlife herbivory. Bark beetles are considered the most destructive biotic agents, especially the European spruce bark beetle (*Ips typographus* (Lineaus, 1758)) (Kautz et al., 2017). Average volume of timber damaged by bark beetles in Europe was estimated to be 2,9 million m^3 per year for the period of 1950 -2000 (Schelhaas et al. 2003). Other insect pest are defoliators from order Lepidoptera (e.g. pine processionary moth (*Thaumetopoea pityocampa,* (Denis & Schiffermüller, 1775)), larch bud moth (*Zeiraphera diniana*, (Hübner, 1799)) and geometer moth (Geomethridae)), although damage by these pests plays minor role compared to that caused by bark beetles. However, serious disturbances have been recently reported from Central European countries (Kautz et al., 2017; Lubojacký et al., 2019).

1.1. Bark beetle pests - knowledge of biology and its practical importance

The Scolytinae subfamily includes around 6,000 species worldwide, which are characterized by a high degree of habitat adaptation and diversity of life histories. The diversity of this subfamily is caused by long-lasting co-existence and adaptation to host trees and the life strategy to spend most of life cycle under the bark of the host. As a result, different types of food and reproductive behavior as well as various types of symbiosis with other organisms have evolved (Kirkendall, 1983; Knížek & Beaver, 2004; Hulcr et al., 2015). Bark beetles are one of the main factors that change forest structure and composition, start the processes of wood decomposition and influence nutrient cycling. Their symbiotic relationships and the transfer of a wide range of microorganisms significantly increase biodiversity, especially fungi and bacteria (Hansen, 2014; Hofstetter et al., 2015). However, only a few species - about 1% - are considered economically important pests capable of rapid population growth, destroying vital trees on large areas and causing significant environmental and economic damage (Wood & Bright, 1992; Cognato, 2015; Raffa et al., 2015; Six & Bracewell, 2015). Occasional local mass outbreaks and subsequent large-scale disturbances were reported in another 5- 10%

of bark beetles species (Kirkendall et al., 2015). The most important forest pests are members of the genus *Ips* in Europe and the genus *Dendroctonus* in North America. Recent mass outbreaks of *I. typographus* in many European countries are unprecedented in history and the annual sum of salvage and sanitation logging (including protective measures i.e. trap trees) reaches up to 50% of the total annual harvest volume (Hlásný et al., 2019). Similar data can be obtained from North America, where 710 million cubic meters of pine wood were extracted in the British Columbia alone within 10 years after outbreaks of *Dendroctonus ponderosae* (Hopkins, 1902). This amount represents half of all the pine forests in this territory (Kreiser et al., 2015). In the Czech Republic, annual sums of wood logging has been reaching record levels since 2015, mainly due to the dry and warm spring and summer months. Two representatives of the genus *Ips* - the spruce bark beetle, *I. typographus*, and the double-spined spuce bark beetle, *Ips duplicatus* (Sahlberg, 1836) - are considered to be the major pests causing massive spruce dieback in the Czech Republic.

The life cycle of both species is very similar and differences can be found predominantly in their overwintering strategies. (Davídková et al., 2017). Activity of *I. typographus* and *I. duplicatus* becomes apparent in spring, when the first adults leave overwintering habitats in the ground or under the bark of infested trees (Davídková et al., 2017; Kasumović et al., 2019) and search for suitable host trees. Male beetles attack first, create a nuptial chamber in the phloem, and attract females with aggregation feromones (Lieutier, 2002). In *I. typographus* number of females that enter a single nuptial chamber varies from 1 to 5, where higher numbers (4 to 5) may result in intraspecific competition and cannibalism of larvae (Anderbrandt, 1990; Weslien, 1994; Krauße-Opatz et al., 1995). In *I. duplicatus* the number of females per one male can be up to 8 females per 1 male. (Knížek & Holuša, 2007). However, the sex ratio oscillates around 1:1 and deviations on both sides may be caused by various factors, e.g. population density

(Lobinger, 1996; Holuša et al., 2012). After mating, the females begin to bore maternal galleries parallel to the trunk axis with eggs laid at the sides. Larval tunnels are perpendicular to the maternal galleries and third instar larvae create oval pupal chambers at the end, where they pupate. Freshly ecdysed beetles are light-colored and the subsequent darkening and sclerotization of cuticle proceeds during so-called maturation feeding, hand in hand with maturation of reproductive organs (Doležal & Sehnal, 2007). Number of generations that complete development to adults in a single vegetation season depends on several factors, e.g. temperature, latitude, food quality and availability etc. Latitude significantly affects the critical photoperiod at which reproduction ceases and the imaginal diapause (i.e. physiological status in which adults of both species overwinter) is induced. While in Central European populations diapause is induced after mid-August, when the day lenght shortens to approximately 15 hours (Schopf 1985, 1989; Doležal & Sehnal, 2007), the threshold is much higher in Scandinavian populations (Doležal & Sehnal, 2007; Schroeder & Dalin, 2016). As a result, the Central European populations from lower altitudes are multivoltine and up to three generations per vegetation season can develop. Scandinavian populations are almost exclusively monovoltine with the only exception from the south of Denmark, where two generations per vegetation season have been repeatedly documented. However, according to several mathematical models, the development of the second generation in Scandinavia is to be expected in near future due to global climate change (Jönnsson et al., 2007, 2009; Bentz et al., 2019). Temperature (and altitude) affect the number of generations per vegetation season directly by influencing reproductive processes as well as developmental rate of subadult stages. Generally, only one filial generation completes development at altitudes above 1000 m a.s.l, but high temperatures of the last few years have allowed the second generation to be established and even partially emerge. Lower elevations support for development of two to three filial broods, but fourth generation of *I. typogrpahus* and *I. duplicatus* has been recently recorded during exceptionally hot and dry year 2018 (Půlpán & Doležal, 2018; Davídková & Doležal, 2019).

Despite the similarities in their life-cycles there are significant differences in the overwintering strategies of the above-mentioned species. In both of them, imaginal diapause is induced in advance before the end of vegetation season. While diapausing adults of *I. typographus* remain under the bark of infested trees where they also overwinter (Doležal & Sehnal, 2007; Kasumovič et al., 2019), adults of *I. duplicatus* actively migrate to the forest litter in the surroundings of the infected trees since the end of August (Davídková & Doležal, 2019). Overwintering in the soil litter has certain specifics that pose both advantages and disadvantages. In the case of warmer winters, adults of *I. duplicatus* cannot replenish their energy reserves by occasional feeding during periods of higher temperatures (contradictory to *I. typographus*). This disadvantage is partially compensated by the insulating properties of the snow cover, so that overwintering individuals frequently don’t need to overcome temperatures deeply below zero degrees. Such adaptation to overwintering habitat properties was confirmed by measurements of supercoolling point (SCP). SCP is the temperature in which the body fluids freeze. Average values of SCP in *I. typographus* oscillated between -20 and -22 °C with minima around -29 °C (winter adults; Koštál et al., 2011). In *I. duplicatus*, the average SCP oscilated around -14 °C with minima slightly below -20 °C (Doležal and Davídková, 2016). From the abovementioned brief literature review it is evident that there is an abundance of available literature on *I. typographus*, whereas information on *I. duplicatus* is much more limited. *I. duplicatus* is a pest that has only been present in Central Europe since the late 19th century (Tredl, 1907; Karpinski, 1925, 1926; Wanka, 1927) and its potential to mass outbreaks did not manifest until early 1990s (Mrkva 1994, 1995, Pfeffer & Knížek, 1995; Holuša et al., 2003). After its expansion from North Moravia and Silesia to almost the whole area of the Czech Republic (Knížek, 2019) insufficient knowledge of its biology and lack of reliable methods of forest protection have been revealed. Information on essential aspects of ecophysiology and bionomy in both species is missing, although it could not only increase the effectiveness of protective measures, but also help in assessing possible changes in this species behavior under the ongoing climate change conditions.

2. Aims and scopes of the thesis

Previous paragraphs demonstrated the gaps in our knowledge of biology of the most ecologically and economically important central European bark beetle species. The experiments presented in this thesis were therefore aimed to shed light on several aspects of *I. typographus* and *I. duplicatus* life cycles, whose knowledge could aid in the optimization of protective measures leading to reduced costs.

1) Questions regarding the spatial dispersion of *I. typographus* are frequently raised but results of large-scale mark-recapture experiments are scarce. The aim of the first study was to test a novel method of passive marking the adults of *Ips typographus* with fluorescent powder (detectable on bark beetle epidermis in amounts as low as one grain of 2 nm in diameter) during their emergence from infested spruce sections and to determine the dispersal of *Ips typographus* by recapture and detection of the marked individuals in outdoor conditions in the Šumava National Park.

2) The most commonly applied protective measures against bark beetles include removal of infested timber and installation of trap trees. However, the effectivity of the above mentioned measures can considerably decrease, when so called sister brood females re-emerge before the timber is removed from spruce stands. The aim of present study was therefore to assess percentage of re-swarming females, their fecundity and timing of re-emergence. The applied methodology has intentionally been similar to that of Martinek (1956, 1957, 1961), which enabled direct comparison of results after almost six decades.

3) *Ips duplicatus* has rapidly spread across the whole area of the Czech Republic. The third study is aimed to characterize temperature effects on the development of *I. duplicatus* under

controlled conditions and to provide basic data for future phenology models and the effective management of this pest.

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CHAPTER II.

Fine fluorescent powder marking study of dispersal in the spruce bark beetle, Ips typographus (Coleoptera: Scolytidae)

EUROPEAN JOURNAL OF ENTOMOLOGY
ISSN (online): 1802-8829
http://www.eje.cz
Eur. J. Entomol. **113**: 1–8, 2016
doi: 10.14411/eje.2016.001
ORIGINAL ARTICLE

Fine fluorescent powder marking study of dispersal in the spruce bark beetle, *Ips typographus* (Coleoptera: Scolytidae)

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Key words. Coleoptera, Scolytidae, *Ips typographus*, bark beetle, dispersal, fluorescent powder, protected areas

Abstract. A novel method was used to study dispersal in the spruce bark beetle, *Ips typographus* (L.), under epidemic conditions (rapidly increasing population density) in the Šumava National Park. Infested spruce logs were coated with a fine fluorescent powder and the passively marked emerging beetles were captured in pheromone baited traps located at various distances from these logs. The number of marked beetles captured decreased exponentially with increasing distance from the release point. The sex ratio of the bark beetles was more female biased the further they were recaptured from the logs, being 57% and 60% at distances of up to 50 and 100 m, respectively. The maximum distance flown by a marked beetle recorded in this experiment was 1094 m. A model fitted to the data on dispersal indicates that 10% of the spruce bark beetles dispersed over distances of 55 m and 4 m in spring (overwintered parental generation) and summer (first filial generation), respectively. Differences between spring and summer swarming are briefly discussed.

INTRODUCTION

Even-aged monocultures of Norway spruce (*Picea abies*) are the main type of forests planted in the Czech Republic (Spiecker, 2003; Knoke et al., 2005; Yousefpour et al., 2010; Mansfeld, 2011). The transformation of natural mixed forests to spruce monocultures has led to changes in forest structure and composition as well as the spread of Norway spruce beyond its natural distribution (Knoke et al., 2005). As a consequence, forest managers are facing decreased resistance of stands to various biotic (insects, fungi) and abiotic (snow, storms, drought) factors (Spiecker, 2003).

The spruce bark beetle, *Ips typographus* (L.), is one of the most important forest pests in Central Europe (Reeve, 1997; Wermelinger & Seifert, 1999; Wichmann & Ravn, 2001). It is commonly considered to be a secondary pest of Norway spruce (Szujecki, 1987; Forster, 1993; Schwenke, 1996), but may occasionally infest also pine and larch. Dispersal of adults is a minor but key part in the life cycle, which may crucially influence the survival and reproductive success of the spruce bark beetle (Hawkes, 2009) and colonization of host trees (Kautz et al., 2011a). Before a host tree is infested, the adults exhibit a series of consecutive behaviours. According to Byers (1996, 2000), the initial phase of each swarming is assumed to be a nonlinear random flight, which continues until beetles respond to attractive stimuli and/or wind drift starts to have an effect. Hietz et al. (2005) report there is a strong correlation between bark temperature and the emission of attractants from spruce trees. The final acceptance of a host spruce tree is probably further conditioned by visual signals, which may (in some bark beetle species) prevail where volatile stimuli are absent, weak or uninformative (Campbell & Borden, 2009). The process of host tree acceptance is finally completed by a positive response of adults to gustatory stimuli and penetration into phloem of the tree (Raffa & Berryman, 1982). *Ips typographus* prefers weakened, damaged or dying trees, predominantly older than 60 years. Favourable climatic conditions, frequently in combination with the late removal of infested timber, may lead to an outbreak of spruce bark beetles (Kautz et al., 2011a; Lausch et al., 2011). During such outbreaks, *Ips typographus* population density increases exponentially and emerging adults are able to infest and kill even healthy trees on a large scale, which changes *Ips typographus* into a primary pest (Reeve, 1997).

Because of the enormous economic losses caused by the spruce bark beetle, it is crucially important to have a

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* Equal contribution.

detailed knowledge of its life cycle as this will aid in the optimization of protective measures leading to reduced costs. Interestingly, there are several aspects of spruce bark beetle biology that remain unclear and on which there is disagreement in the scientific literature. Importantly, questions regarding the spatial dispersion of the spruce bark beetle are frequently raised but rarely resolved. Few studies on the dispersal of *Ips typographus* are published and they used different methods. Most of these studies record the maximum flight distance of *Ips typographus*. Based on the methodology used, these studies may be divided into several groups. The first group includes studies based on more or less random catches or observations of beetles at various distances from the closest infestations or spruce stand. Flight distances reported in these studies are frequently many kilometres. The greatest distance reported, 43 km, is that in a study conducted by Nilssen (1984), who placed logs of spruce at various distances from the nearest spruce forest or bark beetle infestation and recorded the maximum distance at which individuals of various species of bark beetle were found. Nuorteva (1955) found adults of *Ips typographus* on pines approximately 60 km beyond the northern range of spruce in Finland. Fleischer (1875) and Komárek (1931) record spruce bark beetles flying from spruce stands and colonizing solitary spruce trees at distances of 20–30 km. The second group of studies used various methods of capture-mark-recapture, including several methods of marking the beetles prior to release. Duelli et al. (1997) used special pens to place coloured spots onto the pronotum of the beetles, which enabled the recaptured individuals to be sorted based on their release date. Every individual had to be marked manually, which made this method tedious and may also have influenced the behaviour and physiological status of the adults. Werner & Holsten (1997) and Franklin et al. (2000) stained the beetles in a sealed container with fluorescent powder. Thus, the need to handle every specimen was eliminated, but shaking the container to ensure the beetles were coated with the powder may still have influenced their dispersal behaviour. Zumr (1990, 1991, and 1992) captured adults in pheromone traps, marked them using a liquid fluorescent paint and then released them at two localities that differed in forest composition (mixed stand vs. spruce monoculture). He reported a relatively high percentage (63–65%) of marked beetles in pheromone traps installed up to approximately 1.2 km from the release points at both localities. Duelli et al. (1997) studied two categories of adults, those with and without previous flight experience, and marked these with different colours. The adults were then recaptured in pheromone traps arranged in three concentric circles (10, 160 and 400 m in diameter) in a pine (*Pinus sylvestris* L.) stand. Most adults flew less than 500 m but flight distances of more than 6 km were also recorded. Forsse & Solbreck (1985) tested the influence of energy reserves (stored lipid content) on flight distance. Measurements in flight mills indicated that *Ips typographus* adults can fly for distances of more than 19 km. The authors also studied vertical distribution of flying beetles in the field using suction traps placed at four heights (2, 9, 43 and 93 m above ground) on a TV tower, which indicated that only 14% of the beetles flew higher than 20 m above the ground. Zolubas & Byers (1995), who were the first to use fluorescent powder, recaptured marked adults in pheromone-baited traps placed at 10, 30, 60, 90 and 120 m from the release point.

A completely different approach is represented by the so called indirect methods. These methods are based on an analysis of aerial or satellite images of localities taken repeatedly several times a year. A comparison of such photographs provides information on successive activity of the pest and speed of its spreading through the canopy. Kautz et al. (2011b) analysed a dataset of infrared images documenting spruce bark beetle dispersion in the Bavarian Forest National Park since 1988. Similarly, Lausch et al. (2011, 2013) studied an 18 year dataset of colour-infrared aerial photographs of a selected part of the Bavarian Forest National Park. Both studies concluded that the new infestations occurred predominantly at distances of up to 500 m from previous ones. Indirect methods generate datasets on spatio-temporal scale but, unfortunately, with relatively low accuracy since the resolution of satellite images is not high enough to recognise a solitary infested tree. Moreover, it is impossible to identify the source of infestation and therefore the precise distance that the beetles flew before infesting a particular tree.

In the Czech Republic, the distance that *Ips typographus* can fly has become a political topic, mainly in relation to its recent outbreak in unmanaged parts of the Šumava National Park (Šumava NP). Šumava NP is part of the Bohemian Forest that occurs not only within the Czech Republic but also in Germany and Austria. The international character of the problem, together with the fact that neighbouring stands are predominantly commercial monocultures of spruce (except in the Bavarian Forest National Park in Germany), escalated the debate about the outbreak and spread of the spruce bark beetle and resulted in the Czech-Austrian governmental agreement that regulates the protective measures against *Ips typographus* in border areas.

The design of the current experiment was based on the above mentioned scientific literature. Marking the adults with fluorescent powder (detectable on bark beetle epidermis in amounts as low as one grain of 2 nm in diameter) increased the accuracy of flight distance measurements and the passive marking during emergence from logs also eliminated possible influence of handling on adult behaviour.

The aim of the present study was to test this method of marking and detection in outdoor conditions in the Šumava NP and determine the dispersal of *Ips typographus*, especially its spread from the unmanaged core zones to the surrounding intensively managed areas.

MATERIAL AND METHODS

Study site

The study area is within the Šumava National Park and Šumava Protected Landscape Area. Therefore, the process of site selection had to be a compromise between landscape characteristics and the relevant legislation (environmental law in the unmanaged core zone and forestry law in the surrounding areas).

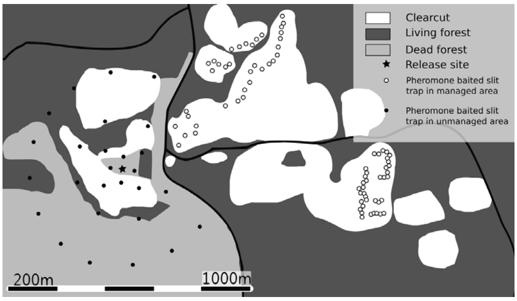

Fig. 1. Schematic map of the experimental site showing the location of the release point and the pheromone baited traps, which were periodically checked for the presence of marked beetles. The furthest clear cut with 24 pheromone baited traps, which was located about 3 km southwest of the release point, is not depicted. North is at the top of the map.

The experimental site (49°03´N, 13°25´E, 1150 m a.s.l.) is located in an unmanaged spruce-dominated forest in the core zone of the Šumava NP. The site consists of a large, south-facing deforested area (20,000 m^2), in which all trees were felled by the hurricane "Kyrill" in 2007. The locality was declared part of the unmanaged core zone in 2008 and the deforested area is surrounded by 60–80 year old spruce stands (Fig. 1). Its eastern side abuts on managed spruce forests and a barrier of pheromone-baited, poisoned spruce trunks was installed on the border in April 2013 to try to prevent the spread of beetles. The outbreak started in 2009 and resulted in an increasing proportion of dead standing trees. The volume of infested timber is not being monitored due to the conservation status of the locality, but an indication of the population density of the spruce bark beetle can be obtained from the maximum yearly catches of monitoring pheromone traps that reached 50,000 to 150,000 beetles per trap in the period 2009–2013. Air temperature at a sun exposed location was recorded at 30 min intervals using Commeter data loggers (Comet Systems, Rožnov pod Radhoštěm, Czech Republic).

Insects, fluorescent marking and data collection

A mark-release-recapture method was used to assess the flight distance of *Ips typographus*. To avoid physical damage during manipulation of beetles, a layer of fine fluorescent powder (Radglo JST-10, Radiant Color NV, Houthalen, Belgium) was dusted onto the surface of spruce logs, containing adult beetles, using a Birchmayer DR 5 CO$_2$-powered duster (Birchmeier Sprühtechnik AG, Stetten, Switzerland). Before flight, emerging beetles walk on the surface of the log, which resulted in 100% of them being passively marked by fine grains of the fluorescent powder that adhered to cuticular hairs, especially those on the apex of the elytra. This enabled their detection in mass trapping devices and on trap trees. The release point was in the middle of the deforested area and 70 infested spruce logs were transferred to the release point in April/May 2013 (spring swarming / overwintered parental generation) and June/July 2013 (summer swarming / first filial generation). The logs were cut from infested trees located on this site. The row of standing logs dusted with fluorescent powder was then covered with a tin roof to prevent the powder from being washed off by rain. Ten logs were randomly selected as soon as the majority of beetles had emerged and debarked to estimate the number of beetles they had harboured.

A total of 124 Theysohn pheromone traps (TPTs) baited with FeSex Typo dispensers (Ubik Karel, Prague, Czech Republic) were installed around the release point. Four concentric circles (50, 100, 200 and 375 m in diameter), each circle consisting of 27 TPTs, surrounded the release point and the numbers of beetles they caught were used for modelling the dispersion. The remaining 97 TPTs were installed in clusters in the surrounding clear cut areas and stand edges at distances ranging from 250 m to 3051 m from the release point (see Fig. 1).

Traps were checked weekly or twice per week during sunny and warm periods, when swarming occurred, and total catch per trap was recorded. The sampling period began on May 6, 2013 and ended on Sept 16, 2013. The presence of marked beetles was detected by illumination using a portable blue light source (cca 1W Luxeon Rebel LED Royal-Blue, Quadica Developments Inc., Brantford, Canada fitted into a cheap CREE hand torch). Yellow goggles filtering out the blue excitation light were used to enhance the effect of illumination and make it easier to identify marked specimens (for detailed spectral characteristics, see Okrouhlík & Foltan, 2015). Horizontal transfer of fluorescent powder onto unmarked specimens in TPTs was unlikely as shown during preliminary laboratory and field experiments performed in 2012 (Doležal & Okrouhlík, unpubl. data). The sex of positively identified beetles was then assessed by dissection in the laboratory; however, this was possible only in about 69% of the cases. The remaining samples were too dry or too decomposed to be dissected.

Dispersion modelling

Only capture data within the unmanaged zone were used for dispersion modelling. The pooled numbers of marked *Ips typographus* captured in each circle were divided by the number of traps in a particular circle. The resulting numbers, i.e. marked beetles per trap at four distances, were fitted using the following the model:

$$mSBB(dst) = a \times \left(e^{b \times dst^{-\frac{2}{3}}} - 1 \right)$$

where, *mSBB(dst)* is the predicted number of marked spruce bark beetles recaptured at distance *dst* from the release point, *e* is the Euler number and *a* and *b* are estimated parameters of the model.

Model parameters were estimated using the Rosenbrock and quasi-Newton method with the following loss function: [ln(*pred*) – ln(*obs*)]^2, where *pred* and *obs* were values predicted by the model and values actually observed, respectively. This loss function enabled more precise fitting of more distant circles as suggested by Turchin & Thoeny (1993).

An estimated maximum distance dispersed by 50% and 10% (median and upper 10% quantile of dispersion distance) of the marked beetles was calculated using the model as follows:

$$y = 100 - \frac{\int\limits_{x=50}^{disp} mSBB(x)}{\int\limits_{x=50}^{1200} mSBB(x)}$$

where *mSBB(x)* is the predicted number of marked spruce bark beetles recaptured at distance *x* from the release point. We used the trapezoidal rule to calculate the definite integral with a step of 1. Starting with 51, the parameter *disp* in the above equation was increased by one until the result *y* reached approximately 50 and 10, respectively.

To evaluate the potential threat of beetles dispersing from unmanaged into managed stands, capture rates predicted by the above model were compared to actual capture rates of the traps located in the neighboring managed area. Prior to analysis, these traps were divided into groups according to their distance from the release point. Mean distances of these groups from the release point were 375, 520, 700, 900 and 1100 m. Counts of marked

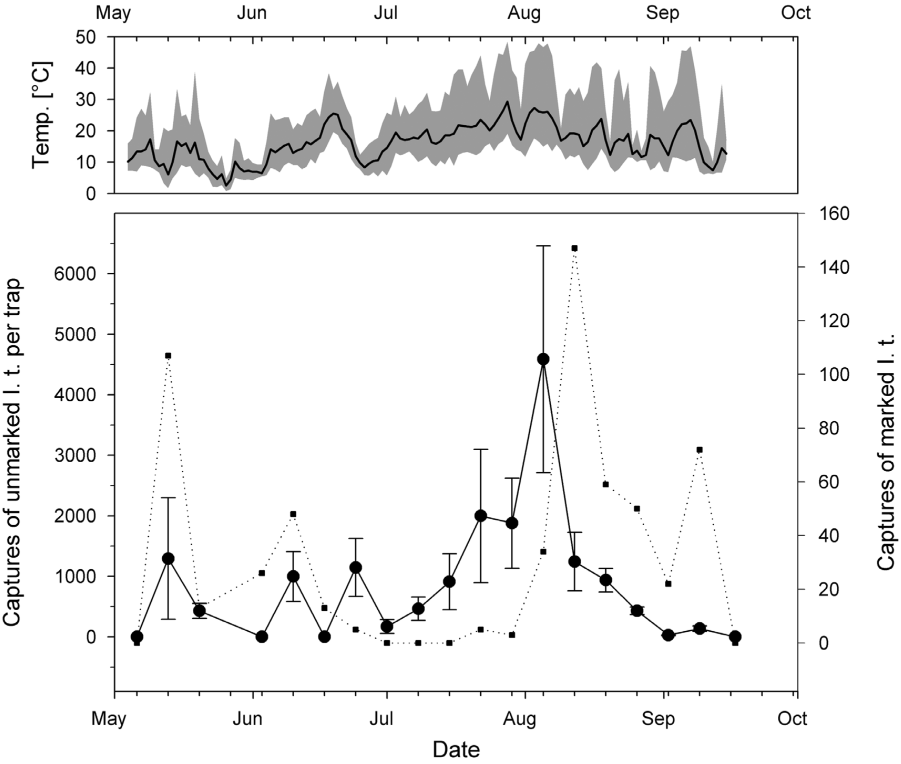

Fig. 2. Spruce bark beetle, *Ips typographus*, (I.t.) density (circles ± S.D., connected with solid line) expressed as average number of beetles captured per pheromone baited slit trap together with absolute counts of marked beetles recaptured (squares connected with dotted line) during 2013. In the upper part, range in daily temperature (grey area) is plotted together with average daily temperatures.

beetles captured by the traps in each group were divided by the respective number of traps.

The direction in which most *Ips typographus* dispersed was evaluated using χ^2 tests. Numbers captured at 50 m and 100 m in spring and summer were evaluated separately assuming they dispersed uniformly in all directions. To evaluate the sex ratios of beetles that dispersed over various distances, captured marked beetles were dissected and their sex determined. Traps were divided into categories based on their distance from the release point and their captures pooled. A χ^2-test was used to test the statistical difference between the actual sex ratio and a 1 : 1 sex ratio (Zumr, 1995; Lobinger, 1996).

χ^2 tests were performed using STATISTICA 12 (Dell, 2015) and no family-wise error correction for multiple tests was applied.

Table 1. Beginning and end dates of trap monitoring, approximate numbers of marked beetles released and numbers of marked beetles captured during the spring and summer swarming at the experimental site in 2013 together with estimated dispersion model parameters and estimated median (ED50) and upper 10% quantile (ED10) of dispersion distances of the marked beetles.

	Swarming	
	spring	summer
Beginning	16th May	23rd July
End	27th June	10th September
Marked *Ips typographus*		
released (approx.)	25000	20000
captured	215	385
Dispersion model		
parameter *a*	76.185	85.597
parameter *b*	0.1548	0.1658
variance explained	99.9%	79.6%
ED10	555 m	432 m
ED50	86 m	76 m

RESULTS

Overwintered adults of *Ips typographus* started to fly in the second week of May. At that time, the number exceeded 1200 unmarked beetles per trap per week (BTW). Low temperatures and rainy weather during the following weeks interrupted the swarming for almost a month during which very few beetles were caught. The swarming then resumed from the second week of June until the end of the month. The average numbers caught were around 1000 BTW. The adults of the filial generation were first caught at the end of July and a maximum number of almost 7000 BTW was recorded at the beginning of August. The activity gradually decreased thereafter and the last capture of approximately 100 BTW was recorded on September 9, 2013 (Fig. 2).

The captures of marked beetles correlated with the general pattern of bark beetle activity (Fig. 2). The only exception occurred at the end of the growth season, when

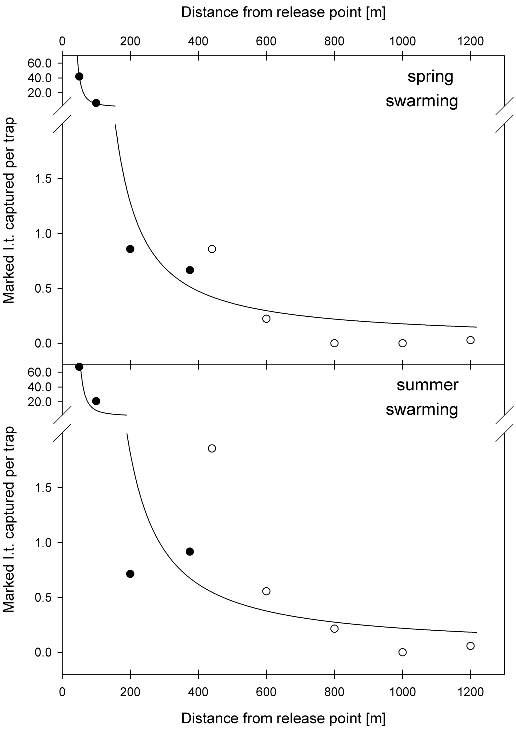

Fig. 3. Counts of marked spruce bark beetles, *Ips typographus*, (I.t.) caught per trap at various distances from the release point in unmanaged (closed circles) and managed areas (open circles) during the spring (top) and the summer (bottom) swarming in 2013. Closed circles were fitted by the model (solid line). See Material and methods section and Table 1 for more details.

an extraordinarily high percentage of marked beetles was recorded.

The total numbers of spruce bark beetles captured, estimated numbers of beetles released and length of the periods sampled during the spring and summer swarming are summarized in Table 1.

A total of 600 marked *Ips typographus* were captured during this study and the maximum distance flown recorded for a marked beetle was 1094 m. Fitted models for the dispersal of *Ips typographus* during spring and summer swarming periods are presented in Fig. 3, which indicates that 10% of the marked beetles in the spring and summer swarmingflew more than 555 m and 432 m, respectively.

More than 70% of the beetles captured were found in traps that were more than 50 m from the release point. In addition, the 200 m trap circle captured surprisingly few marked beetles (6 and 5 beetles, respectively, in the spring and summer swarming).

Table 3. Percentage of females and the number of marked beetles recaptured in pheromone baited traps at various distances around the release point that were dissected. The 1 : 1 sex ratio was tested using a χ^2 test and χ^2 and p are included for reference. Asterisk indicates a statistically significant difference at α = 0.05.

Distance (m)	Females (%)	Dissected *Ips typographus*	χ^2	p
0–50	57.1	340	6.78	0.009*
50–100	59.8	102	3.92	0.048*
100–200	55.6	9	0.11	0.73
200–300	33.3	6	0.66	0.41
300–400	50.0	26	0	1

Catches of marked beetles in neighboring managed stands grouped according to the distances from the release point are depicted together with the model estimates in Fig. 3.

Beetles did not disperse uniformly in all directions, with the north and north-east directions the most commonly recorded (see Table 2).

The sex ratio of recaptured beetles was significantly female biased (57% and 60%) at short distances (50 or 100 m, respectively) from the release point. However, at greater distances the sex ratio was not significantly different from a 1 : 1 ratio (see Table 3).

DISCUSSION

Bark beetle dispersal is influenced by numerous internal (e.g. weight, size, energetic status, population origin – non epidemic vs. epidemic, reaction to visual stimuli etc.) and external factors (e.g. breeding site availability, presence of volatile attractants, temperature, wind etc.) (Franklin & Grégoire, 1999; Wichmann & Ravn, 2001; Campbell & Borden, 2009; Dworschak et al., 2011; Kautz et al., 2011b). The different flight patterns recorded for adults of non-epidemic and epidemic populations are discussed by numerous authors and a possible explanation can be summarized as an interplay between food and breeding source availability, energy reserves (competition) of migrating specimens and presence/absence of either primary or secondary attractants (Weslien & Lindelöw, 1990; Safranyik et al., 1992; Franklin & Grégoire, 1999; Kautz et al., 2011b). The frequency of different flight distances recorded at the site studied decreases exponentially with the distance from the release point. This indicates that higher population densities effectively reduce the average flight distance and beetles search for a host tree close to the original infestation. High numbers of beetles during outbreaks

Table 2. Directional uniformity of *Ips typographus* dispersal. Summary of the statistics of uniformity of dispersal (χ^2, df and p) together with the most commonly recorded (MOD) and the least commonly recorded directions (LOD). N – northward, S – southward, E – eastward, W – westward.

	Spring swarming					Summer swarming				
	χ^2	df	p	MOD	LOD	χ^2	df	p	MOD	LOD
50 m	84.6	3	$<10^{-6}$	N	S+W	41.3	3	$<10^{-6}$	N	S
100 m	7.33	3	0.06	SE	NW+SW	54.5	3	$<10^{-6}$	NE	SE

probably ensure that even healthy trees with strong defense are unable to withstand the attack. The attractiveness of such trees is gradually increased due to the aggregation pheromone produced by each adult that lands on the trees (Franklin & Grégoire, 1999). Infesting the nearest tree is also more advantageous because of the energy demands of flight, although a direct relationship between the total lipid content and flight distance has never been proved (Botterweg, 1982; Dworschak et al., 2011).

The marking and fluorescent detection used in the present study is a unique combination of known methods and a novel application of others. The large scale labelling of logs is fast (using suitable dusters) and only a dust-protection mask and protective overalls are needed. The dye used is non-toxic and, because of its fine grain size, it is unlikely to interfere with insect flight capabilities. Construction of tin roof shelters to prevent the dye being washed off by rain reduces the need for reapplication. We employed, to our knowledge, a unique and simple conversion of a cheap handheld lamp with a CREE LED into a fluorescence detector by refitting it with a LED source of defined emission spectra suitable for excitation of the whole range of JST series of fluorescent powders. It offers several advantages compared to other methods. Mainly, there is no potentially harmful blacklight and the light source is cheap (1W LED is about 10 USD and the lamp is another 15 USD). The yellow goggles are a very beneficial and inexpensive (from 2 USD) replacement for costly low/band-pass filters and can be used for detection of all emission colors except blue. On the other hand, employment of hand-held violet or blue lasers could enable detection from greater distances (Rice et al., 2015).

The bark beetle dispersion model employed here can predict dispersal patterns at greater distances than the more generally accepted models (Turchin & Thoeny, 1993; Duelli et al., 1995) on which it is based. The present model uses data recorded within unmanaged forest, which borders on managed stands, where pheromone baited slit-traps were used as a monitoring and protective measure. The capture of marked beetles in these traps were compared to the captures predicted by the dispersion model. It is clear that, at shorter distances (in this case, 440 m), the risk of *Ips typographus* spreading from an unmanaged to a managed area was higher than predicted by the model, whilst at greater distances (>800 m), the risk of *Ips typographus* dispersion was lower than predicted. Such information is of importance for foresters planning protective measures against the spruce bark beetle. We confirm previous practical experiences in the Bavarian Forest NP (Heurich et al., 2001) and Harz NP (Niemeyer et al., 1995) that the spread of beetles from unmanaged areas with a high population density to managed stands can effectively be prevented by buffer zones located within 100–1500 m. Our model suggests that stands at distances of more than 500 m should be at less risk of infestation and, therefore, it can be concluded that 500 m protective zones should effectively reduce the number of migrating beetles. This finding is in agreement with those of Kautz et al. (2011b) and Lausch et al. (2011, 2013) who record that 95% of the new infestations occurred within 500 m. Similar conclusions are drawn by authors that recently studied the question of spruce bark beetle population levels in unmanaged and surrounding managed forests. Generally, it can be concluded that under non-epidemic conditions, unmanaged stands do not necessarily pose a threat to surrounding managed forests (Schlyter & Lundgren, 1993). However, rapid population growth in unmanaged stands may threaten neighboring managed forests at distances of up to 500 m following abiotic disturbances (e.g. storms or drought) (Wichmann & Ravn, 2001).

The present model estimated that approximately 10% of beetles migrated for distances of more than 500 m, which corresponds with the results of Wichmann & Ravn (2001), who report that 90% of new infestations occurred within 100 m of previous infestations. Thus, it can be concluded that the percentage of long-distance flyers in a population varies between the above mentioned 10% and the figure of 50% estimated by Duelli et al. (1995). That beetles that overwinter (spring swarming) fly greater distances is also reported (Furuta et al., 1996). The higher tendency for the overwintered generation to migrate may be attributed to the resumption of direct development following overwintering and the necessity for these beetles to replenish energy reserves and search for new breeding sites. Such behavior is common in many other species of insects (Košťál, 2006). The maximum distances flown by the spruce bark beetle recorded in the present study and those reported in other studies are very convincing, regardless of differences in the methods used. The most distant catches of marked beetles recorded in this study were almost 1100 m from the release point. Zumr (1990, 1991, 1993) recaptured marked spruce bark beetles at distances up to 1200 m regardless of forest structure and composition, whilst Weslien & Lindelöw (1990) recaptured 2% at 1200–1600 m. Therefore, it can be concluded that a significant percentage migrate longer distances. This observation might explain the occasional observations of mass infestations at localities where bark beetles were not previously reported by foresters. This information may also be of practical importance. Currently, the most widely used protective measures employed against the spruce bark beetle include timely removal of potential breeding material and sanitation felling of infested trees (Wermelinger, 2004). Various trapping devices (e.g. trap trees, poisoned trap trees, pheromone traps etc.) are also being installed in order to prevent attacks on living trees in the sanitation felling area. Although relevant legislation differs between European countries, the exact number of trapping devices deployed usually depends on the number of infested trees that were found and felled on site during the preceding period. Based on the results of this study, some trapping devices should be installed across a wider area (as permitted by terrain / canopy configuration) to restrict the spread of an infestation.

The low catch of the traps in the 200 m trap circle (6 and 5 beetles, respectively, in the spring and summer swarming) recorded in this study can be attributed to the fact that most of the traps in this circle were located inside the canopy or at the boundary between living and dead standing forest. Relatively high catches of marked beetles at the end of the growth season compared to the general activity and catches of unmarked beetles were probably due to the fact that the bark of the logs at the release point was too disturbed by previous development and feeding to provide a suitable overwintering habitat for the remaining beetles. The adults were thus forced to emerge and search for a new habitat in which to overwinter. Such behaviour is common to most pre-diapause insects (Košťál, 2006).

In traps closer to the release point, more marked female beetles were captured than males. A reproductively successful male usually mates with two to three females (Wermelinger, 2004). Males also initiate colonization of a new host tree. Therefore, a greater flight distance of males is to be expected. Unfortunately, there were too few captures at the greater distances to show if there was any significant departure from a 1 : 1 sex ratio (Zumr, 1995; Lobinger, 1996). However, higher captures of females at closer distances may indicate either that males had dispersed further or were not as attracted by synthetic pheromones as females. A lower percentage of males in pheromone trap catches has previously been mentioned by many authors (Annila, 1971; Zumr, 1982; Lindelöw & Weslien, 1986; Schlyter et al., 1987; Weslien & Bylund, 1988). Another possible explanation might be a higher percentage of females developing during periods of high population density. Such a shift in sex ratio (up to 70% females) is reported by Lobinger (1996) in Southern Bavaria.

Although wind speed/direction data were recorded during this study, the resolution of beetle collections (once or twice a week) did not enable a direct comparison of wind speed/direction and position of the marked individuals captured. The fact that beetles did not disperse uniformly in all directions can most probably be attributed to variations in the attractiveness of different areas of the forest. The managed forests in the eastern part of the study area consisted of numerous sunlit stand edges, which would be attractive to bark beetles, whilst the unmanaged stands were characterized by a very high and increasing proportion of dead trees.

ACKNOWLEDGEMENTS. This research was by supported by a project in the framework of the Operation Programme "Cross-Border Cooperation Austria – Czech Republic" of the European Union's European Regional Development Fund, by project LH 12098 from the Ministry of Education, Youth and Sports, and by project 08/2009 from the Forests of the Czech Republic, state enterprises. We would like to thank B. Miklas, M. Moravcová, O. Vojtěch, V. Plchotová and students from the Gymnázium J. Ortena Kutná Hora for the support in the field. The authors would also like to thank C. Stauffer and Y. Moodley for their help with experimental design, two anonymous reviewers, whose comments considerably increased the quality of the manuscript and G. Small and A.F.G. Dixon for English correction.

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Received June 17, 2015; revised and accepted September 29, 2015

CHAPTER III.

Sister broods in the spruce bark beetle, Ips typographus (L.)

Forest Ecology and Management 405 (2017) 13–21

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Sister broods in the spruce bark beetle, *Ips typographus* (L.)

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ARTICLE INFO

Keywords:
Re-emergence
Sister broods
Ips typographus
Climate change
Pest management

ABSTRACT

Establishment of sister broods in the spruce bark beetle, *Ips typographus* (L.), was investigated at three localities of different elevations (600. 800 and 1100 m a.s.l.) in Sumava Mountains during two consecutive years (2011, 2012). Three sister broods were established at 600 and 800 m a.s.l., in both years, while only two occurred at 1100 m a.s.l. in 2011. A third sister brood at 1100 m a.s.l. was recorded only in 2012. Up to100% of females re-swarmed during first re-emergence. Second and third sister broods were established by 8–90% and 0–22% of females, respectively. The number of established broods is highly correlated with infestation density. Data recorded in this study were compared with similar studies conducted in 1950s by Martinek (1956, 1957, 1961). The influence of climate change and rising temperature averages upon number and intensity of sister broods is discussed as a possible explanation.

1. Introduction

The spruce bark beetle, *Ips typographus* (L.), is a serious pest of spruce monocultures in Eurasia (Reeve, 1997; Wermelinger and Seifert, 1999; Wichmann and Ravn, 2001; Wermelinger, 2004), which causes considerable economic and environmental damage throughout its entire distribution area. Yearly volume of timber felled in the Czech Republic due to bark beetle infestations exceeded 650,000 m^3 in 2012 (Knížek and Modlinger, 2013). On the European scale, cost of protective measures and losses on wood products commercial value represent billions of euros every year (Steininger et al. 2015).

The spruce bark beetle is considered a secondary pest that prefers weakened and dying trees over 60 years of age (Szujecki, 1987; Forster, 1993; Schwenke, 1996; Zahradník and Knížek, 2007) and starts the process of wood and bark decomposition. As typical r-strategists, bark beetles are able to exponentially multiply under suitable weather conditions and when food source (vulnerable trees or logs) is provided, for instance, by windthrows and other natural calamities (Wermelinger, 2004). High population densities lead to outbreaks during which bark beetles also attack living healthy trees regardless of their age (Wermelinger, 2004; Zahradník and Knížek, 2007). This way, the spruce bark beetle becomes a primary pest that causes tree mortality in large areas (Kausrud et al., 2012). Most aspects of the spruce bark beetle's life cycle are well-known and reviewed by numerous authors (Zumr, 1995; Wermelinger, 2004). The beetles predominantly overwinter as adults in the state of imaginal diapause. Diapause is induced by short day-length and low night temperatures of late summer. Critical photoperiod that induces diapause in 50% of adult bark beetles of Central European population is 14.7 h. Under natural circumstances, such day-length occurs in mid-August (Doležal & Sehnal, 2007). Similarly to many insect species in the temperate zone, diapause ends in December, but beetles remain inactive due to adverse environmental conditions (post-diapause quiescence) until spring rise of temperature (Košťál, 2006, Doležal and Sehnal, 2007).

In spring, overwintered males attack suitable host trees, bore a mating chamber, and start producing aggregation pheromones. In Central Europe, the timing of their emergence (i.e., spring swarming) depends on temperature and elevation. In lowlands, spring swarming usually starts the end of April, while at elevations above 800 m a.s.l., swarming usually begins one month later (Skuhravý, 2002; Faccoli, 2009). Rainy weather may cause a delay of swarming until the beginning of June (Knížek et al., 2011). Swarming is strongly affected by temperature. In the population from Kalkapen Alps, Austria, the lower temperature threshold for flight activity was 16.5 °C and temperature optimum was between 21 °C and 26 °C (Wermelinger, 2004; Baier et al., 2007). One male mates with one to three females (Wermelinger, 2004; Zahradník and Knížek, 2007). Fertilized females bore maternal galleries parallel with the trunk axis and lay eggs aside. One female lays approximately 50 eggs per ovarian cycle (Merker and Wild, 1954; Zumr and Soldán, 1981; Skuhravý, 2002). After egg laying female ovaries and energetic reserves are depleted and therefore another intense feeding occurs. During this period of so called regeneration feeding ovaries are being restored and egg laying may continue (Merker and Wild, 1954; Zumr and Soldán, 1981; Wermelinger and Seifert, 1999). Three

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http://dx.doi.org/10.1016/j.foreco.2017.08.040
Received 6 June 2017; Received in revised form 22 August 2017; Accepted 23 August 2017

reproductive cycles per female, with equal number of oviposited eggs in each of them, were well-documented by Zumr and Soldán (1981). Oviposition period lasts up to 10 days and females oviposit in temperatures ranging from 12 °C to 33 °C (Wermelinger and Seifert, 1999). Larvae bore galleries perpendicular to maternal tunnels with oval shaped pupation chambers at the end. In these chambers, the metamorphosis from pupae to adults occurs. Gonads of newly emerged bark beetles are not fully developed and their cuticle is not sclerotized. Beetles then pass through the period of so called maturation feeding and gonadal development corresponds to cuticle coloration (Merker and Wild, 1954; Zumr and Soldán, 1981; Wermelinger and Seifert, 1999). Under Central European conditions, the development of one generation lasts 6–10 weeks and is exclusively temperature dependent until shortening day-length prolongs the development of larvae (Doležal and Sehnal, 2007).

Sister broods or re-emergence is a phenomenon common to the spruce bark beetle and several other species of Scolytinae subfamily. Re-emergence means that females finish ovipositon, re-emerge and replenish their energy reserves by so called regeneration feeding (Wermelinger and Seifert, 1999). Depending on phloem quality, regeneration feeding may occur prior to re-emergence in original host trees or in newly infested ones. Once energetic reserves and ovaries are replenished, oviposition continues, without a need to mate again (Martinek, 1956; Anderbrant and Löfqvist, 1988). The most probable advantage of re-emergence is seeking new material for regeneration feeding, egg laying and suitable habitat for development of offspring, and reduction of intraspecific competition. On the other hand, reswarming increases the risk of dying before infesting a new host tree (Kirkendall, 1983). In Central Europe, the re-emergence of sister brood females and emergence of offspring commonly overlap. The timing of sister brood re-emergence depends predominantly on temperature and elevation. Cold and rainy weather delays the spring swarming and if unfavorable conditions prevail, re-emergence is delayed as well. Hence the number of sister broods per vegetation season is reduced. On the contrary, warm and sunny weather shifts spring swarming towards the end of April or beginning of May, which increases the number of sister broods. According to Martinek (1956, 1957, 1961), the second sister brood did not occur above 700 m a.s.l. Over 60% of the females established the first sister brood and 20–35% re-emerged for the second time (Martinek, 1961) in lower elevations. Reproductive potential of females may not be exhausted during a single ovarian cycle, and thus the number of females establishing sister broods may also be restrained by weather or by lack of suitable host trees (Annila, 1969; Anderbrant and Löfqvist, 1988). Under laboratory conditions and exceptionally high infestation densities (8 females/dm^2) the females re-swarmed earlier than ones in logs with low infestation density (2 females/dm^2). One third of females were allowed to repeatedly mate with males after re-emergence. However, repeated mating did not increase the number of eggs laid, when compared to the non-mated females. Furthermore, size of egg-batches did not depend on infestation density and was not affected by first brood size (Anderbrant and Löfqvist, 1988).

The aim of present study was to assess percentage of re-swarming females, their fecundity and timing of re-emergence. Re-emergence was studied in a two-year experiment at three localities differing in elevation within the National Park Šumava. We have intentionally applied similar methodology as Martinek (1956, 1957, 1961), which enabled direct comparison of results after almost six decades. Such knowledge may be of high practical importance because high percentages of reswarming females may considerably reduce effectiveness of two most commonly applied protective measures that include removal of infested timber and installation of trap trees.

2. Material and methods

2.1. Study sites

Experiments were carried out at three localities in the Šumava Mountains that differed in elevation. The study sites were located at altitudes of 600, 800 and 1100 m a.s.l. and all sites were chosen to be situated on southern slopes with spruce stands of the same age structure (80–100 years old). All localities consisted of a dense forest canopy and clearcut patches with sunlit stand edges attractive for bark beetle attack. Local populations of the spruce bark beetle were of the same abundance and in the epidemic (gradation) phase. Population dynamics has been monitored since 1995 and therefore voltinism at all three sites was assessed as follows. At the lowermost polyvoltine site (600 m a.s.l., 49 °4′27.399″N; 13 °55′38.643″E), the spruce bark beetle usually completes two to three filial generations per vegetation season. At 800 m a.s.l. (49 °1′49.231″N; 13 °53′4.448″E), the emergence and development of the second filial generation strongly depends on weather conditions. Therefore, this site was considered partially bivoltine. Only one filial generation per vegetation season completes development to adults at 1100 m a.s.l., (48 °58′9.218″N; 13 °42′3.504″E).

All study sites were located in state owned and managed commercial forests. Standard protective measures against bark beetles included trap trees, poisoned trap trees and pheromone traps. Both pheromone traps and trap trees were used to monitor the population dynamics of the spruce bark beetle. Two series of trap trees were applied during the vegetation seasons 2011 and 2012. Pheromone traps were placed at least 10 meters from stand edges and there were not more than 2 to 3 traps per site. The Theysohn type pheromone traps with FeSex Typo dispensers (Ubik Karel, Prague, Czech Republic) were used in the study.

Air temperature on sunlit stand edges and in the shade was continuously measured with Cometter dataloggers (Comet Systems Ltd., Rožnov pod Radhoštěm, Czech Republic) at 30 - minutes intervals at all the sites.

2.2. Experiments

Experiments were first conducted in 2011 and repeated in 2012. Two cages were placed on each site at the beginning of vegetation season. One cage was placed on the sunlit stand edge and the other one was positioned inside the forest canopy to be fully shaded. All cages were of the same size (1 × 1 × 1 m) and construction. The base consisted of waterproof hardboard, the frame was made of battens (4 × 5 cm) and walls were covered with polypropylene net. Upper part of the cage was hinged and adjusted by lockable clips. Double layer of window seal was glued between lid and frame to prevent bark beetles from escaping.

Twelve logs (each 50–100 cm long and approx. 25 cm in diameter) were cut from infested trap trees at all localities at the end of spring swarming. All logs (on one locality) were cut from the same tree to have similar infestation density and thickness of phloem. Six infested logs were then paired with 6 logs cut from freshly felled uninfested trees (approx. 60 cm long and approx. 25 cm in diameter) and altogether placed into cages (see above). Reemergence of bark beetles was checked weekly or twice a week during exceptionally warm periods. New boreholes found on the surface of uninfested logs were marked with colored sprays. Development of filial generations in the logs that were cut from trap trees was checked twice a week. Logs were removed as soon as occurrence of 3rd instar larvae and pupae were recorded. Removed logs were immediately replaced by freshly cut uninfested ones.

Logs removed from cages were marked; transported to Institute of Entomology and debarked to record the following parameters:

1. Total area of phloem
2. Number of boreholes – date of infestation was assigned to each

borehole/gallery according to the color mark
3. Number and length of maternal galleries
4. Number and length of regeneration feeding galleries
5. Number of eggs laid
6. Number of hatched larvae

Non-emerged parental beetles were collected and frozen for later dissection to assess the sex of adults and status of ovaries in females. Ovaries were photographed using light microscope Leica S6D (Leica Microsystems Inc., Wetzlar, Germany) with camera Canon EOS 500D (Canos Inc., Japan).

Daily averages were derived from temperature records and used to calculate the sums of degree-days (DD) needed for completion of key events in the spruce bark beetle life cycle. Degree-days were calculated as a subtraction of lower developmental threshold (8.3 °C (Baier et al., 2007)) from average daily temperatures. Values below zero were not included in calculations of DD sums.

2.3. *Statistical analysis*

To estimate effects of season, reemergence order, altitude, sun exposure, infestation density and total length of maternal galleries (response variables) on average number of eggs per female, total number of eggs laid, total number of maternal galleries and total length of regeneration feeding galleries (predictor variables) redundancy analysis (RDA) was used and performed in computer program CANOCO 5.0 (Microcomputer Power, Ithaca, USA). Response variables were log-transformed prior to analysis. The significance of ordination results was evaluated by means of the Monte Carlo Permutation test and resulting P values were adjusted by Holm-Bonferroni method to avoid type I errors when performing multiple comparisons.

3. Results

3.1. *Vegetation season 2011*

The weather in 2011 was not significantly different compared to long-term averages. Early onset of spring swarming (early – mid April in lowlands) was induced by supernormal temperatures in March and April. The activity of overwintered bark beetles was then interrupted by night frosts accompanied by snow cover in higher elevations at the beginning of May. Temperatures in May and June were slightly supernormal, but emergence of filial generation was halted by cold and rainy weather in July. Summer swarming started at the beginning of August and peaked in the second August decade (Fig. 1).

3.2. *600 m a.s.l*

Overwintered spruce bark beetles started to swarm massively in the first week of May. No boreholes were recorded in the following weeks and thus, logs from the infested trap trees were cut and placed into cages on May 26. At that time, infestation density was 1.7 boreholes/dm^2 (Table 1).

3.3. *800 m a.s.l*

Spring swarming started in the first May decade when most of the overwintered bark beetles emerged. Logs were cut and placed into the cages on May 26. At that time, infestation density was 1.5 boreholes/dm^2 (Table 1).

3.4. *1100 m a.s.l*

Spruce bark beetles started to emerge in the third week of May, when the majority of beetles swarmed. Logs from infested trap trees were cut and placed into the cages on May 26. Infestation density was 1.3 boreholes/dm^2 (Table 1).

3.5. *Vegetation season 2012*

The temperatures at the beginning of 2012 were supernormal, which led to early start of spring swarming (mid-April in lowlands and one week later in mountains). Sunny weather and high temperatures of following weeks accelerated development of young generation and summer swarming started as early as in mid-June. Second generation finished development and started to swarm in mid-August (Fig. 1).

3.6. *600 m a.s.l*

Overwintered bark beetles started to emerge in the first week of May and the spring swarming culminated one week later. The logs from infested trap trees were cut and placed into the cages on May 15. Infestation density was 2.3 boreholes/dm^2 (Table 2).

3.7. *800 m a.s.l*

The spring swarming started in the first week of May, when the majority of beetles emerged. Logs were cut from trap trees and placed into cages on May 15. At that time, infestation density was 1.8 boreholes/dm^2 (Table 2).

3.8. *1100 m a.s.l*

The first infestations on the surface of the trap trees were recorded in the first week of May, when the swarming culminated. Logs were cut from infested trap trees and placed into cages on May 15. The density of boreholes was 1.7 /dm^2 (Table 2).

3.9. *Oviposition*

Number of eggs laid by a single female was clearly visible as incisions on edges of maternal galleries. In vegetation season 2011, females oviposited on average 19.78 ± 10.38 eggs and recorded maximum was 53 eggs, while in the vegetation season 2012, the number of eggs per female was 29.64 ± 8.7 and maximum number of eggs oviposited by a single female was 72. The difference between the average size of egg batches over the years was significant (ANOVA, $F_{1,186} = 5.88$, $p = 0.016$). The number of eggs per female in the first, second and third ovarian cycle did not differ (27.64 ± 7.88, 21.55 ± 12.47, 24.71 ± 10.39, respectively), but the average number of oviposited eggs in the fourth ovarian cycle is lower (18.24 ± 11.89; non-equal N HSD post hoc test, $p < 0.05$) (Fig. 2)

3.10. *Seasons 2011 and 2012 evaluated together*

The RDA ordination analysis revealed significant effects of infestation density, total length of maternal galleries, third sister brood, altitudes 600 m and 800 m a. s. l., and vegetation season on response variables, i.e. on average number of eggs per female (**EggPerFm**), total number of eggs laid (**Eggs**), total number of maternal galleries (**MatrGall**) and total length of regeneration feeding galleries (**RegnFeed**) (Fig. 3, Table 3). The first two most significant ordination axes explained 46% and 12% of the variation. Total number of eggs laid (**Eggs**), total number of maternal galleries (**MatrGall**) and total length of regeneration feeding galleries (**RegnFeed**) were highly correlated with infestation density (**InfDens**). These response variables are lower at 1100 m altitude as well as during the third sister brood. Although the effect of solar radiation was not significant, there is still some indication of its positive effect on these three response variables. Average number of eggs per female (**EggPerFm**) was unsurprisingly positively correlated with total length of maternal galleries (**GalLen**), lower in third sister broods and higher in the vegetation season 2012. Interestingly, number

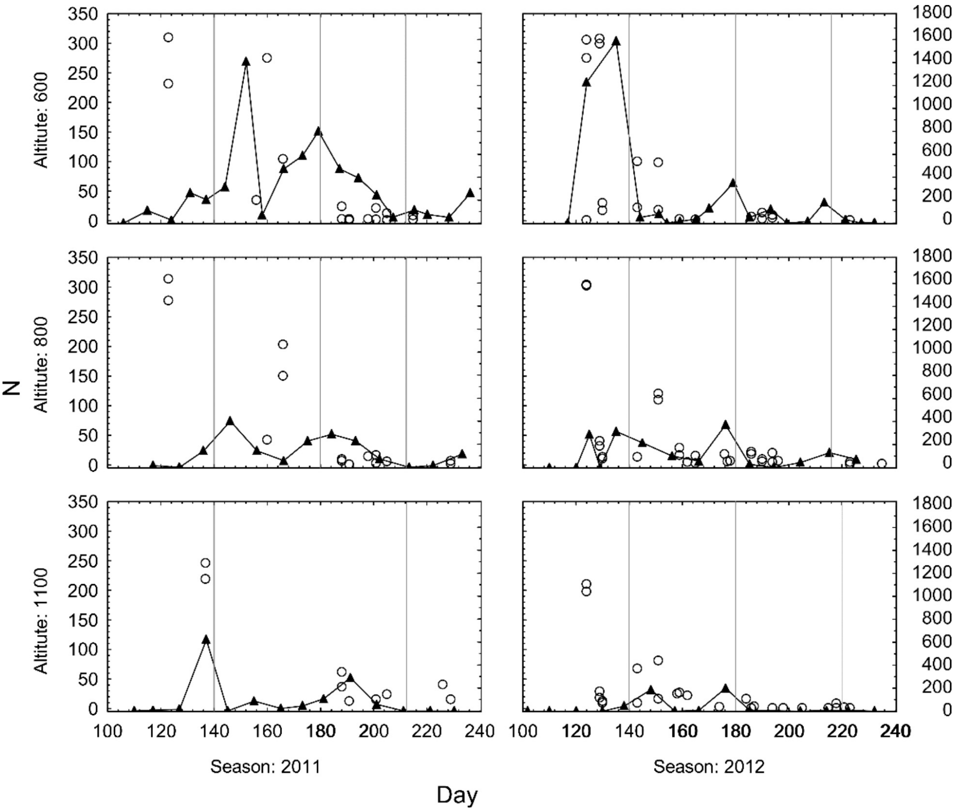

Fig. 1. Timing of sister brood re-emergence in vegetation seasons 2011 and 2012. Data from the shaded and sunlit cages were pooled. Horizontal axis shows time (days from the beginning of the year), left vertical axis and circles display the number of re-emerged females. Grey lines indicate the end of re-swarming. Right vertical axis and black triangles display the catches of spruce bark beetles in the monitoring pheromone traps placed at the localities.

of re-emerged females strongly depends on infestation density (Fig. 4). Further analysis proved that bark beetles undergo regeneration feeding in both old and new logs, which depends exclusively on the quality of phloem (Fig. 5).

3.11. Temperature measurements

Temperature measurements at study sites showed significant increases when compared to data recorded by Martinek (1961) in similar

Table 1
Summary of bark beetle re-emergence in vegetation season 2011. Table shows number of re-emerged beetles, number of degree days (DD) from previous swarming, number of days from previous swarming and the timing of re-emergence during first, second and third re-emregence at elevations of 600, 800 and 1100 m a.s.l. at sunlit and shaded spot.

Elevation		600 m a.s.l.		800 m a.s.l.		1100 m a.s.l.	
Location		Sunlit	Shaded	Sunlit	Shaded	Sunlit	Shaded
Re-emrgence 1	Re-emerged beetles	100%	45%	78%	54%	41%	18%
	degree days	364 DD	472 DD	263 DD	169 DD	337 DD	375 DD
	days	35 days	42 days	35 days	42 days	49 day	49 days
	Date	June-week 1–2	June-week 2	June-week 1–2	June-week 2	July-week 1, 3, 4	July-week 1, 3, 4
Re-emrgence 2	Re-emerged beetles	19%	8%	17%	8%	15%	90%
	Degree days	344 DD	280 DD	23 DD	118 DD	323 DD	266 DD
	Days	28 days	21 days	28 days	21 days	42 days	42 days
	Date	July-week 1–4	July-week 1–4	July-week 1–4	July-week 1, 3, 4	August-week 3	August-week 3
Re-emrgence 3	Re-emerged beetles	15%	22%	16%	13%	Not recorded	Not recorded
	Degree days	364 DD	381 DD	381 DD	275 DD		
	Days	28 days	28 days	28 days	42 days		
	Date	August-week 1	August-week 1	August-week 3	August-week 3		

Table 2
Summary of bark beetle re-emergence in vegetation season 2012. Table shows number of re-emerged beetles, number of degree days (DD) from previous swarming, number of days from previous swarming and the timing of re-emergence during first, second and third re-emregence at elevations of 600, 800 and 1100 m a.s.l. at sunlit and shaded spot.

Elevation		600 m a.s.l.		800 m a.s.l.		1100 m a.s.l.	
Location		Sunlit	Shaded	Sunlit	Shaded	Sunlit	Shaded
Re-emrgence 1	Re-emerged beetles	35%	7%	43%	45%	74%	30%
	Degree days	240 DD	262 DD	127 DD	134 DD	126 DD	103 DD
	Days	22 days	22 days	22 days	29 days	2 days	22 days
	Date	May-week 3–4, June-week 1–2	May-week 3–4, June-week 1–2	May-week 3–4, June-week 1–2	June-week 1–3	May-week 3–4, June-week 1–2	June-week 1–3
Re-emrgence 2	Re-emerged beetles	11%	21%	36%	38%	11%	14%
	Degree days	285 DD	186 DD	260 DD	167 DD	319 DD	284 DD
	Days	18 days	11 days	35 days	28 days	42 days	42 days
	Date	July-week 2	July-week 1–2	June-week 4, July-week 1–2	June-week 4, July-week 1–2	July-week 1	July-week 2–4, August-week 1–2
Re-emrgence 3	Re-emerged beetles	Not recorded	8%	6%	one female (no eggs laid)	17%	Not recorded
	Degree days		517 DD	482 DD	374 DD	228 DD	
	Days		38 days	42 days	42 days	28 days	
	Date		August-week 2	August-week 2	August-week 2	August- week 2	

altitudes. Monthly average temperatures has increased up to 9 °C at 600 and 800 m a.s.l. (Table 4). This increase is caused by higher minimum daily temperatures. The temperatures in 1956 (Martinek, 1957) at 1050 m a.s.l. dropped below 5 °C ten to thirteen times a month in 2011 and 2012, this happened only once or twice a month (Table 5).

4. Discussion

High summer temperatures and lack of rainfalls in the last decades contributed to an increase in forest damage by bark beetles. Bark beetles develop faster and host tree resistance to their attacks is lower,

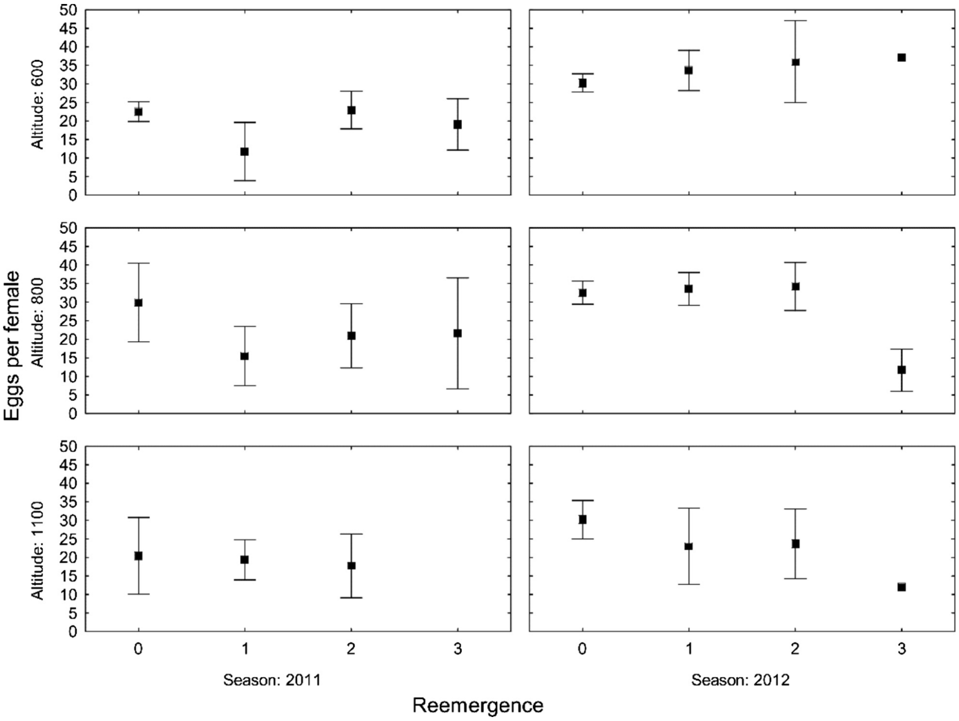

Fig. 2. Average number of eggs laid by a single female per ovarian cycle in vegetation seasons 2011 and 2012. Horizontal axis shows the number of re-emergence (Reemergence 0 marks spring swarming); vertical axis displays the average number of eggs per female.

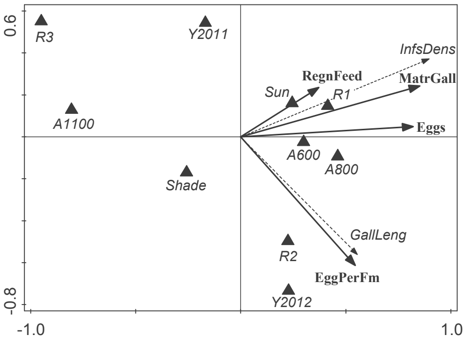

Fig. 3. Ordination diagram of the redundancy analysis of selected response variables during vegetation seasons 2011 and 2012. Response variables (plotted as arrows with a thick solid line; ──▶) are average number of eggs per female (**EggPerFm**), total number of eggs laid (**Eggs**), total number of maternal galleries (**MatrGall**) and total length of regeneration feeding galleries (**RegnFeed**). Continuous predictors (plotted as arrows with a thin dashed line; - - -▶) are total length of maternal galleries (**GallLengh**) and infestation density (**InfsDens**). Factor predictors and their levels (plotted as full triangles; ▲) are altitude (**A600**, **A800** and **A1100**), sunlit or shaded cages (**Shade** and **Sun**) and sister broods (re-emergence **R1**, **R2** and **R3**).

Table 3
Proportion of explained variance in RDA and respective term effects. P(adj) are P values adjusted by Holm-Bonferroni method to avoid type I errors when performing multiple comparisons. P-value and pseudo-F are based on Monte-Carlo Permutation test.

Name[a]	Explains %	Pseudo-F	P	P(adj)
InfsDens	38.6	92.0	0.002	0.024
GallLengh	19.2	34.8	0.002	0.024
R3	10.4	16.9	0.002	0.024
A1100	7.4	11.6	0.002	0.024
Y2011	3.7	5.6	0.004	0.032
Y2012	3.7	5.6	0.004	0.032
A800	3.1	4.6	0.008	0.048
R2	2.8	4.3	0.014	0.07
R1	2.5	3.8	0.028	0.112
Sun	1.4	2.1	0.106	0.288
Shade	1.4	2.1	0.096	0.288
A600	0.9	1.3	0.25	0.288

[a] **A600**, **A800** and **A1100 –** altitude (m a.s.l.), **GallLengh** - total length of maternal galleries, **InfsDens -** infestation density, **R1**, **R2** and **R3 –** first, second and third sister brood re-emergence, **Shade** and **Sun -** sunlit and shaded cages, **Y2011** and **Y2012 –** experimental years.

generally all across the spruce bark beetle distribution area (Bale et al., 2002; Jönsson et al., 2009; Stadelmann et al., 2013; Netherer et al., 2015). Sister broods establishment may considerably contribute to propagation of the spruce bark beetle under conditions of recent climate change, especially at higher elevations and localities with univoltine populations (Marini et al., 2017; Mezei et al., 2017).

In 2011, up to 100% of females established the first sister brood at 600 and 800 m a.s.l. This observation corresponds roughly with the studies of Martinek (1956, 1961) and Öhrn et al. (2014), who found out that 91% of the females re-swarmed at 550 m a.s.l. and up to 74% at 800 m a.s.l., while 95% of females re-emerged in the Swedish study. Re-emergence at 1100 m a.s.l. was considerably lower than it was at two lower-situated localities. Only 41% of females re-swarmed, which is in contrast with 65–70% of re-swarming females recorded by Martinek (1957) at 1050 m a.s.l. Lower percentage of re-swarming females in the present experiment might be caused either by higher elevation of the locality, weather conditions (frequent rainy weather) or by nutritional value and quality of phloem. The number of re-emerging females was generally lower in shade; the minimum was 18% at 1100 m a.s.l. Reduced number of re-swarming females in shade might be due to lack of solar irradiation as cages were placed inside the forest canopy. On the contrary, Martinek (1956, 1957, 1961) placed his cages in sunlit or partially shaded places. Higher precipitation amounts in spring 2012 lowered the number of females establishing the first sister brood. At 600 and 800 m a.s.l. only 35–45% of adults re-swarmed. In contrast, 74% of females established the first sister brood in the sunlit cage at 1100 m a.s.l., which is consistent with results of Martinek (1957).

Up to 19% of females established the second sister brood at 600 m a.s.l., which concurs to 13% at 550 m a.s.l and 20–35% at 500 m a.s.l. observed by Martinek (1956, 1961). At 800 and 1100 m a.s.l., 17 and 15%, respectively, of females re-emerged in the sunlit and 90% in shade cages. Higher percentage of females that re-emerged in shade is probably linked to low proportion of bark beetles that established the first sister brood. The observation of the second re-swarming at higher elevations is contradictory to Martinek (1957, 1961), who did not record its establishment at elevations above 700 m a.s.l. However, results of 2011 were confirmed also in the following vegetation season, when up to 38% of females re-swarmed at 800 m a.s.l. and 11–14% at 1100 m a.s.l. The percentage of adults that established the second sister brood at 600 m a.s.l. was constant in both 2011 and 2012.

The third sister brood was recorded in both vegetation seasons at 600 and 800 m a.s.l. The only exception was caused by entomopathogenic fungi that killed all adults in the sunlit cage at 600 m a.s.l in 2012 and therefore no re-swarming occurred. In 2012, we recorded the third sister brood even at 1100 m a.s.l. in the sunlit cage. This is the first recorded observation since the occurrence of the third brood has never been mentioned in the previous literature. The occurrence of more than one sister brood at higher elevations and third sister brood at all localities in 2012 cannot be explained by a single factor. According to Annila (1969), limiting factors for sister brood establishment are appropriate weather conditions and sufficient amount of suitable host trees for regeneration feeding and oviposition. Bark beetles in our experiments were regularly supplied with fresh logs, so suitable food source was always available. Moreover, laboratory experiments of Zumr and Soldán (1981) proved three ovarian cycles interlaced with periods of regeneration feeding, so sister brood development in suitable conditions is not limited by female internal physiology. In our experiments, re-emergence was positively correlated with infestation density and its onset was strictly density dependent, which is in accordance with results of Andebrant and Löfqvist (1988). Another suggested explanation for the increased number of successfully established sister broods is the effect of climate change. Weather conditions changed considerably since 1950s, when Prof. Martinek's experiments were conducted. Monthly temperature averages increased by 5–10 °C (Table 4). Analysis of temperature recordings proved that this increase is caused exclusively by higher daily minima (Table 5). As the life cycle of the spruce bark beetle is predominantly temperature dependent, higher temperatures may have caused faster development and thus increased number of sister broods (Faccoli, 2009). Similar conclusions were made by Marini et al. (2017), who analyzed the amount of bark beetle damages in 17 time-series from 8 European countries in the last three decades. According to his analysis, climate stressors (warming, drought) itself can increase local population densities even in the absence of storm felled trees. Warm weather also synchronizes and intensifies the re-emergence of parental beetles (Anderbrant, 1986).

Females of the third sister brood in 2012 did not lay any eggs. Only a few exceptions with very limited size of egg batches were found. Similar phenomenon was described by Annila (1969), who observed only exceptional oviposition at the end of vegetation season, when imaginal diapause is being induced (Doležal and Sehnal, 2007).

Number of oviposited eggs per female was higher in 2012, probably due to higher quality of phloem. Overall number of eggs in batches varied from 20 to 40 and it did not differ between ovarian cycles with

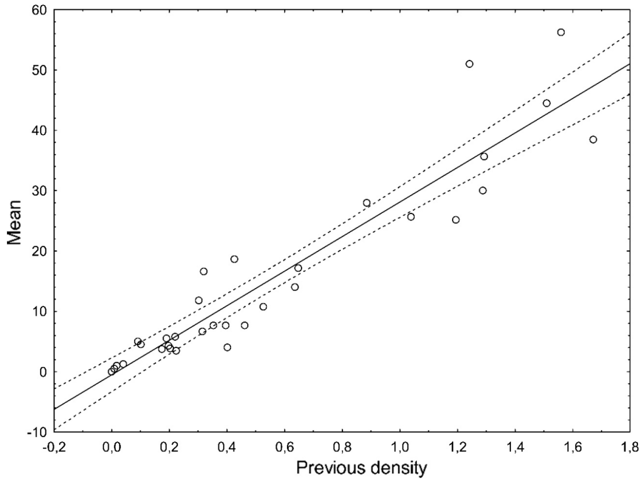

Fig. 4. Dependence of number of re-emerged females on infestation density in old logs. Horizontal axis shows infestation density (bore-holes/dm^2) in old logs, vertical axis displays number of females that re-emerged to new logs. One point marks sunlit and shaded cages pooled and one series of logs. Regression curves with 95% confidence intervals were fitted to the data.

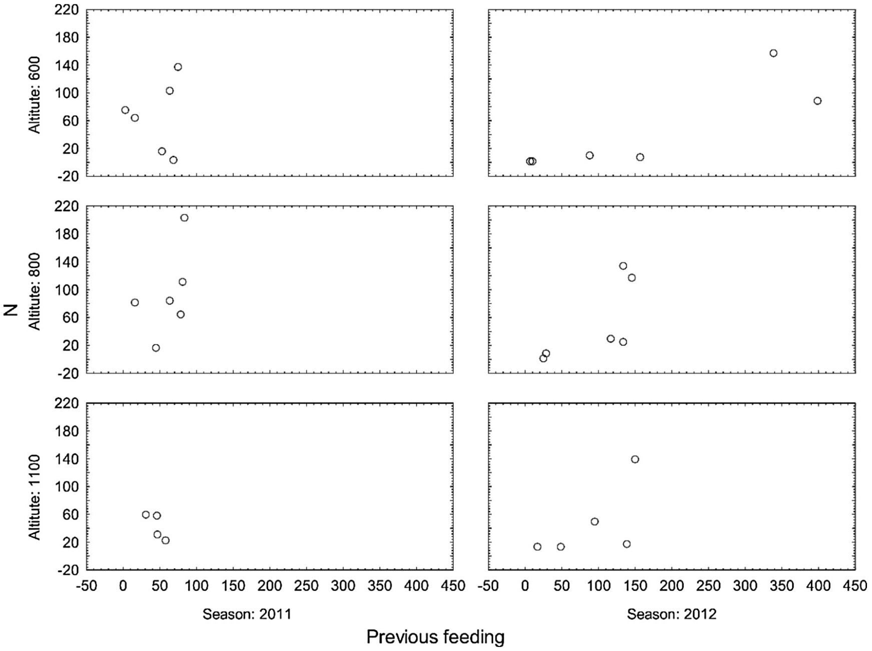

Fig. 5. Total number of regeneration feeding galleries in old and new logs. Horizontal axis shows total number of regeneration feeding galleries in old logs, vertical axis displays total number of regeneration feeding galleries in new logs. One point marks sunlit and shaded cages pooled and one series of logs.

the exception of the third sister brood in vegetation season 2012, when very few eggs were laid. This observation also corresponds with studies of Martinek (1956, 1957, 1961) who observed average numbers of oviposited eggs were 13–46 with no differences between ovarian cycles. Similar conclusions were made by Annila (1969), with an average number of eggs per female varying from 20 to 60, and Anderbrant and Löfqvist (1988), who compared egg batches of regular swarming and sister broods. The number of oviposited eggs did not depend on infestation density. According to Martinek (1957) and Anderbrant and Löfqvist (1988), the number of eggs laid depends on intensity of regeneration feeding. Sufficient length of regeneration feeding gallery needed for complete restoration of ovaries should be at least 1.3 cm (Martinek, 1957), which was confirmed by statistical analysis of the year 2012 and both 2011 and 2012 together. However, in 2011, the

Table 4
Monthly average temperatures (°C). Data from years 1957 and 1958 were recorded by Martinek (1961). Monthly averages of the years 2011 and 2012 were calculated from the temperatures recorded by the datallogers placed at study sites in sunlit (Sun) and shaded (Shade) locations.

Year	1957		1958	2011						2012					
Elevation (m a.s.l.)	600	800	540	600		800		1100		600		800		1100	
				Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade
May	12	7,2	12,5	20,4	20,9	15,1	10,8	13,7	11,9	18,1	18,1	14	12,2	14	12,9
June	13,9	11,5	13,1	21,3	22,5	17	14,2	15,3	14	20,1	21,6	16,6	15	15,6	14,9
July	16,5	13,1	16	20,3	21,4	17,3	14,2	15,5	14,3	21,4	22,1	18	16	16,9	14,3
August	13	12,3	11,6	22,8	22,2	20,5	16,1	18,7	17	23,2	21,2	19	22,2	19,4	16,1

Table 5
The number of days in a month when the daily minimum temperature dropped below 5 °C. Data from year 1956 were recorded by Martinek (1957). The number of days with temperatures below 5 °C in 2011 and 2012 was calculated from the temperatures recorded by the datallogers placed at study sites.

Year	1956	1956	2011			2012		
Elevation (m a.s.l.)	280	1050	600	800	1100	600	800	1100
May	NA	NA	10	9	11	6	11	9
June	0	12	0	0	0	1	2	2
July	0	13	0	0	0	0	0	1
August	0	10	0	0	0	0	0	0

number of oviposited eggs did not depend on the intensity of regeneration feeding. Infestation density is a key factor influencing the number of established sister broods. According to our results, the relation between these two factors is almost linear and number of re-swarming females increases with infestation density. Similar conclusions were made by Annila (1969) and Anderbrant and Löfqvist (1988).

Our results indicate high importance of sister broods for forestry praxis. Depending on actual weather conditions, females of the first and second sister brood may re-emerge already within 20 days after infestation of trees or trap trees. Therefore, timely removal of infested timber from canopy is a key factor that may eliminate consequent damages. If infested timber cannot be removed within 20–30 days, another series of trap trees should be installed prior to re-emergence. The percentage of re-swarming females linearly increases when infestation density reaches approx. 1 borehole per dm^2. Such density (recorded on a trap tree) is considered moderate according to the current legislation in the Czech Republic and if swarming continues and density further increases, additional trap trees should be installed in the surrounding area to prevent damages on healthy standing trees. This protective measure can be effective when trap trees are installed within two weeks after the infestation was recorded.

Acknowledgements

The authors would like to thank Ing. Venuše Plchotová and Ing. Eva Štefaníková for their support in the field, Dr. Jan Okrouhlík for statistical analysis of the data and Prof. Robert J. Van Saun, DVM, MS, PhD, for language editing. This work was supported by Forests of the Czech Republic, state enterprises (project number 08/2009 - 2015).

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CHAPTER IV.

Temperature-dependent development of the double-spined spruce bark beetle Ips duplicatus (Sahlberg, 1836) (Coleoptera; Curculionidae)

Agricultural and Forest Entomology

Agricultural and Forest Entomology (2019), DOI: 10.1111/afe.12345

Temperature-dependent development of the double-spined spruce bark beetle *Ips duplicatus* (Sahlberg, 1836) (Coleoptera; Curculionidae)

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Abstract

1 Development of the double-spined spruce bark beetle *Ips duplicatus* (Sahlberg, 1836) was investigated using the sandwich method under long-day conditions (LD 18 : 6 h) at 10 constant temperatures: 7, 10, 12, 15, 20, 25, 30, 33, 35 and 39 °C. The method proved unsuitable at lower temperatures (7–12 °C), where high mortality occurred.

2 At higher temperatures, development from egg to eclosion of adults shortened from 39.0 days at 15 °C to 10.3 days at 30 °C. Temperatures over 33 °C were lethal to all eggs, larvae and pupae. The developmental rate increased linearly at temperatures between 15 and 25 °C.

3 Stage-specific parameters, such as upper and lower developmental thresholds and optimum temperature for development, were determined by linear and nonlinear (Logan-Lactin) models. Lower developmental thresholds obtained from nonlinear regression were calculated to be 9 °C (eggs), 6.1 °C (larvae), 6.9 °C (pupae) and 6.3 °C (development from eggs to pupae). Upper developmental thresholds for all stages oscillated around 39 °C and optimal temperatures oscillated around 30 °C.

4 The rapid development of *I. duplicatus* at 15 and 30 °C [10 and 4 days faster than *Ips typographus* (L.), respectively] may explain its recent outbreak dynamics and low effectivity of preventive control measures

Keywords Developmental time, forest pest, *Ips duplicatus*, lethal temperature, phenology, sandwich method.

Introduction

The double-spined spruce bark beetle *Ips duplicatus* (Sahlberg, 1836) Coleoptera: Curculionidae, Scolytinae) represents a serious threat to central European spruce stands. It was classified as a quarantine pest in the European Union (Smith *et al.*, 1996) and considered invasive in several countries (Slovakia, Zúbrik *et al.*, 2006). Currently, it is considered as a potentially quarantine pest in protected zones of Greece, Ireland and the U.K. (Jeger *et al.*, 2017). The original distribution area of *I. duplicatus* comprised Euro-Siberian taiga from Scandinavia to the Sakhalin Island (Wood & Bright, 1992; Pfeffer & Knížek, 1995). The southernmost occurrence in Europe was in the Bialowieza Primeval Forest in Poland. However, *I. duplicatus* began to spread southward into non-natural spruce monocultures of lower and middle elevations during the first half of the 20th Century. Its occurrence in Central Europe was first recorded in Poland (Tredl 1907; Karpiński, 1925, 1926) and Silesia, in the northeastern part of the Czech Republic (Wanka 1927). One decade later, the species was reported in Slovakia (Roubal 1937–1941). It is a boreoalpine species because it was also sporadically encountered in the Alps (Postner 1974; Lekander *et al.* 1977; Pfeffer & Knizek 1995). In the Czech Republic, damage by this species was first recorded in the 1990s (Mrkva, 1994, 1995; Holuša *et al.*, 2003), although, as noted above, its occurrence in the northeastern part of the country had been known as early as the 1920s (Wanka, 1927). Currently, *I. duplicatus* has spread southwest and is considered as a devastating species of increasing economic importance (Holuša *et al.*, 2012). Rapid southward expansion from its original range was recorded also in other European countries (Germany: Bussler & Bense, 2003; Austria, Holzschuh, 1989; Slovakia: Turčáni *et al.*, 2001; Romania: Duduman *et al.*, 2011). The beetle's expansion is most likely promoted by mild and warming climate of recent decades, as well as the planting of spruce monocultures at lower

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and middle elevations (Mrkva, 1994; Pfeffer & Knížek, 1995) and the massive transportation of infested timber (Mrkva, 1995; Knížek *et al.*, 2006; Duduman *et al.*, 2011).

Warm and dry weather of the last 3 years (2015–2018) has fostered the largest outbreak of multiple bark beetle species in recent history, which spans across the Czech Republic from north Moravia to south Bohemia (Zahradník & Zahradníková, 2019). The volume of timber infested in 2018 alone is estimated to be almost 15 million m^3, of which a non-negligible proportion can be attributed to *I. duplicatus*, although no precise records exist (Půlpán & Doležal, 2018). The monitoring and management of this species is complicated because beetles attack predominantly the upper parts of the trunk of shaded trees inside the stand, which limits the chances of their timely identification and removal (Mrkva, 1994, 1995; Grodzki, 2012). Similarly to *Ips typographus* (L.), northern populations of *I. duplicatus* above the threshold of approximately 56° N are univoltine (Lange *et al.*, 2008). Central European populations are multivoltine and two or three generations complete development to adults until a shortening day-length in August induces imaginal diapause (Schopf, 1985, 1989; Mrkva, 1995; Holuša *et al.*, 2003; Doležal & Sehnal, 2007; Davídková *et al.*, 2017). An exceptionally warm and dry spring and summer in 2018 permitted rapid development, such that a fourth generation was established in August 2018 and completed development to adults during October and November 2018 (Knížek, 2019).

As a result of the relative novelty and local importance of this pest, temperature effects on development of *I. duplicatus* have not been investigated and only one conference abstract reporting development at three temperatures (20, 22.5 and 27.5 °C) is available (Duduman *et al.*, 2015). Field observations have indicated that the life cycle of *I. duplicatus* can be described by a phenological model similar to *I. typographus*. Both species begin their flight activity at the same time and the mathematical models calculating potential infestation hazards could be identical (Holuša *et al.*, 2003; Holuša *et al.*, 2012). However, the northern origin and smaller body size of *I. duplicatus* suggest that thermal requirements should be lower than those of *I. typographus* (Holuša *et al.*, 2012). This hypothesis is consistent with the data of Duduman *et al.* (2015), who compared the duration of development of both species in sandwich cultures and recorded a faster development in *I. duplicatus*. The present study aimed to characterize temperature effects on the development of *I. duplicatus* under controlled conditions and to provide basic data for future phenology models and the effective management of this pest. Such models exist for *I. typographus* and are used as an online tool for predicting its development in Central European countries (Baier *et al.*, 2009, 2012; Berec *et al.*, 2013) or have been included in various risk assessment frameworks (Hlásný *et al.*, 2011; Mezei *et al.*, 2017). Compared with the basic results reported by Duduman *et al.* (2015), we investigated a broader range of temperatures and modelled temperature optima for development, as well as lower and upper developmental thresholds. Both linear and nonlinear approaches were applied to the data because each of the models calculates different parameters. Although the linear model calculates the lower developmental threshold and the number of degree-days (DD) required to complete development, nonlinear models calculate lower developmental thresholds, optimum temperatures and upper development thresholds. Estimation of the number of DD cannot be calculated from any of nonlinear models commonly used to describe insect temperature-dependent development. Knowledge of such information for this species could help answer questions related to the rapid spread of *I. duplicatus* in recent hot and dry vegetation seasons.

Materials and methods

Insects and sandwich culture

A laboratory culture of *I. duplicatus* has been maintained for several years and, based on experience, we know that adults often refuse to infest fresh logs. Better results are achieved using very fresh logs with approximately 5-cm long branch bases. After several repetitions of initial tests using the original method of Wermelinger & Seifert (1998) failed, such that no males excavated nuptial chambers in the bark, we decided to apply a modification, as described below, to follow the development of single individuals. Parental beetles were collected from a naturally infested standing trap tree baited with pheromone dispenser ID Ecolure (Fytofarma Praha, Czech Republic) in May 2018. The trap tree was cut 3 days after initial infestation and 1-m long bolts transferred from the locality Kružberk (49.8250158N, 17.6330742E) to the laboratory. Logs were carefully debarked so that parental adults remained in their galleries and pieces of bark were embedded between two 0.75-cm thick Plexiglas pieces (25 × 25 cm) and then duct tape (3M, Maplewood, Minnesota) was applied on the sides of each sandwich to prevent precocious drying of phloem. At that time, the galleries consisted predominantly of nuptial chambers and females began to bore maternal galleries. In some cases, a few eggs were laid. The sandwiches were placed into cooled incubators Sanyo MIR 253 (Sanyo Inc., Japan) under long-day conditions (LD 18 : 6 h) at constant temperatures of 7, 10, 12, 15, 20, 25, 30, 33, 35 and 39 °C and 60–70% relative humidity. The length of maternal galleries (if present) was recorded using colour markers and progress, including egg laying, larval hatching, larval feeding, pupation and adult emergence, was recorded daily. For every temperature, three sandwiches with one maternal gallery per sandwich were used.

Data analysis

Datasets were tested for normality using the Kolmogorov–Smirnov test. Data of the mean developmental rates and number of eggs laid were analyzed by analysis of variance and Tukey's post-hoc test using STATISTICA (TIBCO software Inc., Palo Alto, California). Developmental rates (r) were calculated as:

$$r = \frac{1}{\text{developmental time}}$$

A linear model was used to estimate lower developmental thresholds (DT$_\text{L}$) (Cambell *et al.*, 1974). From the regression:

$$r = a + b \cdot T$$

where r is the developmental rate, T is temperature, and a and b are fitted parameters. The lower developmental threshold

Table 1 Mean duration of development and developmental rates of various life cycle stages of *Ips duplicatus* at 15, 20, 25 and 30 °C

	Eggs		Larvae		Pupae		Egg–pupa	
Temperature	Mean ±SD	N	Mean ±SD	*N*	Mean ±SD	*N*	Mean ±SD	*N*
Duration (days)								
15 °C	8.5 ±0.5	16	19.7 ±0.7	16	12.1 ±1.0	9	39.0 ±1.1	9
20 °C	5.1 ±0.35	21	13.5 ±0.9	21	5.9 ±0.8	19	24.2 ±1.1	15
25 °C	3.3 ±0.45	52	10.5 ±0.8	52	3.8 ±0,0.4	29	17.6 ±0.8	29
30 °C	2.0 ±0	18	6.0 ±0	20	2.0 ±0	14	10.3 ±0.5	14
Developmental rate (1/day)								
15 °C	0.118 ±0.007		0.051 ±0.002		0.083 ±0.007		0.026 ±0.001	
20 °C	0.195 ±0.012		0.074 ±0.005		0.171 ±0.024		0.041 ±0.002	
25 °C	0.309 ±0.038		0.096 ±0.008		0.270 ±0.036		0.057 ±0.003	
30 °C	0.5 ±0		$0.167 \pm 5.55 \times 10^{-17}$		0.5 ±0		0.097 ±0.004	

N, number of observations.

(DT_L) was calculated by extrapolating the regression line to $r = 0$.

The standard error of DT_L can be calculated as:

$$SE_{DT_L} = \frac{\bar{r}}{b} \cdot \sqrt{\frac{s^2}{N \cdot \bar{r}^2} + \left(\frac{SE_b}{b}\right)^2}$$

where $\bar{r}$ is the sample mean, b is the fitted parameter from linear regression, s^2 is the residual mean square of regression, N is the number of observations and SE_b is the standard error of b.

The number of DD (K) required to complete development was calculated as the reciprocal of b, where b is the fitted parameter from linear regression (Campbell *et al.*, 1974).

$$K = 1/b$$

The standard error of K can be calculated as:

$$SE_K = \frac{SE_b}{b^2}$$

To describe the developmental rate at temperatures approaching or exceeding the optimum, Lactin modification (Lactin *et al.*, 1995) of the nonlinear Logan model (Logan *et al.*, 1976) was used. The model is:

$$r(T) = e^{\alpha \cdot T} - e^{\left[\alpha \cdot T_{max} - \left(\frac{T_{max} - T}{\beta}\right)\right]} + \gamma$$

where α, β, γ and T_{max} are fitted parameters and T is temperature.

Optimum temperature (T_O) can be calculated after setting first derivate of the Lactin model to zero as:

$$T_O = T_{max} - \frac{\beta \cdot \ln(\alpha \cdot \beta)}{\alpha \cdot \beta - 1}$$

where T_{max}, α and β are fitted parameters from the nonlinear Lactin model.

Linear and nonlinear models were calculated using Matlab (Mathworks Inc., Natick, Massachusetts).

Results

Developmental times

Developmental data for all preimaginal life stages of *I. duplicatus* were recorded at temperatures between 15 and 30 °C. Within this temperature range, the mean developmental time (egg to adult) was in the range 10.3–39.0 days. The duration of the egg stage was, on average, 2.0–8.5 days, the larval stage was between 6.0 and 19.7 days, and the pupal stage developed from 2.0 to 12.1 days (Table 1). Both eggs and pupae developed faster at raising temperatures, which resulted in similar developmental times at 30 °C. Larvae that hatched at temperatures below 15 °C developed very slowly and it was not possible to yield reliable results because of desiccation of the phloem and mortality as a result of entomopathogenic fungi (*Bauveria bassiana*). Temperatures of 33, 35 and 39 °C were lethal for eggs. Supplementary experiments with larvae and pupae showed that, at these temperatures, mortality exceeded 90%. The average number of eggs laid in every treatment is shown in Table 2. This varied from 2.67 at 10 °C to 17.33 at 25 °C. The number of eggs per female gradually increased with temperature and peaked at 25 °C, and then it began to decline. Statistical differences in number of laid eggs were found at temperatures of 7 and 25 °C ($P = 0.017$), 10 and 25 °C ($P = 0.021$) and 25 and 39 °C ($P = 0.037$).

The relative duration of egg development ranged from 17% of total developmental time at 25 °C to 21% at 30 °C; the larval stage ranged from 50% of total developmental time at 15 °C to 60% at 25 °C; and the pupal stage comprised 20–30% of total developmental time (Fig. 1).

Developmental thresholds

The lowest developmental thresholds determined by linear regression (DT_{L1}) were obtained in larvae (9.7 °C). DT_{L1} of eggs (11.6 °C) and pupae (13.6 °C) were higher by approximately 2 °C. Total preimaginal development DT_{L1} (11.1 °C) was close to that of eggs (Fig. 2 and Table 3). The data show a strong

Table 2 Mean number of eggs laid in sandwiches at 7, 10, 12, 15, 20, 25, 30, 33, 35 and 39 °C

Temperature (°C)	$N_{\text{sandwiches}}$	$N_{\text{maternal galleries}}$	Eggs/female	SD
7	3	3	2.67	1.25
10	3	3	3.0	1.42
12	3	3	5.0	0.82
15	3	3	5.33	2.05
20	3	3	7.0	2.94
25	3	3	17.33	5.56
30	3	3	6.67	6.02
33	3	3	7.33	4.19
35	3	3	4.67	3.86
39	3	3	4.0	3.27

$N_{\text{sandwiches}}$, number of sandwich plates at given temperature; $N_{\text{maternal galleries}}$, total number of maternal galleries at given temperature; eggs/female, mean number of eggs per female.

linear relationship between temperature and developmental rate because the correlation coefficient varied from 0.82 to 0.90 (Fig. 1 and Table 4).

The average heat sum K required for development completion of the preimaginal stages was highest in larvae at 140.5 DD. The pupae required a lower heat sum (36.9 DD) than the eggs (40.6 DD) (Table 3).

To describe the developmental rate over a wider range of temperatures, a nonlinear Logan/Lactin model (Lactin *et al.*, 1995) was fitted to the data. The nonlinear model fitted well to the data as indicated by high r^2 values of 0.91 for eggs, 0.83 for larvae, 0.94 for pupae and 0.91 for egg–pupa (Fig. 2 and Table 5). Lower and upper developmental thresholds were estimated from the curve. The upper developmental thresholds (DT_U) varied between 39.6 °C for eggs, 39.7 °C for larvae, 39.9 °C for pupae and 39.8 °C for egg–pupa. From the experiments, it can be seen that temperatures over 33 °C are lethal for all preimaginal stages. The lower developmental thresholds (DT_{L2}) assessed by nonlinear modelling are considerably lower than those calculated from linear regression (DT_{L1}). The DT_{L2} was lowest in larvae (6.1 °C) and an almost similar value was modelled for pupae (7.0 °C). The highest value of DT_{L2} was calculated for eggs (9.0 °C) (Table 3). Slow development at temperatures below 15 °C (12, 10 and 7 °C) resulted in high mortality because of the spread of entomopathogenic fungi and hence these data were excluded from statistical evaluation. The optimal temperatures (T_O) were all under 30 °C: at 27.9 °C for larvae, 29.3 °C for pupae and 28.3 for total pre-imaginal development. T_O in eggs was 33 °C. However, a temperature of 33 °C was lethal to all immature stages, including eggs, as noted above.

Discussion

The sandwich method proved suitable for monitoring the complete development of *I. duplicatus* at temperatures between 15 and 30 °C. Larval hatching was recorded at all temperatures below 15 °C (12, 10 and 7 °C), although a longer development resulted in a high mortality of larvae that, in most cases, could be attributed to infection by entomopathogenic fungi (determined as *Bauveria bassiana*) and possibly also the low quality of phloem. Problems with the drying of phloem inside sandwiches and the growth of the saprophytic fungi that degrade it were previously reported by Wermelinger & Seifert (1998) and Schebeck & Schopf (2017).

Duration of development

At a temperature range of 15–30 °C, larvae of *I. duplicatus* had a longer development time than eggs and pupae, which is consistent with previous studies on *I. typographus* (Wermelinger & Seifert, 1998) and *Ips cembrae* (Schebeck & Schopf, 2017). Larval development represented 50% of the total developmental time at 15 °C and this increased to 60% at 25 °C. A similar percentage was recorded in *I. typographus* by Wermelineger & Seifert (1998).

Developmental times of the immobile stages were similar at temperatures between 20 and 30 °C, whereas, at 15 °C, eggs developed approximately 4 days faster than pupae. Rather

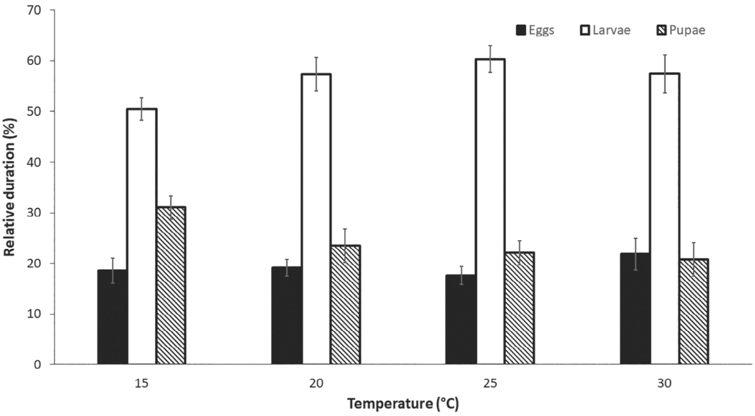

Figure 1 Relative duration of egg, larval and pupal stage of *Ips duplicatus* with respect to total developmental time (mean ± SD) at 15, 20, 25 and 30 °C.

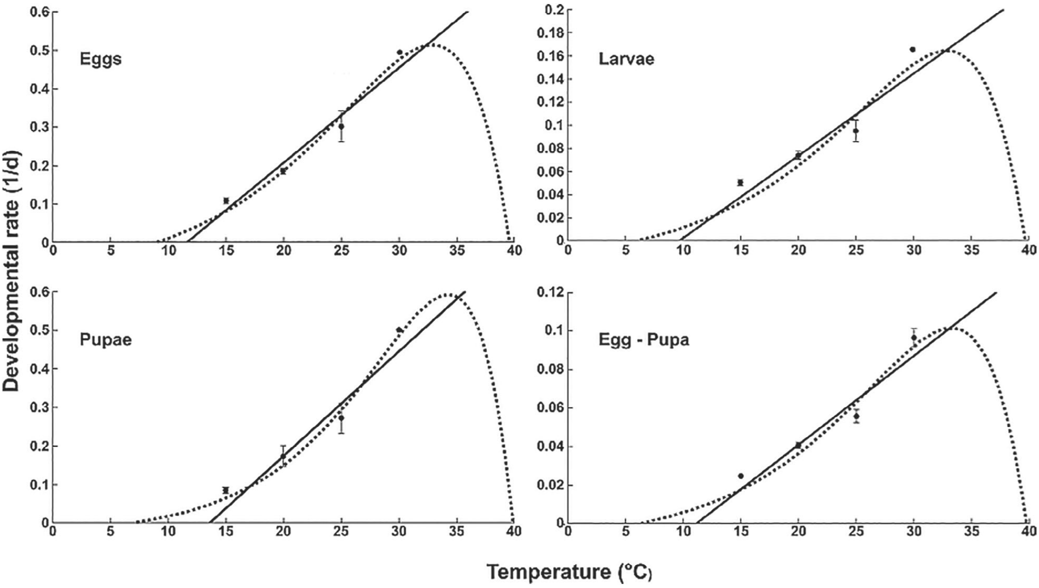

Figure 2 Linear (solid line) and nonlinear (broken line) developmental rates (1/day) of *Ips duplicatus* life cycle stages. Circle markers indicate the measured temperature-based developmental rates (mean ± SD).

Table 3 Developmental thresholds (DT_{L1}), average heat sums (*K*) and corresponding SE based on linear regression model of *Ips duplicatus* development

Life cycle stage	DT_{L1} (°C)	SE of DT_{L1} (°C)	*K* (DD)	SE of *K* (DD)
Eggs	11.6	0.39	40.6	1.35
Larvae	9.7	0.62	140.5	6.31
Pupae	13.6	0.43	36.9	1.63
Egg–pupa	11.1	0.57	217.2	9.93

DD, degree-days.

similar developmental times of eggs and pupae were recorded also in other species of the genus, namely *I. typographus* and *I. cembrae* (Wermelinger & Seifert, 1998; Schebeck & Schopf, 2017). Under epidemic conditions, both *I. typographus* and *I. duplicatus* commonly infest the same trees and inhabit similar parts of the stem, and their seasonal distribution shows a similar pattern (Holuša *et al.*, 2003; Grodzki, 2012; Holuša *et al.*, 2012). However, a faster development of *I. duplicatus* was first implied by Pfeffer & Knížek, 1995, who recorded, at a high laboratory temperature (25–27 °C), that the time from egg-laying to the emergence of fresh *I. duplicatus* adults from spruce logs lasted only 10–14 days. The total developmental time from tree infestation by parental beetles to emergence of the new generation in the field was estimated to be 4–8 weeks in *I. duplicatus* (Mrkva, 1995) and 5–8 weeks in *I. typographus* (Wermerlinger *et al.*, 2012). Therefore, the climatic conditions of Central Europe before the recent (2015 to present) period of hot and dry vegetation seasons allowed the development of two (or exceptionally three) generations per vegetation season (Holuša *et al.*, 2003, 2012; Wermelinger, 2004). However, the development of a third generation and eventually the establishment of fourth generation in *I. duplicatus* was repeatedly recorded as a result of hot and dry weather over the last 3 years (P. Doležal, unpublished results; Knížek, 2019). Duduman *et al.* (2015) recorded a faster development for *I. duplicatus* compared with *I. typographus* of 4–10 days at temperatures ranging from 20 to 27 °C using the sandwich method. The developmental

Table 4 Linear regression parameters between temperature and developmental rates of *Ips duplicatus* instars at 15, 20, 25 and 30 °C

Life cycle stage	*N*	Slope	SE of slope	Intercept	SE of intercept	r^2	s^2
Eggs	107	2.47×10^{-2}	8.19×10^{-4}	-2.86×10^{-1}	1.95×10^{-2}	0.90	7.55×10^{-4}
Larvae	109	7.12×10^{-3}	3.19×10^{-4}	-6.91×10^{-2}	7.65×10^{-3}	0.82	4.02×10^{-5}
Pupae	71	2.71×10^{-2}	1.20×10^{-3}	-3.69×10^{-1}	2.87×10^{-2}	0.88	7.17×10^{-4}
Egg–pupa	67	4.60×10^{-3}	2.11×10^{-4}	-5.11×10^{-2}	5.06×10^{-3}	0.88	8.74×10^{-6}

N, sample size; r^2, adjusted squared multiple correlation coefficient; s^2, residual mean squares. A higher number of larvae than eggs was given by experimental design; some eggs were already laid at the beginning of the experiment, and thus were not included in statistical evaluation

Table 5 Parameter estimates (α, β, T_{max} and γ) of the nonlinear model (Lactin *et al.*, 1995) for the developmental rate of *Ips duplicatus*

Life-cycle stage	α	β	T_{max}	γ	r^2	DT_{L2}	T_O	DT_U
Eggs	0.14050	7.07500	40.0	−0.09000	0.91	9.0	32.9	39.6
Larvae	0.14070	7.09300	40.0	−0.02000	0.83	6.1	27.9	39.7
Pupae	0.17480	5.71200	40.0	−0.03000	0.94	7.0	29.3	39.9
Egg–pupa	0.14840	6.73100	40.0	−0.01002	0.91	6.3	28.3	39.8

r^2, adjusted squared multiple correlation coefficient. Calculated values from the nonlinear model: DT_{L2}, lower developmental threshold (°C); T_O, optimum temperature (°C); DT_U, upper developmental threshold (°C).

times of *I. duplicatus* recorded in the present study are approximately 8–13 days shorter than those reported by Duduman *et al.* (2015), probably as a result of maturation feeding not being included and our data showing only the length of development from eggs to adults. Compared with the data on development of *I. typographus* (Wermelinger & Seifert, 1998), the *I. duplicatus* in the present study developed approximately 3–10 days faster, with greater differences at temperatures of 15–30 °C. Almost no differences were noted at 25 °C. The faster development at 15 °C (approximately 10 days) reflects the northern origin of *I. duplicatus* (Pfeffer & Knížek, 1995), as well as its smaller body size (Hodek & Honěk, 1996; Shi *et al.*, 2013).

Developmental thresholds and optimum temperature

Linear and nonlinear models represent two of the approaches used to describe the effect of temperature on the developmental rate of insects. Linear modelling is used to estimate the lower developmental threshold but may be inaccurate at extreme temperatures and does not allow calculation of the upper developmental threshold and the optimal temperatures for development. Therefore, numerous nonlinear models have been proposed to estimate these parameters (Campbell *et al.*, 1974; Lactin *et al.*, 1995; Logan *et al.*, 1976; Briere *et al.*, 1999, Ikemoto, 2005, Shi *et al.*, 2011). In the present study, linear and nonlinear (Logan/Lactin) models were used to calculate parameters applicable to the management and modelling phenology of *I. duplicatus*. The lowest developmental threshold was estimated for larvae (9.7 °C by linear and 6.1 °C by nonlinear modelling) and pupae (13.6 by linear and 6.9 °C by nonlinear modelling). Although most of the *I. duplicatus* population overwinters as adults in soil litter (Zhang *et al.*, 1995; Onyszko & Starzyk, 2011), the generations established at the end of the vegetation season finish development as adults during the autumn months. Therefore, the low developmental threshold of larvae and pupae probably accounts for such a slow development to adults (i.e. stage with the highest cold hardiness. A similar mechanism has been documented in *I. typographus*., comprising a species that (similar to *I. duplicatus*) overwinters predominantly in the adult stage (Dworschak *et al.*, 2014; Štefková *et al.*, 2017). Adult development completion is crucial because 98% of the *I. duplicatus* population overwinters in soil litter and low winter temperatures are detrimental to subimaginal stages (Onyszko & Starzyk, 2011; M. Davídková & P. Doležal, unpublished results). As a result of all of the above and the frequent observations of living pupae under the bark of infested trees during October and November, we consider the relatively high developmental threshold of pupae (13.6 °C) estimated by linear modelling to be an artefact. The lower developmental threshold in the linear model is estimated by extrapolation of the linear portion of the data into a region that is unlikely to be linear, and so its estimation from linear regression does not provide reliable data in many cases (Bergant & Trdan, 2006; Walgama & Zalucki, 2006).

Eggs had the highest lower developmental threshold (11.6 °C by linear and 9.0 °C by nonlinear modelling), which is consistent with two other species of *I.* previously studied by the sandwich method (Wermelinger & Seifert, 1998; Schebeck & Schopf, 2017). A high lower developmental threshold probably synchronizes the populations because later established broods may catch up on earlier conspecifics, which results in a mass emergence (i.e. a mechanism that helps bark beetles to overcome host tree defence) (Bentz *et al.*, 1991; Logan & Bentz, 1999; Schebeck & Schopf, 2017).

Optimum temperatures of *I. duplicatus* were lower than those of *I. typographus* (Wermelinger & Seifert, 1998), with the highest optimum temperatures being modelled for eggs and pupae in both species. Generally, the values in *I. typographus* were higher by 2–4 °C, except for eggs, which had the higher optimum in *I. duplicatus*.

A high mortality at temperatures over 33 °C (100% of eggs and over 90% of larvae and pupae) and lower optimum temperatures of *I. duplicatus* (compared with *I. typographus*) correspond to the life strategy of the species. *Ips duplicatus* adults prefer shaded trees inside the stand (Holuša *et al.*, 2012) and thus their offspring are not exposed to any solar radiation that may increase temperatures under bark to lethal limits. Modelled upper developmental thresholds DT_U are higher than temperatures that were lethal to most specimens, regardless of the developmental stage.

Practical importance

Ips duplicatus represents a relatively novel pest to Central Europe and many aspects of its life cycle remain unstudied. This species attacks trees that are dispersed within a stand and the infestation concentrates on tree crowns. Beetles commonly complete their development and emerge before changes in the colouration of needles can be observed visually, which complicates the timely identification of infested trees, mainly during initial phase of an outbreak (Holuša *et al.*, 2012; Půlpán & Doležal, 2018). Moreover, *I. duplicatus* rarely invades lying trees and thus trap trees are not an effective measure for controlling this pest (Schneider & Sierpiński, 1955; Grodzki, 1997; Holuša *et al.*, 2012). Overwintering as an adult in the soil litter makes removal of infested trees during autumn and winter completely ineffective (if not infested also by other bark beetle species). During the last 3 years, a fourth generation of *I. duplicatus* has been recorded in numerous localities, which highlights the need for the proper prediction of its occurrence and the timing of control methods. Data on the temperature dependence of the developmental rate represent a key requirement for the reliable modelling of generation development and the phenology of *I. duplicatus* in a changing climate, as well as with respect to an explanation of its rapid spreading and outbreak dynamics in recent years.

Acknowledgements

We thank Ing. Jiří Groda for his support in the field and Professor Robert J. Van Saun, DVM, MS, PhD, for editing the language in the manuscript submitted for publication. This work was supported by Forests of the Czech Republic, state enterprises (project number 02/2014-2018).

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Accepted 26 May 2019

CHAPTER V.

Conclusions

1) Functionality of passive marking of emerging *Ips typographus* (L.) adults by fine fluorescent powder was proven in a field mark-recapture study. The most distant catches of marked beetles were almost 1100 m from the release point and the model applied to the data estimated that approximately 10% of released beetles migrated for distances of more than 500 m. The higher tendency to migrate was recorded in the overwintered generation (spring swarming) and males, which can be attributed to the need to replenish energetic reserves following overwintering and search for new breeding sites. This observation might explain the occasional observations of mass infestations at localities where bark beetles were not previously reported by foresters and implies that at least some trapping devices should be installed across a wider area (as permitted by terrain / canopy configuration) to restrict the spread of an infestation.

2) The importance of so-called sister broods in *I. typographus* for forestry praxis was confirmed. Depending on actual weather conditions, females of the first and second sister brood may re-emerge already within 20 days after infestation of trees or trap trees at relatively high percentages (up to 100 % in some cases). Therefore, timely removal of infested timber from canopy is a key factor that may eliminate consequent damages. If infested timber cannot be removed within 20–30 days, another series of trap trees should be installed prior to re-emergence. However, such protective measure can be effective only when trap trees are installed within two weeks after the infestation was recorded. The percentage of re-swarming females linearly increases when infestation density reaches approx. 1 borehole per dm^2. Compared to the historical data of Martinek (1956, 1957, 1961), number of sister broods increased by one or two at similar elevations, which reflects the influence of changing climate upon bark beetle ecophysiology.

3) Sandwich method was used to study development of the double-spined spruce bark beetle, *Ips duplicatus* (Sahlberg, 1836), under long-day conditions (LD 18 : 6 h) at 10 constant temperatures: 7, 10, 12, 15, 20, 25, 30, 33, 35 and 39 °C. The developmental rate increased linearly at temperatures between 15 and 25 °C and development from egg to eclosion of adults shortened from 39.0 days at 15 °C to 10.3 days at 30 °C. Temperatures over 33 ∘C were lethal to all eggs, larvae and pupae. The rapid development of *I. duplicatus* at 15 and 30 °C [10 and 4 days faster than *I. typographus*, respectively] may explain its recent outbreak dynamics and low effectivity of preventive control measures.

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Neglected aspects of bark beetle (Coleoptera: Scolytinae)
ecophysiology
Ph.D. Thesis Series, 2019, No. 14

Printed in the Czech Republic by Typodesign
Edition of 20 copies

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