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INFLUENCE OF PREDATOR ABUNDANCE AND WINTER MORTALITY ON REPRODUCTION OF BIVOLTINE POPULATIONS OF *Ips typographus* L. (COLEOPTERA: CURCULIONIDAE)

UTJECAJ GUSTOĆE PREDATORA I ZIMSKOG MORTALITETA NA REPRODUKCIJU BIVOLTNIH POPULACIJA SMREKOVOG POTKORNJAKA *Ips typographus* L. (COLEOPTERA: CURCULIONIDAE)

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Summary

The study was aimed at evaluating the influence of winter mortality and predator larvae abundance on breeding performance of bivoltine populations of *Ips. typographus* colonizing felled spruce trees in Croatia. A low colonization density of *I. typographus* expressed as a number of maternal galleries per square meter of bark, usually reflects high reproductive success, defined as a number of daughters per mother beetle (♀/♀). Regarding this study, the mean gallery density on felled trees varied between 27 and 146 per m^2 of bark, while the lowest reproduction rate was only 0.5 ♀/♀. Althought differently suggested by previous findings, the cause of such a low reproduction rate can be explained by high abundance of predator larvae and high winter mortality of larvae, pupae and callow beetles. The results suggest that predators, primarily long-legged flies-of the genus *Medetera* (Fischer von Waldheim) (Diptera: Dolichopodidae), have huge ecological impact on bark beetle populations at endemic levels. At low attack densities, the majority of males (74%) copulate with two females, following the evolutionary trait of avoiding intraspecific larval competition.

KEY WORDS: breeding, low attack, gallery, intraspecific, *Medetera*

INTRODUCTION
UVOD

Most bark beetle species (Coleoptera, Curculionidae, Scolytinae) colonize recently dead trees, but some species are able to attack and kill living trees to reproduce (Lindelöw and Schroeder, 2002; Hedgren, 2004). *Ips typographus* (Linnaeus) (Coleoptera: Curculionidae: Ipini) is the most severe and destructive spruce pest in Europe (Christiansen and Bakke, 1988; Grégoire and Evans, 2004; Wermelinger,

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2004), and it plays an important role in Croatian spruce forests, which is also common for other part of Europe where spruce grows (Hrašovec et al., 2011). *I. typographus* is univoltine in northern Europe (Austarå and Midtgaard, 1986; Schroeder, 2013), and elsewhere in Europe at higher elevations. In central and southern Europe this beetles reproduces two times a year (Wermelinger, 2004; Faccoli and Stergulc, 2006; Jurc et al., 2006; Faccoli, 2009) and overwinters as an adult insect under the bark or in needle litter (Christiansen and Bakke, 1988; Weslien, 1992; Hrašovec et al., 2011; Wermelinger et al., 2012).

Populations of *I. typographus* can remain endemic for a long period of time. In optimal conditions the populations may increase to epidemic proportions when growing trees are attacked and killed (Raffa et al., 2008). Large-scale disturbances, such as storms, e.g. Lothar and Vivian in Switzerland (Wermelinger, 2004), and Gudrun in Sweden (Schroeder, 2010) usually act as triggers of bark beetle outbreaks. *I. typographus* can quickly respond to the appearance of suitable hosts, resulting from favourable weather and stand conditions (Wermelinger, 2004), which happened in the mountain region of Croatia after the ice storm in the late winter of 2014 (Vuletić et al., 2014). The reproduction success of these insects usually differs between living and felled trees due to different host resistance (Elkin and Reid, 2004). For successful colonization of standing trees, beetle attacks need to overcome the defence system of host trees (Mulock and Christiansen, 1986). Living trees defend themselves against bark beetle attacks by a flow of resin-or through the mobilization of dead resin – rich cells around the infected sites to prevent further spread (Francheschi et al., 2000). The availability of these two types of substrate and beetle reproduction success determines their relative importance for the production of bark beetles at the landscape level (Hedgren and Schroeder, 2004). The reproduction rate is related to the intraspecific competition among larvae, particularly when bark beetles shifts from wind felled to live standing trees (Kommonen et al., 2011). A high bark beetle colonization density (maternal galleries per m^2) usually leads to their low reproduction rate (Hedgren and Schroeder, 2004; Faccoli and Bernadinelli, 2011). However, some bark beetle species, precisely those finding additional feeding outside of the host bark can avoid this effect (Sauvard, 1989).

Favourable weather conditions during summer usually allow *I. typographus* to start second or even third generation. In that case some individuals do not complete development before winter and some portion of offspring beetles are forced to hibernate as larvae or pupae. Winter mortality from freezing, especially in pre-adult stages (Faccoli, 2002), complex relationship between host trees and natural enemies (Christiansen et al., 1987), factors stressing trees or inducing variations in the natural enemy abundance (Weslien, 1992) could be an important determinant of population dynamics in *I. typographus*.

The aim of this study was to research the influence of winter mortality and natural enemies on the reproductive success of bivotine populations of *I. typographus* with respect to their colonization density.

MATERIAL AND METHODS
MATERIJAL I METODE

The study was carried out during winter 2014/15 in a 50-year-old spruce stand at 500 m a.s.l. in south-western Croatia (44˚36'49.41" N; 15˚19'13.89" E).

Five spruce trees similar in size were felled and pruned in mid-July, and then left in a stand to be colonized by *I. typographus*. The mean diameter of trees was 29 cm (min-max = 27-32 cm), and medium tree height was 18 m. In the moment of felling all spruce trees were in good health condition without visible needles discoloration. Distance between felled spruces were 30 m to avoid the influence between them at the time of bark beetle colonization. Fist colonization were detected one week after felling. During January, all trees were first cut in 4 m long logs, and then transported to a storehouse where they had been stored at temperatures below 5 ˚C until undergoing analysis in February.

For calculating the bark surface, the log diameter was to be measured first in the middle of each section. What need to be performed before debarking is counting exit holes per each section. During the bark analysis, the number of mating chambers and maternal galleries were counted first. Then the samples were carefully pulled apart, which was followed by counting of *I. typographus* callow beetles, pupae, the biggest larvae (third larval instar) and predator larvae (ant beetle-genus *Thanasimus* (Latreille) (Coleoptera: Cleridae), long-legged flies of the-genus *Medetera* (Fischer von Waldheim) (Diptera: Dolichopodidae) and predatory gall midges (Diptera: Cecidomyiidae)). Living and dead in-

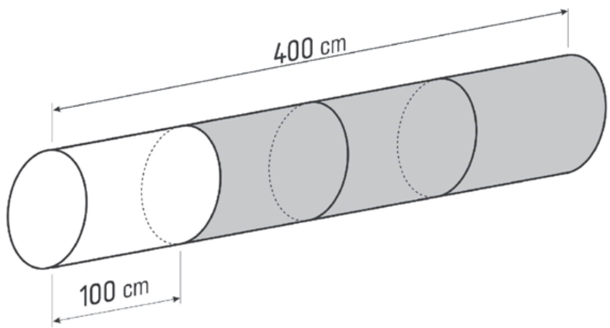

Figure 1. Bark sample (white) on a 4 m long spruce log. The samples were separated with an axe after counting the exit holes.

Slika 1. Uzorak kore (bijelo) na 4 m dugačkom trupcu. Uzorci su otkorani pomoću sjekire nakon brojanja izletnih otvora.

sects were assessed visually. Callow beetles, larvae and pupae were considered dead if they showed no sign of movement at room temperature, or were deformed (Faccoli, 2002).

The reproductive success is defined as a number of daughters per mother beetle (♀/♀), and was calculated as:

$$♀/♀ = [\frac{(a + b) * 0.5}{c}]$$

assuming that one exit hole represents one emerged adult beetle (Schlyter et al., 1984; Komonen et al., 2011), and a balanced sex ratio – 0.5 (Annila, 1971).

Number of:

a – exit holes
b – young living adults in the bark
c – maternal galleries

The measured parameters (reproductive success, total production, gallery number per mating chamber, predator larvae abundance) were first processed in Microsoft® Office 2007, and then compared in Statsoft® Statistica 8 by means of non-parametric Kruskal-Wallis test. The mortality per m² in each development stage were calculated in Microsoft® Office 2007. The Sperman Rank correlation between the predator abundance and the bark beetle attack density were calculated in Statsoft® Statistica 8.

RESULTS
REZULTATI

In total, 55 sections were analysed (table 1.). The number of analysed samples (sections) differed between trees due to the decomposition of bark in top sections or no visible sight of *I. typographus* colonization. Top sections with thinner bark were not analysed because dominant bark beetle species was *Pityogenes chalcographus* (Linnaeus) (Coleoptera: Curculionidae: Ipini). Because of difference in the number of samples taken from a single tree, the non-parametric Kruskal-Wallis test was used in the data analysis.

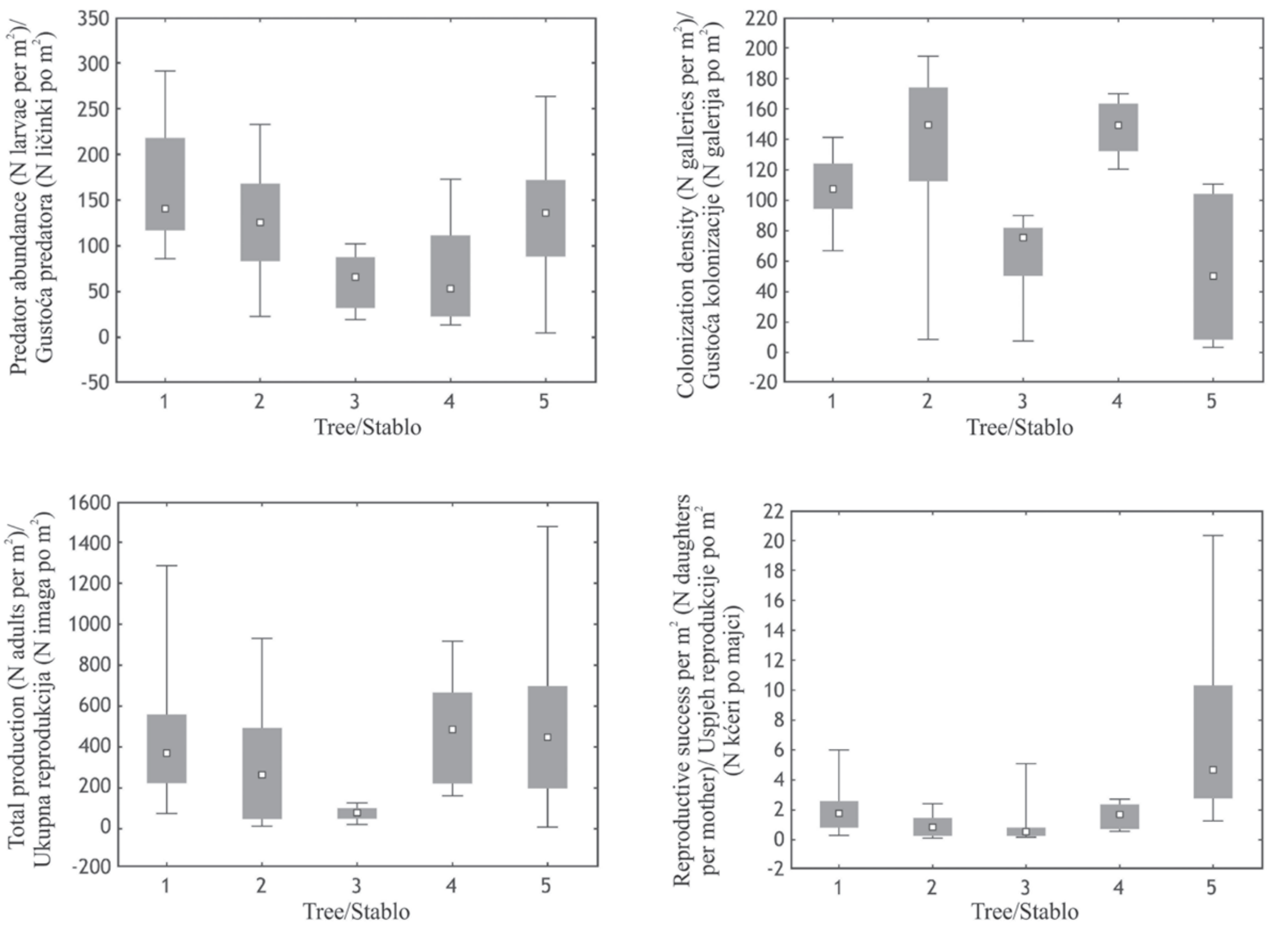

Figure 2. Predator larvae abundance (a), colonization density (b), total production (c) and reproductive success (d) of *Ips typographus* in analyzed stem sections (n = 55). The data are based on bark samples inspected in a laboratory. The boxes indicate 25th and 75th percentiles, whiskers minimum and maximum, and a small square median, respectively.

Slika 2. Gustoća ličinki predatora (a), gustoća napada (b), ukupna produkcija (c) i uspjeh reprodukcije (d) smrekovog potkornjaka *Ips typographus* u analiziranim sekcijama debla (n = 55). Podaci se baziraju na uzorcima kore analiziranim u laboratoriju. Sjenčani pravokutnici obuhvaćaju vrijednosti između prvog i trećeg kvartila, linijski minimalne i maksimalne vrijednosti, a mali kvadratić medijanu.

Table 1. Mortality in different development stages of *Ips typographus* *and number of analysed sections per each tree*
Tablica 1. Mortalitet različitih razvojnih stadija smrekovog pisara *Ips typographus* i broj analiziranih sekcija po pojedinom stablu

Tree/Stablo	Number of analyzed sections/Broj analiziranih sekcija	Adult/*Imago*	Pupae/*Kukuljica*	Larvae/*Ličinka*
			%	
1	16	42.8	14.7	76.8
2	16	34.0	18.9	51.3
3	8	42.6	70.6	100.0
4	8	18.1	22.2	100.0
5	7	26.3	26.8	72.9

The colonization density varied significantly between analysed sections [K-W H(DF = 4, N = 55) = 26.84310, p = 0.0001]. The lowest gallery density in infested trees amounted to 1.1 galleries per m^2, and the highest to 195.4 galleries per m^2. It also come to a significant difference in the reproductive success between analysed sections [K-W H(DF = 4, N = 55) = 1.25745, p = 0.0003]. In some sections, the reproduction success reached 20 ♀/♀, but it was accompanied with a very low colonization density, only 9 maternal galleries per m^2. There was some sections with as many as 1284 filial beetles, but this figure also varied considerably between infested sections [K-W H(DF = 4, N = 55) = 13.11153, p = 0.0107]. The same thing can be said for the number of predator larvae [K-W H(DF = 4, N = 55) = 17.05745, p = 0.0019], which positively correlates with the colonization density (r = 0.896156, N = 55, p < 0.05). In total, 4622 predator larvae were counted (*Medetera* – 4012, Cecidomyidae – 604, *Thanasimus* – 6). The average density ranged from 53 to 135 predator larvae per m^2.

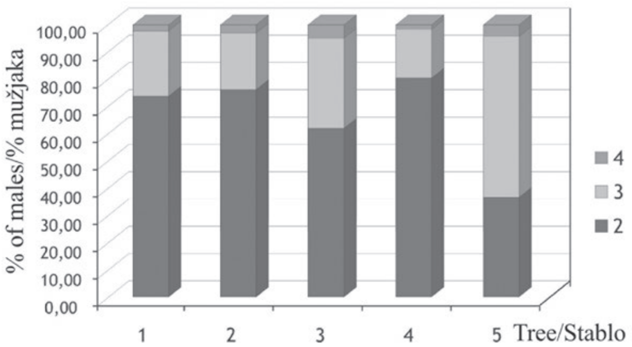

Figure 3. Percentage of males copulating with 2 – 4 females in analysed Norway spruce stem sections per each spruce tree trunk
Slika 3. Postotak kopulacije mužjaka s 2 – 4 ženke u analiziranim sekcijama pojedinog debla smreke.

The maximum winter mortality of callow beetles amounted 42 %, while the peak winter mortality in the pupal stage was 85 %. As far as the biggest larvae are concerned, some sections were even featured by total mortality.

Systems with 2 maternal galleries prevailed (74.2 %). They were followed by systems with 3 maternal galleries which were found in almost one quarter of analysed samples (23.4 %), whereas the 4 maternal gallery systems were very rare (2.4 %).

DISCUSSION
RASPRAVA

The dominant overwintering development stage of *I. typographus* under the bark was the callow beetle. It was followed by pupae while the biggest larvae were the least common. The reproductive success at low attack densities was very low, which is contrary to previous findings (Inouye, 1962; Furuta, 1989). The biological potential of *I. typographus* is extremely high (Christiansen & Bakke, 1988) up to 20 ♀/♀, and it is very likely that most bark beetle females do not have such high biological potential, either on wind felled (Furuta, 1989; Eriksson et al., 2008; Komonen et al., 2011), alive and standing (Hedgren and Schroeder, 2004; Faccoli and Bernandinelli, 2011; Komonen et al., 2011) or felled trees (Hedgren and Schroeder, 2004; Ericsson et al., 2008).

High winter mortality rate of pupae, larvae and callow beetles and high abundance of predator larvae probably influence the reproductive success in *I. typographus*.

Overwintering of pre-adult stages of *I. typographus* is not possible (Austarå et al., 1977; Coeln et al., 1996; Baier et al., 2007) since larvae and pupae are extremely sensitive to low winter temperature (Andebrant et al., 1985; Andebrant, 1988; 1990). This is supported by Faccoli's research (2002) who detected only callow beetles under the bark of attacked trees in spring. The freezing point for larvae and pupae is -13 C˚ and -17 ˚C, respectively, and concerning callow beetles, this figure ranges from -20 ˚C to -30 ˚C (Annila, 1969), though, more recent studies (Koštal et al., 2007; 2011) narrow this range between -20 ˚C and -22 ˚C. Winter temperatures in the area where the research was conducted commonly drop below the above thresholds relating to larvae and pupae, but lethal temperatures for the callow of fully mature beetles are rarely measured. The attack time is mainly triggered by favourable weather conditions while delayed attacks in summer could result in high winter mortality rates (Wermelinger and Seifert, 1999). Adults with low lipid content heavily survive winter (Botterweg, 1982).

Positive correlation between the bark beetle attack density and the predator abundance has been observed. Unlike recent Swedish research (Hedgren and Schroeder, 2004), this study has disclosed high abundance of *Medetera* accompanied with low attack densities on felled trees. *Medetera* larvae turn out to be the most abundant predator off all in this context (86 %). The results suggest that their ecological impact on *I. typographus* populations is not present only at outbreak conditions, but also at endemic levels. High predator abundance can even result in an 80 % reduction of bark beetle populations (Weslien, 1992). Assessing the predator abundance and its impact on the size of bark beetle populations is important in determining the impact of tree removal from infested stands on the outspread of this pest (Hedgren and Schroeder, 2004).

The majority of male beetle comprised this research copulated with two females, which is compliant with some recent research (Anilla, 1971; Starzyk et al., 2000; Grodzki et al., 2014). Pursuant to the calculation made within this research the average number of females per male was 2.3, while according to Wermelinger (2004), optimal number of females per male is 3. This figure depends on host susceptibility, and it differs between wind felled (Grégoire et al., 1997) and standing killed trees (Vakula et al., 2014). When males copulate with more than two females, it comes to a significant reduction in the breeding success (Schlyter and Zhang, 1995). Contrary to the expectations, gallery systems with two maternal galleries as an evolutionary adaptation to avoid intraspecific larval competition at high attack, were the prevalent form at low attack densities.

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SAŽETAK

Smrekov pisar, *Ips typographus* je jedan od najštetnijih i najistraživanijih štetnika smreke u Europi. Istraživanje je provedeno s ciljem utvrđivanja utjecaja zimskog mortaliteta i gustoće predatora na uspjeh reprodukcije bivoltnih populacija smrekovog potkornjaka, *Ips typographus* L., koje koloniziraju posječena stabla u smrekovim kulturama jugozapadne Hrvatske. Početkom srpnja 2014. u kulturi smreke oboreno je 5 stabla istih dimenzija. Stabla su ostavljena u sjeni okolnih stabala kako bi ih kolonizirale jedinke smrekvog pisara. Početkom siječnja 2015. stabla su prevezena u skladište, gdje su detaljno analizirana. Najprije su podijeljena u sekcije dužine 1 m kojima je na temelju promjera na sredini sekcije izračunata površina kore (m^2). Prije otkoravanja svake sekcije najprije su izbrojani izletni otvori. Nakon otkoravanja utvrđen je broj ličinki (prvog, drugog i trećeg larvalnog stadija), kukuljica, mladih imaga potkornjaka te broj ličinki predatora. Mortalitet ličinki, kukuljica i mladih imaga utvrđen je na temelju njihove pokretljivosti na sobnoj temperaturi. Na svakom uzorku kore izbrojane su galerije te je utvrđen broj galerija po bračnoj komorici, odnosno prosječan broj ženki po jednom mužjaku. Kod izračuna uspjeha reprodukcije izraženog brojem kćeri po majci (♀/♀) uzet je u obzir omjer spolova 50:50.

Niska gustoća kolonizacije izražena brojem majčinskih galerija po kvadratu kore rezultira visokim uspjehom reprodukcije izraženim brojem kćeri po majci (♀/♀). Suprotno od već provedenih istraživanja, mala srednja gustoća galerija po m^2 kore (27 do 146) rezultirala je s malim uspjehom reprodukcije (0.5 do 4.2 ♀/♀). Mali uspjeh reprodukcije posljedica je visoke stope mortaliteta ličinki, kukuljica i mladog imaga tijekom zime, ali i visoke gustoće ličinki predatora. Rezultati upućuju na činjenicu da predatori, ponajprije muhe gusjeničarke–rod *Medetera* (Diptera: Dolichopodidae) imaju važan utjecaj na populaciju potkornjaka i pri niskim gustoćama populacije, za razliku od već provedenih istraživanja. U provedenom istraživanju sustavi s dvije galerije bili su najzastupljeniji (74 %), što znači da je mehanizam izbjegavanja unutarvrsne kompeticije ličinki za ishranu svježim floemom prisutan i kod endemičnih gustoća populacija kao svojevrsna evolucijska prilagodba, za razliku od dosadašnjih istraživanja koja potvrđuju njegovu prisutnost samo kod visokih gustoća populacija.

KLJUČNE RIJEČI: kopulacija, niska gustoća, galerije, unutarvrsna, *Medetera*