OVERWINTERING STRATEGY OF
IPS TYPOGRAPHUS L. (COLEOPTERA,
CURCULIONIDAE, SCOLYTINAE) IN CROATIAN
SPRUCE FORESTS ON LOWEST ELEVATION

STRATEGIJA PREZIMLJAVANJA SMREKOVOG PISARA
Ips typographus L. (COLEOPTERA, CURCULIONIDAE,
SCOLYTINAE) U HRVATSKIM SMREKOVIM ŠUMAMA
NA NAJNIŽOJ NADMORSKOJ VISINI

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SUMMARY
Better understanding of overwintering strategy in Ips typographus is crucial in planning of sanitation felling as hot spots recovery measure. Bark and needle litter are present as overwintering niches within the species. At the lowest elevation (500 m a. s. l.) in spruce stands 85% of beetles overwinter under the bark. Overwintering behavior is elevation adaptable, and portion of beetles which overwinters under the bark of attacked trees increase with decreasing of elevation. The results suggest presence of high plasticity within the species which is well adaptable to changeable habitat and temperature conditions. High in the mountains sanitation felling need to be implemented early in autumn before beetles end the development, while at lower elevations a good result can be achieved with felling early in spring before the start of new generation. During the winter bark peels off the dense attacked tress very often and changes the beetle ratio between niches. This fact needs to be considered in planning of sanitation felling early in spring before fly period of Ips typographus.

KEY WORDS: bark beetles, overwintering niches, predators, ecological plasticity, temperature, felling

INTRODUCTION
Forests are the largest terrestrial ecosystem on our planet with more than 80% of total terrestrial biodiversity (Pan et al., 2013). Conifer bark beetles and phloem-feeding insects belong to group of important disturbance agents in forest ecosystems (Byers, 2012; Linnakoski et al., 2012). Ips typographus L. (Coleoptera, Curculionidae, Scolytinae) is one of the most severe pest insects in mature spruce stands in the whole palearctic region (Christiansen and Bakke, 1988; Wermelinger, 2004). During the period from 1990

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to 2001 more than 31 million m³ of spruce wood in Europe was killed (Grégoire and Evans, 2004). At low population densities, *I. typographus* usually breeds in trees with low or no defense, or in those which are physiologically stressed, particularly in warm spring weather, long drought periods during summer (Christiansen and Bakke, 1997) or after severe storms (Lindelöw and Weslien, 1986; Weslien et al., 1989; Weslien and Lindelöw, 1990; Wermelinger, 2004; Gutowski and Krzysztofiak, 2005; Schroeder, 2010). This species is capable to respond to changes quickly by increasing its population density if there is suitable material in stands (Schroeder and Lindelöw, 2002) which happened in the mountain region of Croatia after the ice storm in the late winter of 2014 (Vuletić et al., 2014). Effective aggregation pheromones (Bakke et al., 1977) and symbiosis with blue stain fungi (Viiri, 1997; Krokene and Solheim, 1998; Kirisits, 2010) enable *I. typographus* to colonize and kill stressed or healthy growing trees (Botterweg, 1982; Weslien et al., 1989) depending on population density. The species is univoltine in northern Europe (Annila, 1969; Andebrant, 1986; Schroeder, 2013), while in southern and central Europe, it reproduces one to three times a year (Wermelinger, 2004; Faccoli and Stergulc, 2006; Jurc et al., 2006; Zúbrik et al., 2008; Wermelinger et al., 2012), depending on climatic conditions, an elevation and a geographic position (Zúbrik et al., 2008; Faccoli, 2009; Wermelinger et al., 2012; Kasumović, 2016).

*I. typographus* overwinters in the adult stage (Austara et al., 1977; Coeln et al., 1996; Faccoli, 2002; Baier et al., 2007) either in the bark of attacked trees (Annila, 1971; Hrašovec et al., 2011; Dworschak et al., 2014) or in the litter (Botterweg, 1982; Weslien and Bakke, 1988; Hrašovec et al., 2011). Beetle in subadult stages can survive the winter when it is mild (Zumr, 1982; Wermelinger and Seifert, 1999; Dworschak et al., 2014; Štefková et al., 2017) but in more cases, they do not make it to spring (Austarà et al., 1977; Coeln et al., 1996) since winter temperatures often fall below lethal thresholds, which are -13 °C and -17 °C for subadult (Annila, 1969). More rarely, winter temperatures drop below -20 °C or -22 °C, which seem to be the lethal temperatures for callow or fully matured beetles (Koštál et al., 2007; 2011), thought this is not exception in the research area - Žitnik, northern Europe and higher elevations elsewhere. E.g. only callow beetles under the bark of attacked trees in spring have been detect (Faccoli, 2002).

Similar to *Ips grandicollis* E. in North America (Lombardo et al., 2000), the majority of northern European *I. typographus* populations overwinter in the litter (Annila, 1971; Botterweg, 1982; Weslien and Lindelöw, 1989; Weslien, 1992), while in central and southern Europe most bark beetles stay under the bark during the winter period (Zumr, 1982; Faccoli, 2002; Hrašovec et al., 2011).

Norway spruce (*Picea abies* L. (Karst.)) trees growing in Dinaric mountain range, usually in mixed stands with silver fir (*Abies alba* Mill.) or beech (*Fagus sylvatica* L.), or in monocultures where early or late frosts are more frequent. Good knowledge of the overwintering behavior of this pest related to elevation can be helpful for foresters dealing with sanitation felling. This paper aimed at investigating the proportion of *I. typographus* populations and their natural enemies which overwinter under the bark of attacked trees in a spruce culture at 550 m a.s.l. in southwestern Croatia.

**MATERIAL AND METHODS**

The study was conducted in a 50-year-old spruce stand at 550 m a.s.l. in SW Croatia (44°36'49.41'' N; 15°19'13.89'' E). In mid-July 2014, five spruce trees similar in size (*d₂₀=27-32 cm*) were first felled and then left in the stand to be colonized by *I. typographus*. In January 2015, trees were cut in 4-m-long logs, and transported to a storehouse. Logs were stored in cold, shadow place where temperature did not exceed 5 °C.

During the first three weeks in February, all the logs were analyzed. Before debarking, one-meter-long sections (bark samples) were marked with spray and for the purpose of calculation of the bark surface, their diameter in the middle of each section had to be measured. The bark was removed with an axe after the exit holes had been counted. All the bark samples were carefully pulled apart in small pieces, which was followed by counting filial beetles, pupae, larvae and predator larvae (*Thanasimus* (Coleoptera: Cleridae), *Medetera* (Diptera: Dolichopodidae), predatory gall midges (Diptera: Cecidomyiidae)). Adults, pupae or larvae were considered alive if they showed any sign of movements at room temperature (Faccoli, 2002).

In terms of calculations, one exit hole represents one emerged adult beetle (Schlyter et al., 1984; Komonen et al., 2011). The number of adult beetles which remained under the bark and number of adult beetles which had left the bark were first calculated per m² and then compared between trees using a nonparametric Kruskal-Wallis test. Spearman’s Rank correlation between the number of beetles which had left the logs actively (number of exit holes) and the predator abundance under the bark was calculated in Statsoft® Statistica 8.

**RESULTS**

In total, 55 samples (43.5 m² of the bark) were analyzed. The number of samples differs between trees because wood peckers destroyed a part of the bark in some trunk sections and those samples were not included in analysis.
The percentage of beetles remaining under the bark differs significantly between sections \( [\text{K-W } H(DF = 4, N = 55) = 21.55579, p = 0.0002] \). The proportion of adult bark beetles remained in the bark varies between 79.4 and 95.1 % among trees, with the average proportion to 84.7 %. There is a positive correlation between the number of adults beetles which left the bark and the abundance of predator larvae \( (r = 0.487693, N = 55, p < 0.05) \). In total, 4622 predator larvae were detected, among which *Medetera* larvae were the most abundant larval form.

The results indicate that the proportion of a beetle population which stays under the bark during the winter increases with a decrease of elevation. It can be explained by the genetic variability (Stauffer et al., 1999) and plasticity (Hrašovec et al., 2011; Dworschak et al., 2014) within the oldest European populations of *I. typographus* which are present in south and central Europe (Stauffer et al., 1999). This species is adaptable to spatially and temporally changeable habitat conditions. The beetles of southern latitudes and lower elevations are not forced to leave the bark during the winter to avoid chilling injuries caused by long-lasting low air temperatures, which are typical for northern Europe and higher elevations elsewhere. Higher portion of beetles leave the bark in sections with their higher total production or predator abundance. This fact can be viewed as a further confirmation of the plasticity of species and the possibility of adaption to changeable habitat conditions. Most of the natural enemies of *I. typographus* overwinter as larvae in bark beetle galleries, which is similar to the situation in Switzerland (Wermelinger et al., 2012).

Overwintering behavior is the key factor in planning sanitation felling as recovery measure within hot spots of *I. typographus* attacks. In regard to spruce stand growing at 550 m. a. s. l., the second generation of spruce bark beetles finishes full development in late September or mid-October (Kasumović, 2016), but a shortage of photoperiod in mid-August can cause a swarming, copulation or gradual disruption of egg hatching (Baier et al., 2007; Kasumović, 2016). Moreover, 15 % of beetles which leave the logs actively through exit holes overwinter in the needle litter. As far as the zone of Velebit peaks is concerned, half of bark beetle population overwinter in the needle litter while in altimontane region, this figure is smaller, around 40 % (Hrašovec et al., 2011). The life cycle and voltinism of *I. typographus* is elevation adaptable (Faccioli 2002; Kasumović, 2016), and have significant influence on the share of beetles which leave the bark during the winter (Wermelinger et al., 2012).

Despite temperature fluctuation and super cooling injuries (Annila, 1969), bark is believed to be a good overwintering niche. This thesis is supported by the following facts: beetles stay in dry bark where the freezing risk is very low (Koštál et al., 2011); the risk of infection is minimal in dry conditions (Doležal et al., 2009); bark heated by sun isolation in spring results with earlier nutrients exploitation, development completion (Dworschak et al., 2014) and a prolonged fly period for the new host search (Hrašovec et al., 2011).

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The number of beetles overwintering under the bark, which is inversely proportional with elevation, highlights the difficulties in sanitation felling which needs to be adapted to

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*Figure 1.* Percentage of adult beetles under the bark. Boxes indicate the 25th and 75th percentiles, whiskers minimum and maximum, and small square medium, respectively

*Slika 1.* Postotak prezimljavanja odraslih potkornjaka pod korom. Pravokutnici obuhvaćaju vrijednosti između prvog i trećeg kvartila, linjski minimalne i maksimalne vrijednosti, a mali kvadratić medijanu.

*Figure 2.* Percentage of overwintering beetles per two niches at different elevations in Dinaric spruce forests, including the data from a recent study (Hrašovec et al., 2011)

*Slika 2.* Postotak zimujućih potkornjaka u dvije niše u Dinarskim smrekovim šumama na različitim nadmorskim višinama, uključujući podatke nedavnih istraživanja (Hrašovec i dr., 2011)
elevation and season. At higher elevations, sanitation measures aimed at reduction of the emergence of new infestation spots (Stadelmann et al., 2013) need to be implemented in early autumn when most of the beetles are still under the bark while in lowlands, felling in early spring or late autumn can achieved high efficiency. Winter felling does not only kill most bark beetles within bivoltine populations, but also eliminates a huge fraction of their natural enemies whereas with univoltine populations of this pest, this is much less detrimental (Wermelinger et al., 2012). In regions with beetle outbreaks, the priority need to be salvage logging of damaged timber, particularly in years affected by storm events (Stadelmann et al., 2013). Salvage logging should be followed by sanitation felling which ought to comprise the area within 100 m from previous infestations (Esseen et al., 2007). The removal of attacked standing trees may additionally cause edge effect in subsequent spring (Dworschak et al., 2014) when colonized wind felled trees (Esseen, 1994; Peltonen, 1999) or killed standing trees (Hedgren, 2002) can be frequent occurrence due to the beetles that overwinter in the litter and constitute the local population within the spots of attacks.

Foresters need to consider the fact that bark falls off in upper parts of standing trees during the winter period (Dworschak et al., 2014) and changes the portion of beetles between niches. It could have a negative impact on the success of sanitation recovery planned for spring. Upper parts of standing trees are often heavily infested, which can modify insulator characteristics of the bark and result in peeling and higher winter mortality (Faccoli, 2002) as well as in a higher proportion of upper tree beetles which leave the bark during the winter (Komonen et al., 2011). During sanitation felling, the removal of attacked standing trees with needles discoloration need to be carried out first. For that purpose, individual inspection of symptoms (resin flow, boring dust around the trunk) in each tree is necessary. Sometimes it is difficult to conduct such an inspection due to a shortage of time and manpower. If beetles complete their development and leave trees, it might be good to leave those trees in stands for some time because the bark beetle antagonist can be removed with them (Wermelinger et al., 2012). The impact on the natural enemies can be minimized if heavy infested trees are removed out of stands before the emergence of bark beetles.

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REFERENCES

- Annila E., 1969: Influence of temperature upon the development and voltinism of Ips typographus L. (Coleoptera: Scolytidae). Ann. Entomol. Fenn. 6: 161-208
- Annila E., 1971: Sex ratio in Ips typographus L. (Coleoptera: Scolytidae). Entomol. Fennica 37:7-14
- Aandbrant O., 1986: A model for temperature and density dependent reemergence of the bark beetle Ips typographus. Entomol. Exp. Appl. 40:81-88
- Austarå O., Pettersen H., Bakke A., 1977: Bivoltinism in Ips typographus in Norway and winter mortality in second generation. Medd. Norweg. Inst. Skogforsk. 33: 269-281
- Baier P., Pennerstorfer J., Schopf A., 2007: PHENIPS – A comprehensive phenology model of Ips typographus (L.) (Col., Scolytinae) as a tool for hazard rating of bark beetle infestation. Forest. Ecol. Manag. 249: 171-186. doi:10.1016/j.foreco.2007.05.020
- Bakke A., Frøyen P., Skatseth L., 1977: Field response to a new pheromonal compound isolated from Ips typographus. Naturwissenschaften 64:98-99
- Botterweg P.F., 1982: Dispersal and flight behaviour of the spruce bark beetle Ips typographus in relation to sex, size and fat—content. J. Appl. Entomol. 94:466-489. doi:10.1111/j.1399-0418.1982.tb02594.x
- Byers J. A., 2012: Ecological Interactions of Bark Beetles with Host Trees. Psyche 2012:1-3. doi:10.1155/2012/252961
- Christiansen E., Bakke A., 1997: Does drought really enhance Ips typographus epidemics? A Scandinavian perspective. Proceedings: Integrating cultural tactics into the management of bark beetles and reforestation pests, USDA Forest Service General Technical Report NE-236, p 163-171
- 10. Christiansen E., Bakke A., 1988: The spruce bark beetle of Eurasia, Dynamics of Forests Insect Populations. Patterns, Causes, Implications. Plenum Press, p 479-503, New York-London
- Coeln M., Niu Y., Fuhrer E., 1996: Temperature-related Development of Spruce Bark Beetles in Montane Forests Formations (Coleoptera: Scolytidae). Entomol. Gen. 21:37-54
- Doležal P., Husáková J., Sehnal F., 2009: Effect of temperature on the termination of imaginal diapause in the spruce bark beetle Ips typographus (L.) hibernating under the bark or in the litter. Ann. Entomol. Fenn. 6: 161-208
- Dworschak K., Meyer D., Gruppe A., Schopf R., 2014: Choice or constraint: Plasticity in overwintering sites of the European spruce bark beetle. Forest. Ecol. Manag. 328:20-25. doi:10.2016/j.foreco.2007.05.020
- Esseen P.A., 1994: Tree mortality patterns after experimental fragmentation of an old-growth conifers forest. Biol Conserv 68, 19-28.
- Faccoli M., 2002: Winter mortality in sub-corticolous populations of Ips typographus (Coleoptera: Scolytidae) and its parasites in the south-eastern Alps. J. Pest Sci. 75:62-68. doi:10.1034/j.1399-5488.2002.02017.x
- Faccoli M., 2009: Effect of Weather on Ips typographus (Coleoptera, Curculionidae) Phenology, Voltinism and Associated
Spruce Mortality in the Southeastern Alps. Environ. Entomol. 38(2):307-316. doi:10.1603/022.038.0202

Faccoli M., Stergulc F., 2006: A practical method for predicting the short-time trend of bivoltine populations of Ips typographus (L.) (Coleoptera, Scolytidae). J. Appl. Entomol. 130: 61-66. doi:10.1111/j.1439-0418.2005.01019.x

Grégoire J. C., Evans H. F., 2004: Damage and control of BAW-BILT organisms—an overview. Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis, Kluwer Academic Publisher, p 19-37, London

Gutowski M. J., Krzysztofiak L., 2005: Directions and intensity of migration of the spruce bark beetle and accompanying species at the border between reserves and managed forests in north-eastern Poland. Ecological Questions 6:81-92

Hedgren P. O. 2002: Dead Wood Retention and the Risk of Bark Beetle Attack. Dissertation. Swedish University of Agricultural Sciences

Hrvašovec B., Kasumović L., Franjević M., 2011: Prezimljanje smrkovog pisara (Ips typographus L.) u smrkovim šumama sjevernog Velebita (Overwintering of Eight Toothed Spruce Bark Beetle (Ips typographus L.) in Spruce Forests of North Velebit). Croat. J. For. Eng. 32:211-222 (in Croatian with English abstract)

Jurc M., Perko M., Džeroki S., Desar D., Hravašovec B., 2006: Spruce bark beetle (Ips typographus, Pityogenes chalcographus, Col: Scolytidae) in the Dinaric mountain forests of Slovenia: Monitoring and modeling. Ecol. Model. 194:219-226. doi:10.1016/j.ecolmodel.2005.10.014

Kasumović L. i dr.: OVERWINTERING STRATEGY OF IPS TYPOGRAPHUS L. (COLEOPTERA, CURCULIONIDAE, SCOLYTINAE) IN CROATIAN SPRUCE FORESTS ...
SAŽETAK
Pokus je postavljen u ljeto 2014. s ciljem boljeg razumijevanja strategije zimovanja smrekovog pisara, ali djelomično i zbog dopune zaključaka nedavno provedenih istraživanja (Hrašovec i dr., 2011). U kulturi smreke na nadmorskoj visini od 550 m. u mjesecu srpnju oboreno je 5 potpuno zdravih smrekovih stabala koja su okresana i ostavljena u sjeni okolnih stabala. Prva ubušivanja smrekovog pisara primijetima su već nakon tjedan dana. Početkom mjeseca siječnja 2015. godine stabla su izrezana u trupce dužine 4 m radi lakšeg prijevoza do skladišta gdje su u potpunosti analizirana. Svaki trupac podijeljen je u 4 sekcije dužine jedan metar, a na sredini sekcije izmjeren je srednji promjer zbog izračuna površine kore pojedine sekcije i samog trupca, odnosno stabla. Prije otkoravanja obilježeni su i prebrojani izletni otvori gdje je svaki izletni otvor predstavljao jednog odraslog potkornjaka koji je prezimio u tlu. Osim broja potkornjaka utvrđen je i broj prirodnih neprijatelja (Thanasimus (Coleoptera: Cleridae), Medetera (Diptera: Dolichopodidae), predatory gall midges (Diptera: Cecidomyiidae) koji prezimljavaju pod korom napadnutih stabala. Gledajući na razini same vrste kao mjesta prezimljanja prisutne su dvije ekološke niše – tlo i kora. U smrekovoj kulturi na najnižoj nadmorskoj visini na kojoj smreka raste 85 % potkornjaka prezimljuje pod korom napadnutih stabala, dok na višim nadmorskim visinama postotak značajno opada. Rezultati ukazuju na vjerovatnost prilagodbe prezimljanja promjenjivim stanišnim uvjetima i temperaturnim prilikama, što ponajprije proizlazi iz plastičnosti same vrste. Visoko u planinama sanitarna sječa treba se provesti krajem ljeta ili rano u jesen kada je većina potkornjaka još uvijek pod korom, dok se na nižim nadmorskim visinama dobri rezultati mogu postići i sječom u rano proljeće prije leta potkornjaka. Ova mogućnost uvelike pomaže operativi na terenu, budući da često žarišta napada nije moguće sanirati u jesen, dijelom zbog nesto pod korom nesavršene odnose mehanizacije. Kod primjene ovih rezultata operativa mora biti opreza jer kora s napadnutih dubećih stabala tijekom tijekom zime otpada i mijenja odnos potkornjaka između niša zimovanja što izravno može utjecati na uspjeh planiranih sanacija u proljeće.

KLJUČNE RIJEČI: kora, tlo, prirodni neprijatelji, plastičnost, temperatura, sanitarna sječa