

Article

Evaluation of Attractant Composition, Application Rate, and Trap Type for Potential Mass Trapping of *Ips typographus* (L.)

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Abstract: This study focused on elucidating the possibilities of improving current trapping methods for *Ips typographus* (Linnaeus, 1758). Three field experiments were conducted simultaneously in one study area in the German federal state of Saxony. A comparison of six different commercial attractants revealed a significant superiority of Typosan[®], especially for adult beetles after hibernation in the phase of their first swarming. It also attracted fewer individuals of *Thanasimus* spp. than the other highly attractive products Pheroprax[®] and IT Ecolure Extra[®]. Increasing the Pheroprax[®] application rate by using four instead of one dispenser in a single trap increased the total catch of *I. typographus* only by 15.5%. In contrast, *Thanasimus* spp. catch increased by 195.5% when four dispensers were used. A test of different trap types showed a species-specific catching capability, with the 12-funnel WitaTrap[®] being the most effective in catching *I. typographus*. The quantity of *Thanasimus* spp. bycatch in multiple-funnel traps demonstrated the necessity of a selective mechanism to minimize impacts on predator populations. Although we were not able to identify new milestones towards mass trapping, this study contributes to necessary improvements of current trapping methods. Especially in future stands with a smaller share of Norway spruce (*Picea abies* Karsten, 1881) the weakened beetle population in spring could be effectively reduced by properly conducted mass trapping.

Keywords: *Ips typographus*; *Thanasimus* spp.; bark beetles; Norway spruce; mass trapping; attractants; release rate; trap type; integrated pest management



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1. Introduction

Climate change impacts on forests are a worldwide phenomenon [1–3]. For Europe, an increase in extreme weather events is predicted to cause physiological stress for trees and forests as well as promoting the reproduction of forest insects with high damage potential [4,5]. Consequently, millions of hectares of forest land are annually damaged by insects and pathogens in Europe [6]. The eight-toothed spruce bark beetle (*Ips typographus* Linnaeus, 1758) particularly benefits from more frequent droughts, storms, and rising temperatures [1,7,8]. The species is able to undergo eruptive population outbreaks and is known as the most destructive pest in forests of Norway spruce (*Picea abies* Karsten, 1881) where it has killed extensive areas in recent years [7,9,10].

Enormous amounts of suitable breeding material following disastrous storms, a drought-induced raised susceptibility of trees and high temperatures accelerating the development of *I. typographus* increase the probability of outbreaks [1,11–13]. These factors coincided in Central Europe from 2017 to 2020. Six devastating storm events [14–19] and unprecedented hot and dry summers [20] gave rise to a perennial large-scale outbreak of *I. typographus*. In such situations, the species is able to overcome the defense mechanism of healthy trees and not depend on susceptible stands [7,21–23]. As a result, large amounts of calamity wood accumulated, especially in Germany, the Czech Republic, and Austria [24–26], which exceeded the capacity of the regular forestry and wood industry, thus resulting in severe logistical problems [9,27]. For example, in the German federal

state of Saxony, unplanned wood logging due to bark beetle infestations alone added up to 2.2 million m³ in 2019, which is almost as much as the annual mean for Europe from 1950 to 2000 with 2.9 million m³ [26,28]. Historically, bark beetle induced calamities are a frequent phenomenon. A total of 7000 hectares of spruce forest were killed during an outbreak of *I. typographus* from 1781 to 1786 in the Harz mountains [29]. Several other eruptive population outbreaks followed in the 19th and 20th century in Europe [28,30,31].

Even though *I. typographus* is considered to be a crucial ecosystem engineer and key-stone species in natural forests, its management in forests, serving ecological, social, and economic purposes, is often inevitable to sustain a multifunctional forestry [8]. Trap-based monitoring programs are an important part of managing spruce forests [13,32]. Since trap trees were replaced by artificial traps after the discovery of the species-specific aggregation pheromone of *I. typographus* [33,34], trapping methods have been constantly developed and improved [35–39]. Salvage logging and sanitation felling are based on the monitoring data and are still the most effective measures in bark beetle management [11,13,32]. Consequently, the enormous amount of unplanned logging caused a drop in wood prices due to a saturated wood market [9]. The preventive application of pheromone traps to protect spruce stands and avoid calamity logging has been, however, discussed intensively. Various studies have proven that effective trap-based management can prevent attacks by *I. typographus* and decrease unplanned logging [40–45]. In contrast, many studies exist in which no significant reduction in population sizes and protection of living trees were achieved by trapping despite great effort [30,46,47], or where the cause for the decline in damage cannot be explicitly assigned to mass trapping [31,45]. The critical factor for success or failure appears to be the stage of population development in which mass trapping was conducted [13,42]. The increasing restrictions for the application of insecticides in forests due to strict formalities of the European Union [48] and the side effects of calamity logging draw interest to mass trapping options without insecticides. Such methods aim to reduce the population density of the target species in a way that secures the ecological, social, and economic objectives of the forest.

In our study we conducted alterations of current trapping methods for *I. typographus* to improve the state of knowledge for future mass trapping as part of bark beetle management. With regard to the “surveillance with the intent to control” approach by Vité (1989) [34], and in consideration of important antagonists, three main components of current monitoring techniques were tested concerning their potential for mass trapping of *I. typographus*. These are:

- (1) attractant composition,
- (2) application rate, and
- (3) trap type.

2. Materials and Methods

2.1. Study Site

The study took place in Germany in the federal state of Saxony in the Tharandt forest from the 6 April 2020 to the 29 June 2020. Three different clearings were selected in the forest district Bärenfels between the villages of Grillenburg and Naundorf, north and south of the state road S194 and within a radius of 1700 m to ensure similar climate conditions. The study sites are located at an altitude of 400 to 430 m above sea level and are categorized as humid lower mountainous region. The mean annual temperature is 9.8 °C, long-term precipitation mean is 843 mm, but was distinctly lower in 2018 (496.4 mm), 2019 (676.1 mm), and 2020 (644.7 mm). The distance between the three clearings was at least 100 m to avoid interdependence.

In the study area, a mass outbreak of *I. typographus* started in 2018 and has caused large amounts of calamity wood. The clearings selected for this study are the result of sanitation felling or salvage logging. The adjacent stands consist mainly of Norway spruce, 40 to 70 years old and colonizable by *I. typographus*. Scots pine (*Pinus sylvestris*), European larch (*Larix decidua*), and European beech (*Fagus sylvatica*) are secondary tree species. Silver birch

(*Betula pendula*), common ash (*Fraxinus excelsior*), sycamore maple (*Acer pseudoplatanus*), and European alder (*Alnus glutinosa*) are present as single trees.

2.2. Species Identification

I. typographus, *Thanasimus femoralis* (Zetterstedt, 1828), and *T. formicarius* (Linnaeus, 1758) were defined as target species, which are considered to be two of the most important antagonists of *I. typographus* [49,50]. In the process of further analyses, *T. femoralis* and *T. formicarius* were regularly grouped as *Thanasimus* spp. *Pityogenes chalcographus* (Linnaeus, 1761), another important bark beetle on Norway spruce [51–53] was additionally included in the trap trial analysis to study species-specific behavior within the group of bark beetles. A stereomicroscope Zeiss Stemi 508 was used for species identification with keys [54–57].

I. typographus was identified and counted individually at least in the first collection of all three trials. With increasing numbers, individual counting became too time-consuming and catches were quantified using a mean weight value. For its determination, catches were dried and 50 individuals of each trap in each collection were weighed using a precision balance (Kern EW 150-3M) to derive a trap-specific mean beetle weight. Individuals of the genus *Thanasimus* were always identified and counted individually.

2.3. Study Design

2.3.1. General Design

The experiments were based on the trap island methodology [58], which was also applied in other field trials with bark beetles [59,60]. For each of the three trials five trap islands were set up with a minimum distance of 50 m to each other. Within a trap island the different test variants were arranged depending on the number of variants: an isosceles triangle for three, a square for four, and a circle for more than four variants. The circular arrangement enables the integration of more than four variants while ensuring that each trap has only two adjacent traps. Traps on the same trap island were spaced at least 10 m from each other. The distance between traps was set in a way to both guarantee a targeted approach of the insects to the respective variants to avoid mutual interference due to too narrow spacing [61] and to reduce the probability of catching different beetle populations on the same trap island [58]. Traps were activated on the 6 April 2020 by attaching the attractants inside the trap analogous to Miller (2013) [62]. Trap catches were then collected six times in a 14-day interval beginning with the first on the 20 April 2020. Saturated benzoic acid solution with a drop of dishwashing detergent to lower surface tension was used as killing and preservative agent and renewed at every collection date. The attractants were replaced with a new attractant according to the specifications given by the manufacturer (Table 1).

2.3.2. Attractant Composition Trial

Since the first commercially produced attractant Pheroprax[®] in 1979 [34], various alternative attractants have been developed, differing in release rate and composition. Out of these, six were selected and tested regarding their attractivity to *I. typographus* as well as its antagonists *T. femoralis* and *T. formicarius* with Theysohn[®] slot traps (FLÜGEL GmbH, Lower Saxony, Germany). All products have been included in several other studies. Pheroprax[®] was specifically examined [63] and has been the standard attractant in many other experiments [41,61,64,65]. It is also part of the standardized bark beetle monitoring applied in the study area [26]. The attractants IT Ecolure classic[®], IT Ecolure Extra[®], and IT Ecolure Mega[®] are also known from literature [44,66,67] as well as Ipsowit[®] [68–71] and Typosan[®] [70–72]. Table 1 summarizes the duration of attractivity, release rate and composition of the tested products. The release rate has been determined by weekly weighing the products with a precision balance (Kern EW 150-3M), while the composition of the attractants was obtained from literature [71], where only information for IT Ecolure Extra[®] was available. Since it had the same manufacturer as IT Ecolure classic[®] and IT Ecolure Mega[®], information was transferred. However, it seems that only the pheromonal

components were specified [71]. *Cis*-Verbenol was mentioned as the only constituent for the Ecolure products, but since it is crystalline and solid in pure state [73], it needs a solvent, which was not listed.

Table 1. Composition of products tested in the attractant composition trial modified after Sramel et al. (2021) [71].

Dispenser	IT Ecolure Classic®	IT Ecolure Extra®	IT Ecolure Mega®	Ipsowit®	Pheroprax®	Typosan®
Duration of attractivity (weeks)	8–10	6–8	18–20	6–8	6–8	10
Release rate (mg/d)	36.5	70.4	69.5	16.2	33.8	30.0
Composition	(<i>S</i>)- <i>cis</i> -Verbenol	(<i>S</i>)- <i>cis</i> -Verbenol	(<i>S</i>)- <i>cis</i> -Verbenol	<i>S</i> -Ipsdienol, (<i>S</i>)- <i>cis</i> -Verbenol	<i>S</i> -Ipsdienol, (<i>S</i>)- <i>cis</i> -Verbenol, 2-Methyl-3-buten-1-ol	(<i>S</i>)- <i>cis</i> -Verbenol, 2-Methyl-3-buten-1-ol
Dispenser type	blotter (aluminum foil)	blotter (aluminum foil)	blotter (aluminum foil)	blotter (membrane foil)	ampoule	blotter (membrane foil)
Producer	Fytofarm	Fytofarm	Fytofarm	Witasek	BASF	Sintagro AG
Country of production	Slovakia	Slovakia	Slovakia	Austria	Germany	Switzerland

2.3.3. Application Rate Trial

In this experiment, the attractivity of different dosages of Pheroprax® was tested. In addition to single-baited Theysohn® slot traps the dispenser was applied twice and four times within one trap. The attractants were individually distributed in the center of the trap over the entire trap width.

2.3.4. Trap Type Trial

The development of trap types began parallel to the first commercial attractants in the late 1970s [34] resulting in a variety of existing types, two of which were tested in this study. WitaTraps® (WITASEK PflanzenSchutz GmbH, Kärnten, Austria) designed after Lindgren (1983) [74] with 8, 12, and 16 funnels were compared with the Theysohn® slot trap [75], in terms of trapping efficacy. By reducing the number of funnels from the standard 12 to 8 and increasing it to 16, we wanted to examine whether the size of the trap surface affects its trapping efficacy. All tested trap types were baited with one dispenser of Pheroprax®. *P. chalcographus* individuals were only identified and counted for the first two collections.

2.4. Data Analysis

Statistical analysis was performed using the R software, version 4.1.1 with the ggplot2, ggpubr, PMCMRplus, pgirmess, plyr, tidyverse, and readxl packages [76–82]. First absolute numbers of caught beetles were transformed into relative ones. This approach has the advantage of compensating different population densities as well as varying trapping periods during the study [58–60]. The relative values represent the percentage of caught individuals of one species in one variant per trap island and collection date. The numbers of trap islands and collections were used as replications, assuming that new individuals emerge every week [58–60]. The data was then tested for normal distribution using the Shapiro–Wilk test and for homogeneity of variances using the Levene test. If these conditions were not met, a Kruskal–Wallis test was applied as a nonparametric test for independent samples. Subsequently pairwise Iman–Conover tests located the significant differences between the variants. A *p* value of 0.05 was applied as threshold of significance.

3. Results

During the study period, a total of 1,245,835 individuals of *I. typographus* were caught in the traps on the three study sites, with most individuals in the application rate trial

and the fewest in the attractant composition trial. Figure 1 shows the numbers during the course of the study. A first maximum was reached at the collection on the 4 May, a second more distinctive one followed six weeks later.

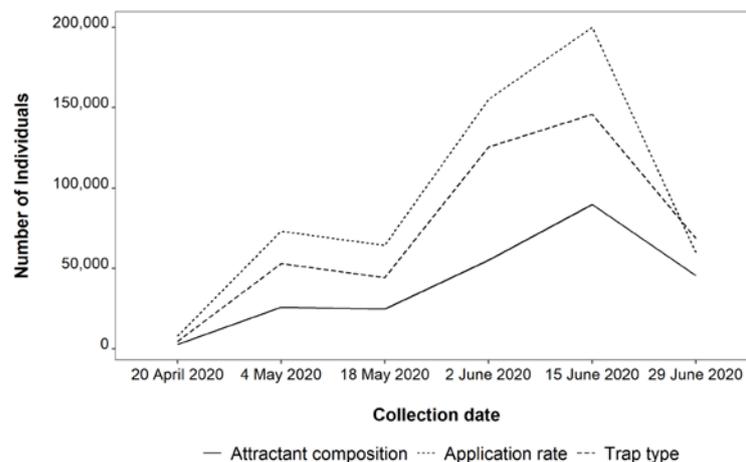


Figure 1. Total number of *I. typographus* caught in the three trials within the study period.

3.1. Attractant Composition Trial

A total of 243,491 individuals of *I. typographus* were caught in this trial. Additionally, 211 specimen of *T. formicarius* and 163 specimen of *T. femoralis* were present. In terms of attractivity to *I. typographus* the products can be distinguished in two groups: a group with higher trapping numbers consisting of Typosan[®] with a median of 23.5%, IT Ecolure Extra[®] with a median of 18.7%, Pheroprax[®] with a median of 16.7%, a group with lower trapping results consisting of IT Ecolure classic[®] with a median of 14.8%, Ipsowit[®] with a median of 13.5%, and IT Ecolure Mega[®] with a median of 13.3% (Figure 2a). All products of the first group caught significantly more individuals than Ipsowit[®] and IT Ecolure Mega[®] (Table A1 in Appendix A), while IT Ecolure classic[®] took a middle position. Within the first group Typosan[®] stood out from the other two products with significant higher catching numbers than Pheroprax[®].

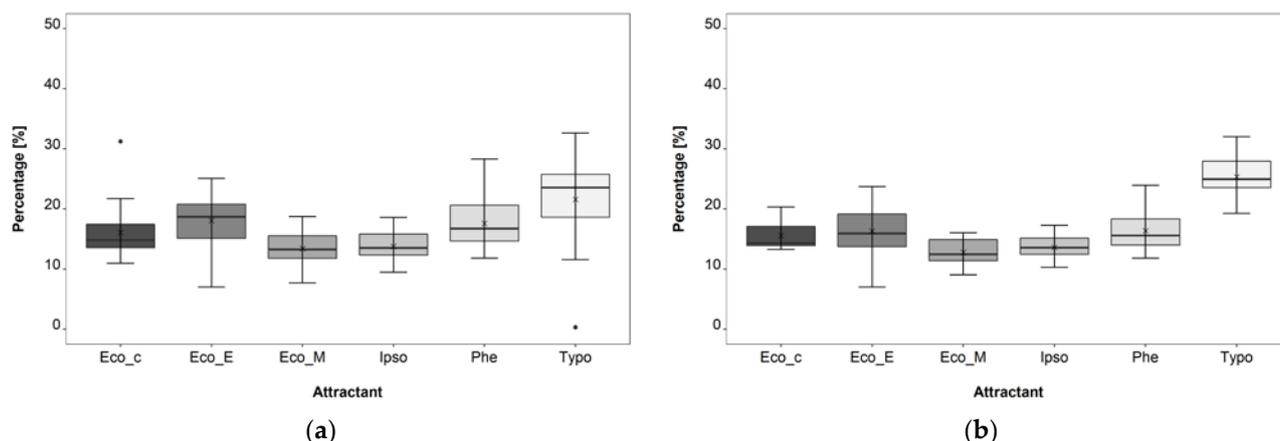


Figure 2. Mean percentage of *I. typographus* catches in Theysohn[®] slot traps baited with different attractant products per trap island and collection date in the study period (a) 6 April 2020 to 29 June 2020, $n = 30$; (b) 6 April 2020 to 18 May 2020, $n = 15$; Eco_c = IT Ecolure classic[®], Eco_E = IT Ecolure Extra[®], Eco_M = IT Ecolure Mega[®], Ipso = Ipsowit[®], Phe = Pheroprax[®], Typo = Typosan[®].

Typosan[®], Pheroprax[®], and IT Ecolure Extra[®] also showed superior results in terms of absolute trapping numbers. Their total catches of 44,357, 45,542, and 47,378 individuals of *I. typographus* represent increases of 29.9%, 33.4%, and 38.8% compared to the least effective

product Ipsowit[®], which caught 34,146 individuals. Although the absolute number of individuals for Typosan[®] was lower than for Pheroprax[®] and IT Ecolure Extra[®], a significantly higher attractivity of Typosan, considering relative numbers, is given. This is a result of the first three trapping periods displayed in Figure 2b, in which Typosan[®] is clearly superior and caught significantly more individuals of *I. typographus* than any other product (Table A2 in Appendix A), which is also reflected in the absolute numbers for this period. In total, catches of *I. typographus* were distinctively lower during the first three collections with 53,119 individuals than in the second half of the trial, when 190,372 individuals were caught. However, during the second half only three significant differences were verifiable (Table A3 in Appendix A).

Regarding the trapping results for *T. femoralis* and *T. formicarius* all three Ecolure products showed a high attractivity for both species (Figure 3). Together they caught 82.9% of all 374 *Thanasimus* spp. individuals in this trial, with IT Ecolure classic[®] and IT Ecolure Extra[®] attracting significantly more individuals than Ipsowit[®] and Typosan[®] (Table A4 in Appendix A).

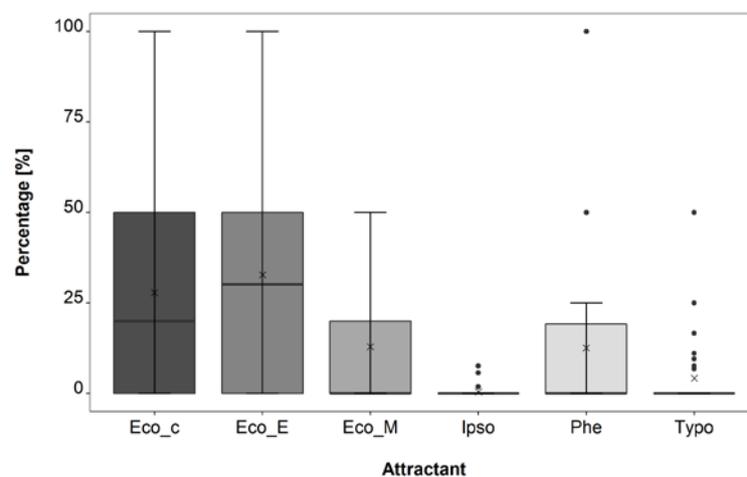


Figure 3. Mean percentage of *Thanasimus* spp. catches in Theysohn[®] slot traps baited with different attractants per trap island and collection date in the study period from 6 April 2020 to 19 June 2020, Eco_c = IT Ecolure classic[®], Eco_E = IT Ecolure Extra[®], Eco_M = IT Ecolure Mega[®], Ipso = Ipsowit[®], Phe = Pheroprax[®], Typo = Typosan[®], $n = 30$.

3.2. Application Rate Trial

In this trial a total of 560,598 individuals of *I. typographus* were caught, whereas *T. femoralis* and *T. formicarius* were present with 474 and 599 individuals, respectively.

Increasing the number of Pheroprax[®] dispensers per trap led to an increase in attractivity for *I. typographus* (Figure 4). Thus, the median of traps with a single Pheroprax[®] was 31.8%, with two Pheroprax[®] 32.5% and the fourfold application 34.7%. The statistical analysis showed significantly higher trapping percentages of the variant with four Pheroprax[®] compared to the variants with a single or two Pheroprax[®] (Table A5 in Appendix A), whereas no significant difference existed between the single and double application variants. However, increasing the application of Pheroprax[®] by four times only resulted in a 15.5% increase in absolute numbers of caught *I. typographus* compared to the regular single application.

Applying four dispensers of Pheroprax[®] in one trap resulted in a significant increase in *Thanasimus* spp. bycatch by 195.5% from 199 to 588 individuals (Table A6 in Appendix A). Double application of Pheroprax[®] increased trap attractivity for the considered antagonists as well (Figure 5), however, this was not statistically significant.

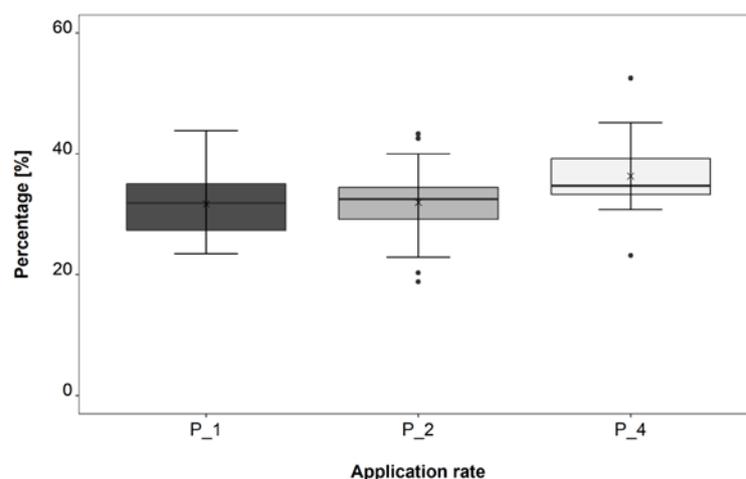


Figure 4. Mean percentage of *I. typographus* catches in Theysohn® slot traps baited with different numbers of Pheroprax® dispensers per trap island and collection date in the study period from 6 April 2020 to 29 June 2020, P_1 = one Pheroprax®, P_2 = two Pheroprax®, P_4 = four Pheroprax®, $n = 30$.

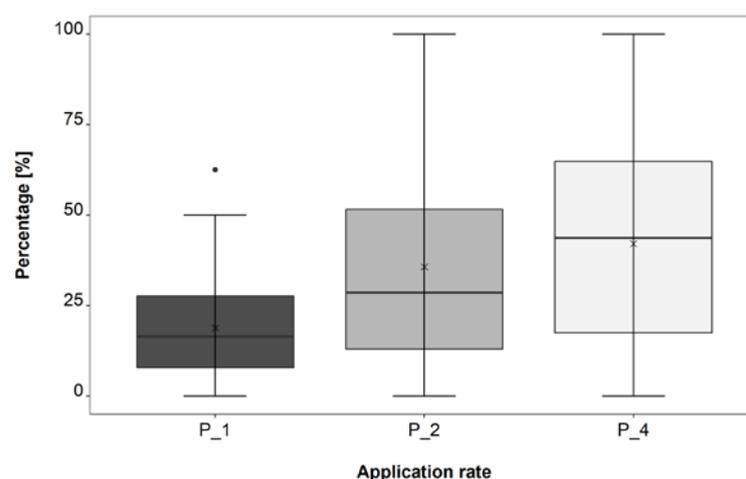


Figure 5. Mean percentage of *Thanasimus* spp. catches in Theysohn® slot traps baited with different numbers of Pheroprax® dispensers per trap island and collection date in the study period from 6 April 2020 to 29 June 2020, P_1 = one Pheroprax®, P_2 = two Pheroprax®, P_4 = four Pheroprax®, $n = 30$.

3.3. Trap Type Trial

A total of 441,746 individuals of *I. typographus*, 492 individuals of *T. femoralis* and 490 individuals of *T. formicarius* were caught in this trial comparing trapping efficacy of different trap types.

The tested trap types showed clear differences in their trapping efficacy for *I. typographus* (Figure 6) and revealed a significant superiority of the 12-funnel WitaTrap® (Table A7 in Appendix A) with a median of 30.4%, whereas the median for the 16-funnel WitaTrap® was 23.9%, for the Theysohn® slot trap 22.1%, and for the 8-funnel WitaTrap® 20.4%. Both increase and reduction in the number of funnels led to a decrease in trapping numbers compared to the standard 12-funnel WitaTrap®. With regard to absolute numbers, the 12-funnel WitaTraps® caught 45.5% more individuals than Theysohn® slot traps.

The results for *P. chalcographus*, with 7225 individuals, the second most frequent species in the first two collections, differed from those of *I. typographus* (Figure 7). With a total of 3012 individuals the Theysohn® slot trap was the most effective trap type for this species (Table A8 in Appendix A).

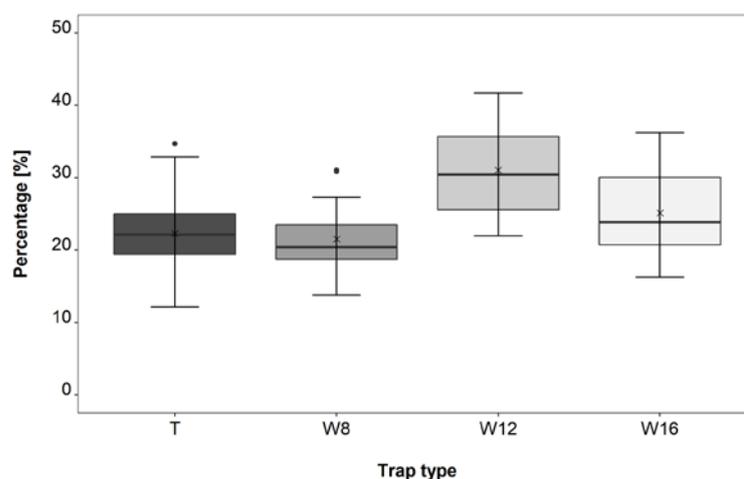


Figure 6. Mean percentage of *I. typographus* catches in different trap types per trap island and collection date in the study period from 6 April 2020 to 29 June 2020, T = Theysohn[®] slot trap, W8 = 8-funnel WitaTrap[®], W12 = 12-funnel WitaTrap[®], W16 = 16-funnel WitaTrap[®], $n = 30$.

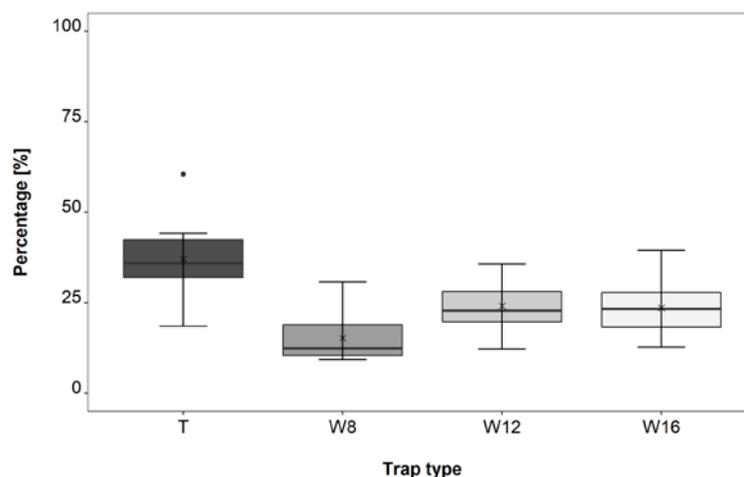


Figure 7. Mean percentage of *P. chalcographus* catches to different trap types per trap island and collection date in the study period from 6 April 2020 to 29 June 2020, T = Theysohn[®] slot trap, W8 = 8-funnel WitaTrap[®], W12 = 12-funnel WitaTrap[®], W16 = 16-funnel WitaTrap[®], $n = 30$.

The majority of *Thanasimus* spp. showed a preference for the WitaTrap[®] types (Figure 8), whereas the Theysohn[®] slot trap caught the fewest individuals of these antagonists with a median of 8.2%. Within the three WitaTrap[®] types, the more funnels were installed, the more individuals of *Thanasimus* spp. were caught. The median of the 8-funnel WitaTrap[®] was 18.9%, of the 12-funnel WitaTrap[®] 24.2%, and of the 16-funnel WitaTrap[®] 37.8%, with the latter catching significantly more individuals than any other tested trap type (Table A9 in Appendix A).

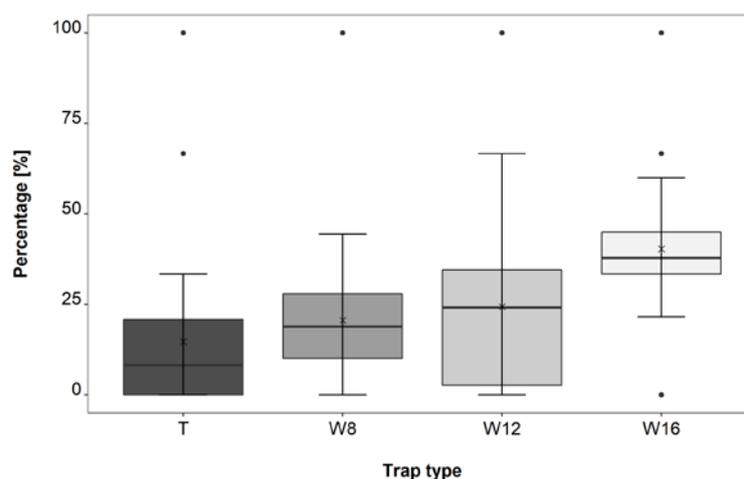


Figure 8. Mean percentage of *Thanasisimus* spp. catches in different trap types per trap island and collection date in the study period from 6 April 2020 to 29 June 2020, T = Theysohn[®] slot trap, W8 = 8-funnel WitaTrap[®], W12 = 12-funnel WitaTrap[®], W16 = 16-funnel WitaTrap[®], $n = 30$.

4. Discussion

4.1. Attractant Composition Trial

After the development of the first commercial pheromone attractant for *I. typographus* in 1979 [34], the manufacturing of other products with varying compositions and release rates followed. According to the results of this study, they also differ significantly in their attractivity to *I. typographus*. The compositions of the attractants are based on the components of the species-specific aggregation pheromone. Based on findings on olfactory communication of *Ips confusus* (LeConte, 1876) [83–85], the attractivity of the three genus-specific components Ipsenol, Ipsdienol, and *cis*-Verbenol was proved under natural conditions [86]. The existence of an aggregation pheromone was also demonstrated for *I. typographus* and further components were discovered [87–89]. After advances in the knowledge on the complex chemical communication of bark beetles [90], 2-Methyl-3-buten-1-ol was identified as the species-specific pheromonal component [33]. The variation in trapping results among the tested products illustrates the potential of attractant composition to optimize the trapping efficacy for *I. typographus*.

All products tested in this study contain merely a part of the entire known bouquet of attractive components of the *I. typographus* aggregation pheromone (Table 1). The reason for this is their main application in the monitoring of the species [13,32,71,91], which only requires the attraction of a sufficient number of beetles. The best trapping results were obtained by Typosan[®], which is the only product containing nothing more than the synergistically acting pheromone components *cis*-Verbenol and 2-Methyl-3-buten-1-ol. While the former acts as long-range orientation component of the aggregation pheromone, the latter has been indicated as landing stimulus [92]. In contrast, Pheroprax[®] and Ipsowit[®] contain Ipsdienol, which is known to trigger a reaction on receptor neurons [93] and has an aggregating effect [94]. However, the addition of Ipsdienol to a combination of *cis*-Verbenol and 2-Methyl-3-buten-1-ol does not increase attractivity [61,95,96], which is supported by the results of this study. *Cis*-Verbenol is the only pheromone component in the Ecolure products. It might be the absence of 2-Methyl-3-buten-1-ol that causes a lower attractivity of these products for *I. typographus*, which was particularly apparent for IT Ecolure classic[®] and IT Ecolure Mega[®]. The high efficacy of IT Ecolure Extra[®], on the other hand, could be explained by its high release rate, which is the highest in the group of most attractive products. *I. typographus* catches tend to increase with increasing release rate of pheromones [34,61,64,67,97]. Apparently, the lower release rate of Typosan[®] and Pheroprax[®] compared to IT Ecolure Extra[®] was compensated by a more suitable attractant composition.

The aforementioned high efficacy of Typosan[®] was manifested particularly in the first half of the trial. Assuming a start of swarming at an air temperature of 16.5 °C [98,99], the first three collections consisted of overwintered adult beetles from the previous year. Since favorable conditions allow a complete development from egg to emerging young beetle within 29 days [100], the last three collections consisted partly of individuals of the first generation. This hypothesis is supported by the PHENIPS model [101] based on the climate data of the station at Dippoldiswalde-Reinberg located close to the study site. The combination of *cis*-Verbenol and 2-Methyl-3-buten-1-ol in Typosan[®] seems to have the most attractive effect on overwintered adult beetles, whereas the emerging young beetles of the first generation appear to be much less selective when approaching the traps. Such intraspecific variability in olfactory perception is already known for *I. typographus*. A distinction between primary and secondary attraction referring to different attack phases of *I. typographus* was established [90]. Moreover, an increased attractivity of monoterpenes for pioneer beetles was assumed [102], as well as specific primary attractants favoring the initial selection of a breeding habitat were described [93]. Even during colonization of a host tree the composition of produced pheromones varies considerably [103]. The overwintered generation, weakened by winter mortality of approximately 50%, continues to be exposed to high mortality during the first swarming, which is more intense than the flight of subsequent generations [7,104]. The increased risk possibly leads to an increased olfactory sensitivity of overwintered adult beetles compared to the vital young beetles of the first generation.

In contrast to the high attractivity of Typosan[®] to *I. typographus* a low attractivity to its antagonists *T. femoralis* and *T. formicarius* was found, thus emphasizing its suitability for potential mass trapping. The reciprocal behavior to *I. typographus* seems unusual at first, since *Thanasimus* spp. responds to similar volatiles as its prey, so similar results were expectable [63,105–107]. However, for *Thanasimus* spp. as generalists [108] genus-specific semiochemicals such as Ipsdienol, Ipsenol, or *cis*-Verbenol [86] are more important than species-specific attractants such as 2-Methyl-3-buten-1-ol [105]. *Thanasimus* spp. do not have olfactory receptor cells for the latter, triggering no reaction as single component for these species [105,106]. Furthermore, *cis*-Verbenol elicits a lower antennal response in *Thanasimus* spp. than Ipsenol and Ipsdienol [105]. Both *cis*-Verbenol and 2-Methyl-3-buten-1-ol are pheromone components in Typosan[®] and explain its low attractivity to *Thanasimus* spp. However, the Ecolure products containing solely *cis*-Verbenol showed the highest attractivity. This does not seem to be a behavior induced by attractant composition but by higher release rates. The results of the application rate trial show that *Thanasimus* spp. reacts strongly to a higher attractant concentration. This behavior can be transferred to the results of the attractant composition trial as cause for the high catches of *Thanasimus* spp. with the Ecolure products characterized by the highest release rates and low catches with Ipsowit[®], which has the lowest release rate of the tested products.

Similar results regarding the trapping of *I. typographus* with Typosan[®] can be found with the evidence of its higher attractivity compared to Pheroprax[®] [72] and its relatively low number of bycatch [71]. However, Pheroprax[®] is considered to be an effective attractant for *I. typographus* when compared with different products in other studies [44,71,109]. IT Ecolure Mega[®] was previously described as comparatively less attractive for *I. typographus* [110] according to the results of our study. On the contrary, numerous studies contradict our results. In Šramel et al. (2021) the lowest trapping numbers of *I. typographus* were achieved with Typosan[®] compared to Pheroprax[®], IT Ecolure Extra[®], Ipstyp[®], and Ipsowit[®] [71]. In Otto (2005), Typosan[®] performed significantly worse than Pheroprax[®] [70]. IT Ecolure classic[®] achieved higher trapping results in Nakládal et al. (2013) than IT Ecolure Mega[®] [110], whereas no significant differences between both products were detected in our study. Zahradník and Zahradníková (2014) described IT Ecolure Mega[®] as the most efficient attractant [109], while in this study it belongs to the group of less effective products. In studies by Pfister (1997, 1998), Ipsowit[®] showed similar trapping results as Pheroprax[®] [68,69], which could not be confirmed in our study. The reasons for

these differences in trapping results of various products are likely to be found in differing methodological approaches. In the above-mentioned studies trapping was conducted over the entire activity phase of *I. typographus*, while this study only considered twelve weeks of its flight starting with the first swarming of overwintered adult beetles in spring. Moreover, the experimental design used in this study [58,59] was not applied in the other studies.

4.2. Application Rate Trial

The increased release rate by the application of more than one Pheroprax[®] dispenser resulted in higher trapping numbers of *I. typographus*, which is consistent with other studies [61,64,67]. However, while a proportional increase in trapping numbers when increasing the release rate was observed in previous studies [61], the fourfold application of Pheroprax[®] in our study only resulted in an increase of 15.5% with regard to absolute numbers. Instead of a proportional relationship between application rate and attractivity, trapping numbers followed the principle of the Weber–Fechner law, which states that “linear increments in sensation are proportional to the logarithm of stimulus magnitude” [111]. A behavior according to the Weber–Fechner law was observed for several insect species, such as *Drosophila melanogaster* (Meigen, 1830), *Hylobius abietis* (Linnaeus, 1758), *Trypodendron lineatum* (Olivier, 1795) [112–114], and also *I. typographus*. For this species the number of caught beetles cannot be increased perpetually by increasing the release rate of an attractant. Instead it asymptotically approaches a saturation level, since very high release rates do not exert relevant effects on behavior [34,92].

Thanasimus spp. exhibited a stronger reaction to a high application of Pheroprax[®] than *I. typographus*. This behavior is consistent with their general ecology, since such predators aggregate at sites of increased prey abundance. They follow an aggregation reaction that describes an increase in local population densities of predators due to increased prey abundance [115,116]. Such a response was observed for *Nemozoma elongatum* (Linnaeus, 1761) as predator of *Taphrorychus bicolor* (Herbst, 1793) [117] and applied in the form of allochthonous kairomones as part of a nature-based bark beetle management [58]. In this context, the increased release of pheromonal components in our trial simulated a higher abundance of *I. typographus*. The antennal receptors of *Thanasimus* spp. have the same olfactory sensitivity as their potential prey [63,105–107]. Thus, they are able to perceive the semiochemicals emitted by Pheroprax[®] and aggregate at sites of higher concentrations.

4.3. Trap Type Trial

The results of this trial showed that trapping numbers of *I. typographus* can be significantly influenced by the choice of the trap type. The previously known superiority of the multiple funnel trap with 12 funnels over the Theysohn[®] slot trap [38,39] was confirmed. The reduction to eight funnels caused a decline in trapping efficacy, since trap surface and trapping numbers correlate positively [34,39]. Correspondingly, increasing the trap surface by adding more funnels should result in higher numbers of caught individuals. However, this effect only occurred when comparing the 8-funnel with the 12-funnel WitaTrap[®], while trapping efficacy declined when using the 16-funnel WitaTrap[®]. This can be explained with the increasing trap height by adding additional funnels. Insects are then able to spread their wings within the trap and leave it before reaching the trapping container like discussed in other studies [74,118]. The trap design also affects the emission of semiochemicals causing higher or lower release rates into the environment [32,62,118,119]. Multiple-funnel traps probably allow a higher emission of the used attractants due to the larger gaps between funnels compared to the Theysohn[®] slot trap. Even the position of the dispenser within the trap can affect trapping efficacy [62,119], which is why attractants in this trial were always placed in the same position.

In contrast to *I. typographus* we found a significant preference of the Theysohn[®] slot trap for *P. chalcographus*. A species-specific trapping efficacy of different trap types was described in many other studies [39,118,120–123]. With regard to *I. typographus* and *P. chalcographus* a possible explanation is the visual similarity of trap design and preferred

beetle habitat, since both species use visual cues for orientation [124,125]. *I. typographus* primarily colonizes the trunk below the crown of trees, while *P. chalcographus* usually breeds in the canopy [126]. On one hand, multiple-funnel traps better resemble a tree trunk than the Theysohn[®] slot trap due to their vertical, elongated appearance and are preferred by *I. typographus*. On the other hand, the Theysohn[®] slot trap has similarities to the silhouette of a tree canopy due to its rectangular, planar shape, and is therefore more attractive to *P. chalcographus*.

Thanasimus spp. showed similar preferences as *I. typographus* favoring WitaTraps[®]. The higher trapping numbers of antagonists in multiple-funnel traps are consistent with the results of other studies [39,127]. The critical factor seems to be the visual orientation used by *Thanasimus* spp. to locate its prey [125]. Since *I. typographus* is the more important prey, the trap that more closely resembles its habitat is also more attractive to *Thanasimus* spp. In addition, a potentially better attractant emission from WitaTraps[®] might contribute to the higher numbers of *T. femoralis* and *T. formicarius* in these traps. In contrast to *I. typographus* *Thanasimus* spp. is apparently not able to spread its wings and escape before dropping into the trapping container, resulting in higher numbers the more funnels were installed. The amount of caught antagonists emphasizes the necessity of having more selective trap types, which has also been mentioned in former studies [44], and has already been developed for *Ips sexdentatus* [128]. *Thanasimus* spp. is essential for the natural regulation of bark beetle populations [49,50,129] requiring highly selective mass trapping devices to minimize the impacts on predators [130].

5. Conclusions

The data of our study prove that an optimization of the analyzed three-directional approach to mass trapping results in a significant increase in catches of *I. typographus*. The attractant composition seems to be the most powerful tool to reach further improvements, especially since neither of the tested attractants contains all known pheromone components. Increasing the application rate had an unwanted side effect on antagonists similar to some of the tested trap types. Improving the selectivity of traps is required if mass trapping programs are to be implemented. Furthermore, trap types showed a species-specific efficacy exacerbating the chances of a universally applicable mass trapping technology for bark beetles.

The high efficacy of Typosan[®] for hibernated *I. typographus* shows a promising time dependent reaction to volatiles. Further research such as gas chromatographic analysis of attractants and electroantennogram responses are crucial to understand the differences in olfactory receptors of hibernating adult beetles and their offspring. It is desirable to develop a mass trapping attractant specifically designed for the first swarming period of *I. typographus* when the population size is at its lowest level due to high winter mortality. During early spring pheromone traps are highly attractive to individuals in search for breeding sites, meaning it is the best time for mass trapping. A temporary increase in the application rate for this first swarming period could contribute to a more pronounced reduction of population sizes, while trap types with a high selectivity would spare antagonists. This would increase the chances to sustainably reduce the population of *I. typographus* to a level not harmful for standing trees or at the least mitigate the peak of a mass outbreak. Hence, mass trapping of *I. typographus* without insecticides might be applicable in the future. Considering the forest conversion in Central Europe from monocultures towards mixed stands, a reduction in local outbreaks and protection of smaller spruce stands has higher chances to succeed than under current circumstances. In future stands, it might be economically sensible to protect rare spruce wood by traps. It remains disputable if mass trapping can cause an abrupt end to ongoing eruptive population outbreaks in pure spruce stands on a large scale, even though successful small-scale operations are known. However, the significant increase in total trap catches achieved by the three-directional approach of this study does not seem sufficient to reduce the number of beetles in an outbreak situation

effectively. Thus, the replacement of salvage logging and sanitation felling as most effective treatments in bark beetle management by mass trapping is not yet an option.

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Appendix A

Table A1. Significance table of the results of pairwise comparisons with the Iman–Conover test for the attractant composition trial from 6 April 2020 to 29 June 2020 for *I. typographus*, $n = 30$, Eco_c = IT Ecolure classic[®], Eco_E = IT Ecolure Extra[®], Eco_M = IT Ecolure Mega[®], Ipso = Ipsowit[®], Phe = Pheroprax[®], Typo = Typosan[®], $0.05 \geq * > 0.01 \geq ** > 0.001 \geq ***$.

Pairwise Comparison	<i>p</i> Value	Significance Code
Eco_E–Eco_M	2.5×10^{-5}	***
Eco_E–Ipso	0.0001	***
Phe–Eco_M	0.00045	***
Phe–Ipso	0.00156	**
Typo–Eco_c	0.00013	***
Typo–Eco_M	2.3×10^{-10}	***
Typo–Ipso	1.4×10^{-9}	***
Typo–Phe	0.04111	*

Table A2. Significance table of the results of pairwise comparisons with the Iman–Conover test for the attractant composition trial from 6 April 2020 to 18 May 2020 for *I. typographus*, $n = 15$, Eco_c = IT Ecolure classic[®], Eco_E = IT Ecolure Extra[®], Eco_M = IT Ecolure Mega[®], Ipso = Ipsowit[®], Phe = Pheroprax[®], Typo = Typosan[®], $0.05 \geq * > 0.01 \geq ** > 0.001 \geq ***$.

Pairwise Comparison	<i>p</i> Value	Significance Code
Eco_c–Eco_M	0.0413	*
Eco_E–Eco_M	0.0098	**
Phe–Eco_M	0.0135	*
Typo–Eco_c	9.4×10^{-6}	***
Typo–Eco_E	5.9×10^{-5}	***
Typo–Eco_M	1.0×10^{-11}	***
Typo–Ipso	5.3×10^{-10}	***
Typo–Phe	4.0×10^{-5}	***

Table A3. Significance table of the results of pairwise comparisons with the Iman–Conover test for the attractant composition trial from 19 May 2020 to 29 June 2020 for *I. typographus*, $n = 15$, Eco_c = IT Ecolure classic[®], Eco_E = IT Ecolure Extra[®], Eco_M = IT Ecolure Mega[®], Ipso = Ipsowit[®], Phe = Pheroprax[®], Typo = Typosan[®], $0.05 \geq * > 0.01 \geq ** > 0.001 \geq ***$.

Pairwise Comparison	<i>p</i> Value	Significance Code
Eco_E–Eco_M	0.0052	**
Eco_E–Ipso	0.0022	**
Phe–Ipso	0.0277	*

Table A4. Significance table of the results of pairwise comparisons with the Iman–Conover test for the attractant composition trial from 6 April 2020 to 29 June 2020 for *Thanasimus* spp., $n = 30$, Eco_c = IT Ecolure classic[®], Eco_E = IT Ecolure Extra[®], Eco_M = IT Ecolure Mega[®], Ipso = Ipsowit[®], Phe = Pheroprax[®], Typo = Typosan[®], $0.05 \geq * > 0.01 \geq ** > 0.001 \geq ***$.

Pairwise Comparison	<i>p</i> Value	Significance Code
Eco_c–Ipso	1.6×10^{-5}	***
Eco_c–Typo	0.0013	**
Eco_E–Ipso	1.9×10^{-7}	***
Eco_E–Phe	0.0441	*
Eco_E–Typo	2.8×10^{-5}	***
Eco_M–Ipso	0.03	*

Table A5. Significance table of the results of pairwise comparisons with the Iman–Conover test for the application rate trial from 6 April 2020 to 29 June 2020 for *I. typographus*, $n = 30$, P_1 = one Pheroprax[®] applied, P_2 = two Pheroprax[®] applied, P_4 = four Pheroprax[®] applied, $0.05 \geq * > 0.01 \geq ** > 0.001 \geq ***$.

Pairwise Comparison	<i>p</i> Value	Significance Code
P_4–P_1	0.0059	**
P_4–P_2	0.0108	*

Table A6. Significance table of the results of pairwise comparisons with the Iman–Conover test for the application rate trial from 6 April 2020 to 29 June 2020 for *Thanasimus* spp., $n = 30$, P_1 = one Pheroprax[®] applied, P_2 = two Pheroprax[®] applied, P_4 = four Pheroprax[®] applied, $0.05 \geq * > 0.01 \geq ** > 0.001 \geq ***$.

Pairwise Comparison	<i>p</i> Value	Significance Code
P_4–P_1	0.0052	**

Table A7. Significance table of the results of pairwise comparisons with the Iman–Conover test for the trap type trial from 6 April 2020 to 29 June 2020 for *I. typographus*, $n = 30$, W8 = 8-funnel WitaTrap[®], W12 = 12-funnel WitaTrap[®], W16 = 16-funnel WitaTrap[®], T = Theysohn[®] slot trap, $0.05 \geq * > 0.01 \geq ** > 0.001 \geq ***$.

Pairwise Comparison	<i>p</i> Value	Significance Code
W12–T	6.1×10^{-8}	***
W12–W8	6.7×10^{-10}	***
W12–W16	0.00046	***
W16–W8	0.02047	*

Table A8. Significance table of the results of pairwise comparisons with the Iman–Conover test for the trap type trial from 6 April 2020 to 29 June 2020 for *P. chalcographus*, $n = 10$, W8 = 8-funnel WitaTrap[®], W12 = 12-funnel WitaTrap[®], W16 = 16-funnel WitaTrap[®], T = Theysohn[®] slot trap, $0.05 \geq * > 0.01 \geq ** > 0.001 \geq ***$.

Pairwise Comparison	<i>p</i> Value	Significance Code
T–W8	1.0×10^{-5}	***
T–W12	0.044	*
T–W16	0.028	*
W12–W8	0.041	*

Table A9. Significance table of the results of pairwise comparisons with the Iman–Conover test for the trap type trial from 6 April 2020 to 29 June 2020 for *Thanasimus* spp., $n = 30$, W8 = 8-funnel WitaTrap[®], W12 = 12-funnel WitaTrap[®], W16 = 16-funnel WitaTrap[®], T = Theysohn[®] slot trap, $0.05 \geq * > 0.01 \geq ** > 0.001 \geq ***$.

Pairwise Comparison	<i>p</i> Value	Significance Code
W16–T	1.6×10^{-6}	***
W16–W8	0.0009	***
W16–W12	0.0186	*

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