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Thermal sum requirements for development and flight initiation of new-generation spruce bark beetles based on seasonal change in cuticular colour of trapped beetles

Danja Fritscher[1] | Martin Schroeder[2]

[1]Weinbergstraße, Münchsteinach, Germany

[2]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

Correspondence
Martin Schroeder, Department of Ecology, Swedish University of Agricultural Sciences, P.O. Box 7044, S 750 07 Uppsala, Sweden.
Email: martin.schroeder@slu.se

Abstract

1. The spruce bark beetle *Ips typographus* is the most important pest on Norway spruce in Europe. To improve predictions of bark beetle phenology in a warmer climate, correct thermal sums representing the development time of the new generation are needed.

2. A standardized method for classifying adults into five different colours was used for describing the seasonal change in colour of beetles in breeding substrate and in weekly trap catches from regions located in southern, central and northern Sweden in 2015–2020.

3. Repeated sampling of *I. typographus* from breeding substrate demonstrated that the adults get gradually darker, from light brown when newly moulted to dark brown or black in the following summer.

4. In spring, four to five colours co-occurred among trapped beetles. Over time, the proportions of darker individuals increased until the two lightest colours were absent except for 2 cases out of 21 trapping locations/years. Thereafter, the individuals of the two lightest colours started to occur again, indicating that they belonged to the new generation.

5. The average thermal sum from start of flight of parental generation in spring until onset of new-generation flight in summer was higher for southern Sweden [lower developmental threshold (LDT) $5°C = 744$ degree-days (dd); LDT $8.3°C = 467$ dd] than for northern Sweden (LDT $5°C = 668$ dd; LDT $8.3°C = 418$ dd).

6. New-generation flight occurred in every year and region, but generally constituted only a small proportion of total seasonal flight activity.

KEYWORDS
brood development, cuticle colour change, degree days, flight activity, *Ips typographus*, pheromone traps, population dynamics, spruce bark beetle, temperature models, voltinism

INTRODUCTION

The spruce bark beetle *Ips typographus* (L.) is the most important insect pest on Norway spruce *Picea abies* (L.) Karst in Europe, killing large volumes of mature trees. Tree mortality caused by *I. typographus* exceeded 150 million m³ from 1950 to 2000 in Europe, and damages have increased substantially in recent years (Grégoire et al., 2015; Hlásny et al., 2021; Jönsson et al., 2012; Schelhaas et al., 2003;

Seidl et al., 2011). Due to climate change, damage levels are predicted to increase even more in the future (Seidl et al., 2014). One factor that may contribute to increased damages is an increase in number of generations per year (voltinism) in a warmer climate. Models, based on different climate scenarios and on thermal sums required for *I. typographus* development, have been used for predicting the increase in voltinism in different parts of Europe in the future (Bentz et al., 2019; Jönsson et al., 2012). It is important that the thermal sums used in such models are based on data for the specific areas included in the models.

Lower developmental threshold (LDT) temperatures limiting *I. typographus* development have been determined by rearing beetles at different constant temperatures in the laboratory (Annila, 1969; Wermelinger & Seifert, 1998). Most commonly, LDTs of 5 and 8.3°C are assumed for modelling *I. typographus* generation development. Similarly, accumulated effective thermal sums (accumulated daily mean temperatures above LDT) required for complete development from egg to mature adult were determined either in laboratory (Annila, 1969; Wermelinger & Seifert, 1998) or in field studies (Baier et al., 2007; Berec et al., 2013; Harding & Ravn, 1985; Ogris et al., 2019; Öhrn et al., 2014). In the field studies, thermal sums were calculated from colonization of trap trees to start of emergence of new-generation beetles. Models predicting development rates and generation development, and thus when emergence of the new generation can be expected, are based on known thermal requirements and information about air temperature, topography and solar radiation for a given locality (Baier et al., 2007). A major drawback of studies using trap trees is that, unless beetles are dissected and examined for the presence of mature eggs, it is not known whether emerging new-generation beetles are in a reproductive state or in reproductive diapause (i.e. just emerging from breeding material for hibernation in the litter). No dissections were conducted in the field studies mentioned above. Another issue is the difficulty to apply the results from local studies including a few trap trees to landscape level. That is because it is generally not known to what extent breeding substrates are utilized (or available) at different altitudes and sun exposures which will influence developmental rates. In addition, there may also be local *I. typographus* adaptations to differences in regional climatic conditions.

An alternative approach to the trap tree studies mentioned above is to investigate weekly trap catches of *I. typographus* from monitoring programs for the first date of occurrence of new-generation beetles in the summer. Based on the information on start of flight in spring, and temperature data from climate stations, thermal sums required for completion of development and start of flight of new-generation beetles can then be determined. This approach has several advantages: (1) The fact that beetles were attracted by a pheromone bait is a strong indication that they were not in reproductive diapause. (2) The trapped beetles originate from many different localities and types of breeding substrates in the surrounding landscape and thus give a good estimate for when, and at which temperature sum, the flight of the landscape-wide population of new-generation beetles is initiated. (3) Weekly monitoring of *I. typographus* is conducted in many regions and thus offers easy access to trapping materials.

In northern Europe, bivoltine populations of *I. typographus* are not predominant. Thus, from a population dynamic perspective, it is important to determine to what extent new-generation beetles reproduce before the winter. Climate chamber experiments, including Swedish *I. typographus* populations, demonstrated that at shorter day lengths, an increasing proportion of the new-generation beetles entered reproductive diapause and that some of the beetles from northern regions showed an obligatory diapause (Schebeck et al., 2022; M. Schroeder & Dalin, 2017). However, it is very likely that laboratory results regarding induction of diapause do not correspond with field observations under fluctuating temperatures and natural light conditions. Thus, it is difficult to translate laboratory results to certain proportions of reproductive new-generation beetles under field conditions. Analyses of trapping materials may offer a possibility to determine the proportion of total *I. typographus* seasonal flight activity that is constituted by new-generation flight. This proportion can then be used as a proxy for the influence of new-generation beetles on the population dynamics.

Two morphological traits have been used to distinguish between parent and new-generation beetles of *I. typographus*: density of bristles on the pronotum and elytra (Harding & Ravn, 1985) and body colour (Öhrn et al., 2014). Harding and Ravn (1985) separated beetles emerging from trap logs into parent beetles and new-generation beetles by the lower density of bristles on the pronotum and elytra of the former. However, the practicality of this method for classifying beetles from trap catches is questionable. Friction between the beetles in the trap, and the possibility that some new-generation adults may already have bored into trees before being trapped, can damage the bristles. Thus, differentiation by colour appears to be a more useful method for classifying the age of beetles collected in pheromone traps.

When beetles develop from pupae to adults, the cuticle is first soft and pale. As the proteins in the cuticle become sclerotized and melanized, the exoskeleton hardens and darkens (Moret & Moreau, 2012; Noh et al., 2016; Thompson et al., 2002). Merker and Wild (1954) reported that yellow/light brown to black beetles were present both in early spring (before flight period) and later in summer in colonized trees. Knowledge of the long-term change in cuticle colour of *I. typographus* is limited. Thus, a detailed understanding of colour change over the season is required in order to use colours as indicator of new-generation flight activity in the summer. So far, no study on *I. typographus* or any other bark beetle species has recorded the transitions in colour from the newly-moulted adults until colonization of new trees for a particular cohort of beetles. In addition, no earlier study has used a standardized method to classify *I. typographus* based on colour.

The aims of this study were: (1) to develop a standardized method to classify *I. typographus* individuals based on their cuticular colour; (2) to describe the seasonal colour change of *I. typographus* in breeding material and from trap catches in Sweden, and based on this information to determine the date of flight initiation of the new generation; (3) to determine the thermal sum required from start of flight of parent beetles in spring until onset of new-generation flight in summer along a climatic gradient; and (4) to estimate the proportion of total seasonal trap catch constituted by new-generation beetles as a proxy for their potential influence on population dynamics.

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MATERIALS AND METHODS

In the study, we (1) develop a standardized method for colour classification of *I. typographus*; (2) describe the seasonal colour changes of *I. typographus* in breeding substrate; (3) determine the start of flight of new-generation *I. typographus* based on colour classification of trap catches; (4) determine the thermal sum required from start of flight in spring until onset of new-generation flight in summer; (5) estimate the proportion of total seasonal trap catch constituted by new-generation beetles; (6) estimate the proportion of trapped *I. typographus* attracted by the pheromone bait per se and thus assumed to be in reproductive state.

Colour classification

The cuticular colour of *I. typographus* was classified by the same person with a stereo microscope at ×10 magnification. Five different colours were selected from the Natural Colour System®© (NCS). The NCS provides a straight-forward method to evaluate colours by plain eyesight. The system is based on the six psychological primaries: white, black and the elementary colours green (G), yellow (Y), red (R) and blue (B). Nonelementary colours are described as a relationship between two of the elementary colours. Thus, a red-brown hue will be more reddish than yellowish, for example, 70% red, which would result in the colour Y70R. In addition, lightness is expressed in percentages as the degree of blackness. Chromaticness is shown in percentages as a degree of saturation, where 0 is monochrome. For instance, the individual nuance of a red-brown bark beetle with the hue Y70R can have 60% blackness and 20% chromaticness. This results in the NCS colour notation S 6020-Y70R, where S denotes NCS 1950 standards.

Both blackness and reddishness were used in the classification of beetle development. The following five colours were chosen and referred to as: light brown (S 6020-Y30R), intermediate brown (S 8010-Y30R), red brown (S 8010-Y70R), dark brown (S 8502-R) and black (S 9000-N). When classified, the beetles were placed individually on a neutral-coloured background (grey: S 6500-N) next to a colour palette with the five colours and the closest match was determined for both ventral side of thorax and elytra (Figure 1).

Seasonal colour change of *I. typographus* in breeding material

The development, and colour change of new-generation beetles, was recorded in two wind-felled spruces in central Sweden in 2019. One tree was located in Fiby Urskog (59°52′52.4″N, 17°21′03.2″E) and the other in Kronåsen (59°49′33.7″N, 17°39′31.9″E) in Uppsala (distance between localities 18 km). Both trees were situated in semi-shaded conditions and colonized during the first flight of *I. typographus* in spring. By debarking small areas of bark at several occasions, the development of the offspring was monitored. In addition, the bark of the trees was checked for the presence of *I. typographus* emergence holes. Samples of live new-generation beetles were collected from the wind-felled trees from 25 June 2019 to 21 April 2020, 15 times in Kronåsen and 11 times in Fiby. At each collection, three to 13 live beetles were collected except for the last collection in spring 2020 when 100 beetles were collected in Kronåsen and 101 in Fiby. In addition, catches from a pheromone-baited trap (500 m from wind-felled tree in Kronåsen) were colour classified in 2019 in order to compare with the beetles from the wind-felled trees.

From 20 May 2020 to 6 August 2020, beetles were collected from attacked wind-felled and standing trees to record the colour change of parent beetles over time. In Kronåsen, beetles were collected four times from a wind-felled tree. In Fiby, beetles were collected four times from two wind-felled trees from 1 June 2020 to 24 June 2020. The first attacks on these trees were recorded on
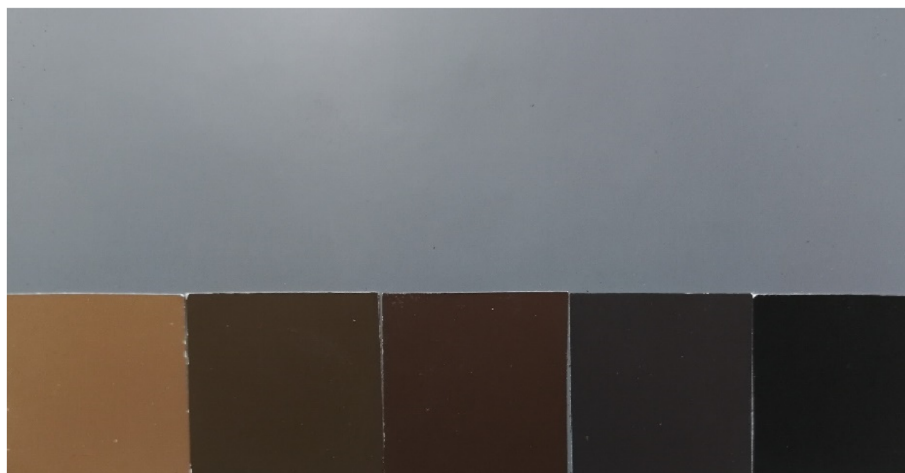

FIGURE 1   Colour palette used in the classification of *Ips typographus*. From left to right: light brown (S 6020-Y30R), intermediate brown (S 8010-Y30R), red brown (S 8010-Y70R), dark brown (S 8502-R) and black (S 9000-N). The beetles were placed on the palette and the closest match was determined for both ventral side of thorax and elytra under 10 times magnification

20 May 2020. In addition, beetles were collected from one standing tree under attack on 26 May 2020 and from five standing trees, attacked later in the season, from 29 June 2020 to 8 August 2020. The beetles were stored in the freezer before the colour of each individual was classified with the method described above.

Start of flight of new-generation *I. typographus* based on colour classification of trap catches

Ips typographus trapped in a long-term monitoring survey with pheromone-baited traps (Ipslure® Kjemikonsult, Norway) conducted by the Swedish University of Agricultural Sciences (SLU), were colour classified with the method described above. The analysis included beetles from three regions (Figure 2) close to SLUs research stations Tönnersjöheden in southern Sweden (56°42′51.7″N 13°7′14.5″E), Siljansfors in central Sweden (60°53′0.2″N 14°22′37.6″E) and Vindeln in northern Sweden (64°14′29.9″N 19°45′28.5″E). In each region, a group of three pheromone-baited funnel traps (Nordforest Novefella) is set up on five fresh spruce clear-cuts every year. The pheromone bait is changed two times during the summer and the traps are emptied weekly during the flight period. The trap catches are sent to SLU and kept in the freezer. Low catches up to about 100 beetles are counted, higher catch numbers are estimated by volume. In the colour classification analyses, we included 5 years of trappings from Tönnersjöheden (2015, 2017, 2018, 2019, 2020), 4 years from Siljansfors (2015, 2018, 2019, 2020) and 5 years from Vindeln (2015, 2016, 2018, 2019, 2020) which were the only years for which samples were available.

From each region and year, we determined the colour of 100 beetles per weekly catch if the trapped numbers allowed. If available, we analysed 50 beetles from 2 different trapping sites (out of the 5 available sites in each region). We chose the localities with the highest catch numbers per week with particular focus on the early and late season when catches were generally lower. In case the samples of the two chosen localities in each region contained less than 100 beetles, we included beetles from the three remaining trapping sites.

In addition, in 2020 we included beetles trapped in seven other localities in Sweden: Örsundsbro, Svenljunga, Misterhult, Nordmaling, Ljungsbro, Karlskrona and Åmål (Figure 2). In these localities, only one trapping location with a group of three traps was used for monitoring. Otherwise, the trapping and the analysis was conducted in the same way as for the three regions described above. Thus, we classified 100 beetles per week for each locality if the catch number allowed.

Based on the results of the colour classification of trap catches, the start of new-generation flight was determined to occur when light brown and intermediate brown beetles occurred after a period of at least 1 week with catches of only darker beetles (see Results). We used two levels for how large proportion of the catch that light brown and intermediate brown beetles together should constitute: at least 5% and at least 10%. Choosing lower proportions, such as 1% or 2%, appeared imprecise considering that the sample size was only 100 beetles per week.
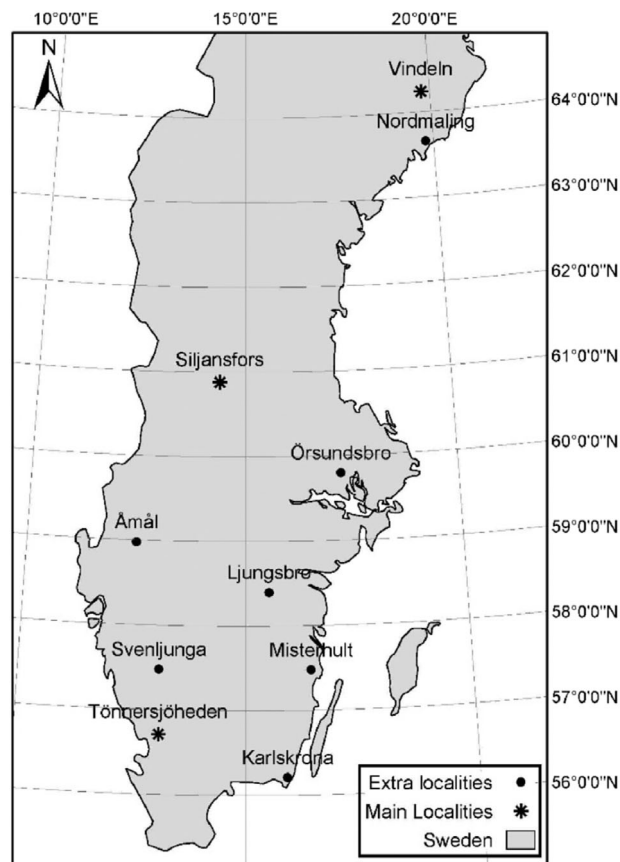

FIGURE 2 Trapping locations in Sweden for *Ips typographus* individuals that were classified by colour. Main localities represent the three regions in which several years of trapping were conducted, while beetles were trapped in the extra localities in 2020 only. The attacked wind-felled and standing trees from which beetles were colour classified were situated about 30 km from the trapping location Örsundsbro

Thermal sum required from start of flight in spring until onset of new-generation flight in summer

Thermal sums were calculated from start of *I. typographus* flight in the spring until the samples constituted at least 5% and 10% new-generation beetles for 5 years of trappings from Tönnersjöheden (2015, 2017, 2018, 2019, 2020), and 4 years for Vindeln (2015, 2016, 2018, 2019) and Siljansfors (2015, 2018, 2019, 2020). Vindeln 2020 was not included in the thermal sum analysis due to a 3-week period with zero catches prior to the start of flight of new generation. Based on previous studies, we decided to use the two most commonly applied LDTs of 5°C (Annila, 1969; Harding & Ravn, 1985; Öhrn et al., 2014) and 8.3°C (Baier et al., 2007; Wermelinger & Seifert, 1998). The thermal sum was calculated in degree-days (dd) as the accumulated sum of the daily mean air temperatures subtracted by the LDT. Starting date of flight in spring was defined as the first day of at least 16.5°C maximum air temperature in the first week with an accumulated catch sum of at least 100 beetles (including catches from prior weeks). The traps were set up prior to the expected start

of the spring flight based on the weather forecast and snow conditions in the north (Figures S1–S3). Only in Vindeln 2018, the maximum air temperature exceeded 16.5°C during the 4 days prior to the baiting date (maximum air temperature varied between 19.4 and 23.1°C). Hence, we decided to include the four warm days prior to baiting in the calculation of the thermal sum for this year in Vindeln.

For Tönnersjöheden, Siljansfors and Vindeln, we used temperature data from climate stations at the research stations, which also were the closest climate stations to the trapping localities. Mean daily temperatures were calculated from 1440 readings per day (1 per minute). The distance of the trap sites to the climate stations varied from 3 to 43 km (Table 1). We could not acquire our own temperature measurements

TABLE 1 Coordinates, distances to climate stations, total number of *Ips typographus* caught and the estimated percentage of this catch constituted by new-generation beetles in the three main regions Tönnersjöheden, Siljansfors and Vindeln, and in the seven additional localities included in 2020

Region	Year	Trapping site	Latitude	Longitude	Distance climate station (km)	Total catch	New generation (%)
Tönnersjöheden	2015	Site 1	56.77532	13.21142	9	183,249	4.62
		Site 2	56.63039	13.11348	9		
	2017	Site 1	56.68063	13.06474	5	216,867	6.95
		Site 2	56.69230	13.06020	5		
	2018	Site 1	56.74907	13.16673	5	344,279	17.67
		Site 2	56.74907	13.16673	8		
	2019	Site 1	56.71255	13.01470	7	249,892	14.74
		Site 2	56.80924	12.82057	21		
	2020	Site 1	56.69841	13.08369	3	131,898	3.77
		Site 2	56.71254	13.35151	14		
Siljansfors	2015	Site 1	60.97230	15.07309	17	125,759	0.05
		Site 2	60.98087	14.61528	39		
	2018	Site 1	61.18695	14.77856	40	168,821	13.36
		Site 2	61.06552	14.64544	25		
	2019	Site 1	60.94214	15.01819	35	110,154	2.26
		Site 2	60.89885	15.16991	43		
	2020	Site 1	60.95922	14.46879	10	94,932	0.37
		Site 2	60.88316	14.55829	9		
Vindeln	2015	Site 1	64.12464	19.44078	21	198,593	0.06
		Site 2	64.11839	19.20798	31		
	2016	Site 1	64.12038	19.47287	20	255,756	0.31
		Site 2	64.19540	19.45842	16		
	2018	Site 1	64.28066	19.62121	8	186,454	7.1
		Site 2	64.12619	19.42889	21		
	2019	Site 1	64.15519	19.67556	11	138,121	0.3
		Site 2	64.19450	19.56795	11		
	2020	Site 1	64.17816	19.48328	15	195,459	0.2
		Site 2	64.16847	19.62714	10		
Karlskrona	2020		56.21101	15.89421	20	21,280	0.48
Misterhult	2020		57.48036	16.43941	34	19,444	3.56
Svenljunga	2020		57.48368	13.09772	18	4707	2.65
Ljungsbro	2020		58.49887	15.51102	25	35,011	8.83
Åmål	2020		58.97552	12.50173	37	22,097	3.12
Örsundsbro	2020		59.79783	17.23036	17	39,196	4.63
Nordmaling	2020		63.65389	19.79078	29	18,242	0.45

Note: For the main regions beetles were colour classified from two different trapping sites each year. Total catch was summed up for 15 pheromone-baited traps each year for the three main regions and from tree traps for the seven additional localities. The percentage of new-generation beetles was defined as the part of total catch constituted by light brown, intermediate brown and red brown beetles trapped from the week when new-generation beetles constituted at least 5% of the catch.

because to a large extent our study included beetles trapped during previous years. In addition, trapped beetles may have developed far from the trapping locations. Both climate stations and trapping locations were situated on open areas (fresh clear-cuts for traps). The thermal sums for the extra localities in 2020 were calculated from mean daily temperature data based on 24 readings per day (1 every hour) measured at the Swedish Meteorological and Hydrological Institute (SMHI) climate stations. The distance between climate stations and these extra trapping sites varied from 17 to 37 km (Table 1).

Proportion of total seasonal trap catch constituted by new-generation beetles

We estimated how much the new generation of beetles made up of the total seasonal *I. typographus* catch by: (1) summing up all catches of light brown, intermediate brown and red brown beetles accumulated from the first week when at least 5% of the beetles were classified as new-generation beetles until the end of the season and (2) dividing this catch with the total seasonal catch. We decided to also include red brown beetles (i.e. not only light brown and intermediate brown) because new-generation beetles also changed colour over time resulting in increased proportions of red brown individuals (see Results section).

Proportion of trapped beetles attracted by pheromone bait per se

Our assumption that the trapped new-generation *I. typographus* were in reproductive state (i.e. not in reproductive diapause) is based on the further condition that the beetles were in fact attracted by the pheromone bait and not trapped by chance or only visually responding to the silhouette of the traps. To test for pheromone attraction, data from an unpublished trapping study were used. The study included 10 pairs of unbaited and pheromone-baited (Ipslure®, Kjemikonsult) multi-funnel traps (Econex) and was conducted on fresh clear-cuts in northern Sweden from 15 May 2018 to 18 September 2018. The distance between traps was 50 m and the traps were emptied four times during the season. By comparing catches from unbaited and pheromone-baited traps, we estimated the proportion of trapped *I. typographus* attracted by the pheromone.

Statistics

We only included the two climatic extremes, the southernmost (Tönnersjöheden) and the northernmost (Vindeln) regions, in the statistical test for differences in thermal sum and proportions of new-generation beetles since replicate numbers were too low for comparing three test sites including the intermediate region Siljansfors. The Welch two-sample *t* test or Kruskal–Wallis test was used depending on the distribution of the data. The data were tested for normal distribution by means of the Shapiro–Wilks test of normality. If normal

distribution did not apply to the data set, even after data transformation, the comparison was performed with the Kruskal–Wallis test. To compare the mean proportions of new-generation beetles between the southernmost and northernmost regions *t*-test with arcsin transformed values was used. The analyses were performed in R (RStudio Team, 2019; Wickham, 2016).

RESULTS

Colour classification

When comparing the colour of ventral side of thorax with the colour of elytra of 24,797 checked beetles from the three main regions, 61.1% had the same colour, 37.1% differed one step, 1.8% two steps and 0.04% three steps on our five-step colour classification. The proportions of beetles among the five colours were somewhat more even for ventral side of thorax than for elytra (Figure 3). The elytra colour of some of the beetles was not homogenous making classification difficult. Thus, we decided to use data from the thorax in the analyses.

Seasonal colour change of *I. typographus* in breeding material

The wind-felled trees in Kronåsen and Fiby were colonized by *I. typographus* in the last days of April 2019. In the wind-felled tree in Kronåsen, newly-developed adults were first recorded on 25 June 2019 (1 week earlier there were only pupae). Light brown adults dominated during the following 4 weeks (Figure 4a). In Fiby, the first newly-developed adults were recorded on 26 June 2019. The first sampling of adult beetles was conducted on 16 July 2019 and then light brown adults dominated (Figure 4b). Thereafter, intermediate brown beetles were most prevalent with some red brown and dark brown individuals until October–November in both localities. In January 2020, both intermediate brown and red brown beetles were present while in late April, before start of spring flight, red brown
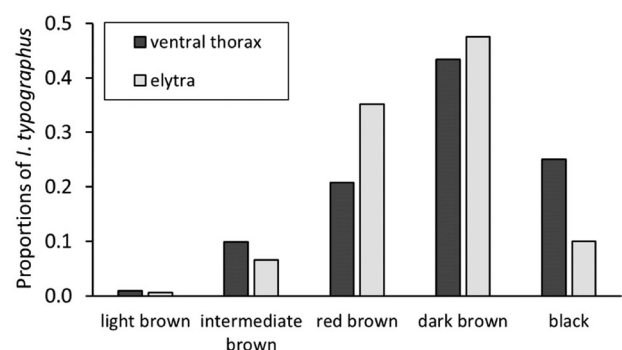

FIGURE 3 Proportions of *Ips typographus* classified into five different colours. Beetle colour was assessed for the ventral side of the thorax and for the elytra for 24,797 beetles trapped in the three main regions
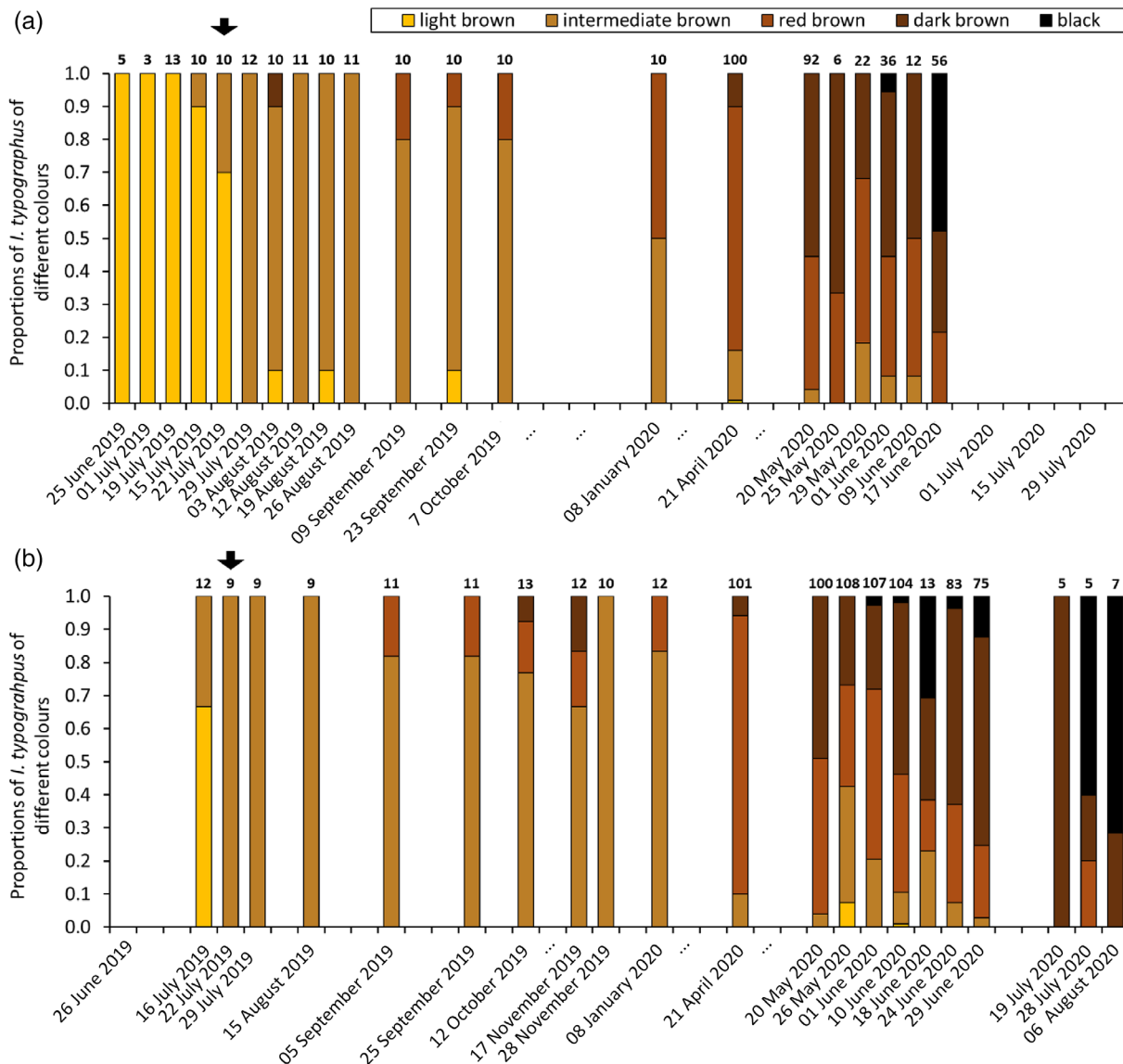
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FIGURE 4 Colour change of *Ips typographus* beetles from newly-moulted adults in 25 June 2019 to after hibernation in 21 April 2020 in one wind-felled tree in Kronåsen (a) and one in Fiby Urskog (b). From 20 May 2020 to 17 June 2020, the beetles were collected from a newly-colonized wind-felled tree in Kronåsen. In Fiby Urskog the beetles were collected from a wind-felled and standing tree currently under attack in 20 May 2020 and 26 May 2020, respectively, a wind-felled tree from 01 June 2020 to 24 June 2020, and a group of five standing trees from 29 June 2020 to 06 August 2020. Each date at the *X*-axis represents one inspection. The arrow indicates the first date with *Ips typographus* emergence holes in 2019. Observe that the *X*-axis is "broken" for the winter and spring inspections. The number of beetles checked each date is given above the bars

beetles dominated in both localities. In late May 2020, intermediate brown, red brown and dark brown adults dominated during attack of the wind-felled and standing tree in Fiby and in the newly-colonized wind-felled tree in Kronåsen (Figure 4). During June 2020, the proportion of dark brown and black adults increased while intermediate and red brown decreased in the wind-felled tree colonized in Fiby. To a lesser extent, this was also the case in the wind-felled tree in Kronåsen (but here we only had samples from a short period in the spring). In July 2020, only a few parent beetles were collected in Fiby with dark brown and black individuals dominating (47% each) and only a small proportion being red brown (6%).

On 22 July 2019, the first *I. typographus* emergence holes were detected in the wind-felled trees in both Kronåsen and Fiby. At this

date, only light brown and intermediate brown beetles were present (Figure 4). On the same day, the first adults classified as the new generation (light brown and intermediate brown, see below) were caught in the pheromone-baited trap in Uppsala (10% of the catch) (Figure S4). One week later, the catch contained 36% light brown and intermediate brown beetles.

Start of flight of new generation *I. typographus* based on colour classification of trap catches

During the first weeks of the *I. typographus* flight period, four to five of the colours occurred among the trapped beetles in all three regions
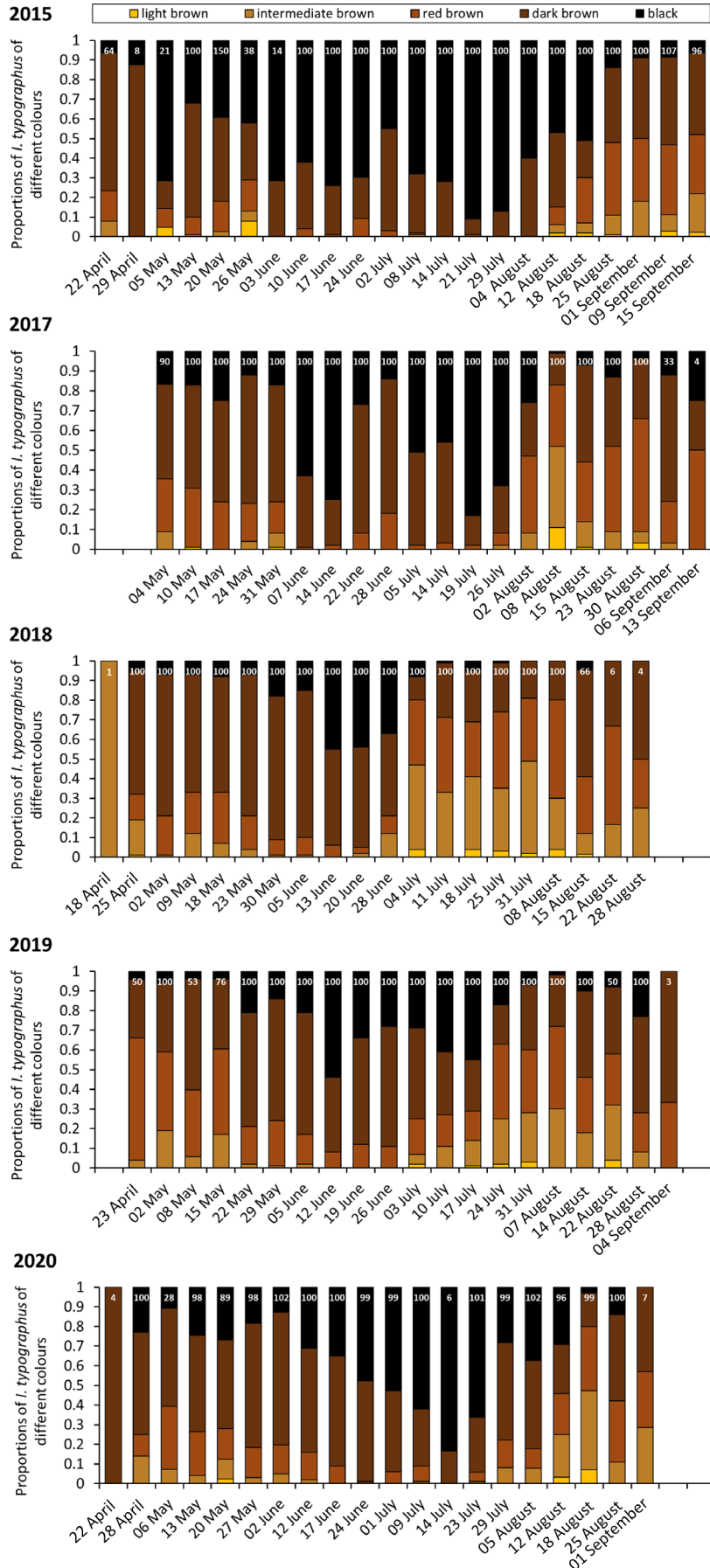
FIGURE 5 Proportions of *Ips typographus* of different colours at different trapping dates over 5 years in Tönnersjöheden. The number of beetles checked for each date is given at the top of the bars. Traps were emptied once a week. The dates when the traps were emptied are given at the *X*-axis
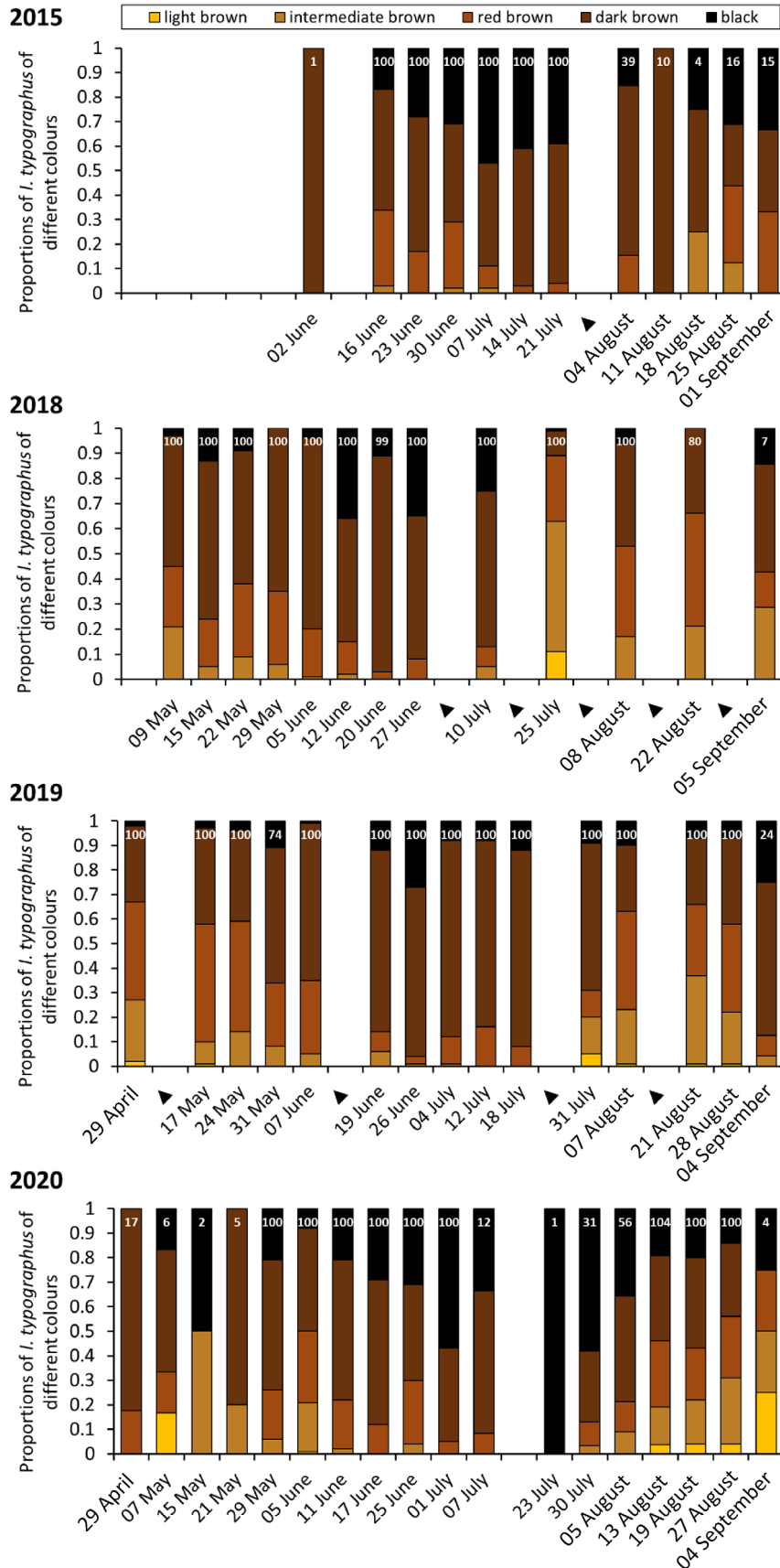
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FIGURE 6 Proportions of *Ips typographus* of different colours at different trapping dates over 5 years in Siljansfors. The number of beetles checked for each date is given at the top of the bars. Traps were emptied once a week except for in Siljansfors where traps were emptied after 2 weeks in a few cases (indicated below the *X*-axis with black triangle). The dates when the traps were emptied are given at the *X*-axis
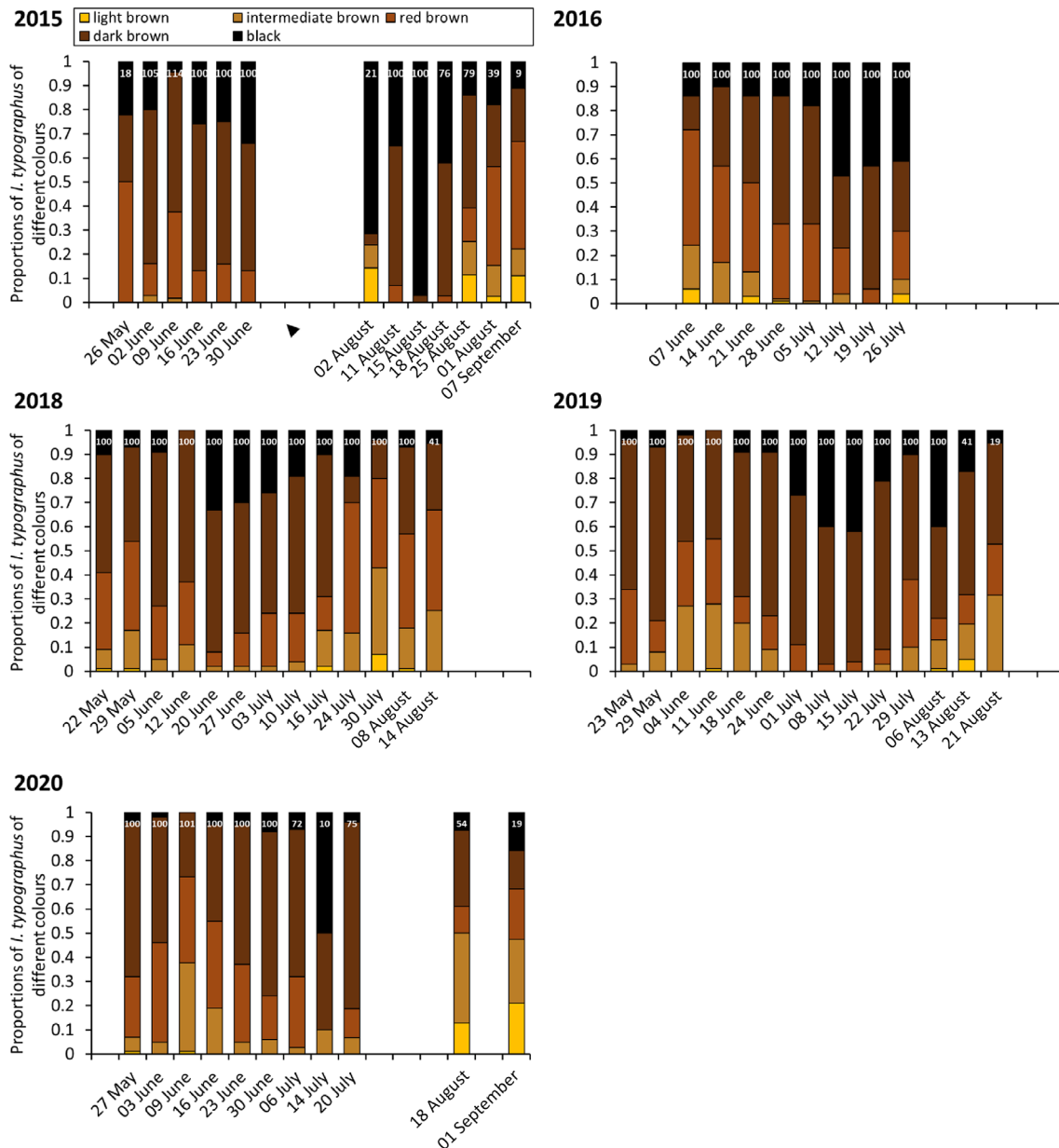
FIGURE 7 Proportions of *Ips typographus* of different colours at different trapping dates over 5 years in Vindeln. The number of beetles checked for each date is given at the top of the bars. Traps were emptied once a week except for one period in 2015 where traps were not emptied for 4 weeks (indicated below the *X*-axis with black triangle). The dates when the traps were emptied are given at the *X*-axis

and years (Figures 5–7). The most common ones were intermediate brown, red brown and dark brown beetles. The proportions of individuals of the darker colours generally increased over time, until the two lightest colours (light brown and intermediate brown) did not occur at all any more except in two cases: Vindeln 2018 and 2020 (Figure 7). After that, light brown and intermediate brown beetles started to occur again in the catches indicating that they belonged to the new generation of beetles that had developed during the summer. In Vindeln 2018, a low proportion (2%–4%) of intermediate brown beetles occurred during 4 weeks before the first light brown started to appear on 16 July 2018. In addition, an increased proportion of intermediate brown beetles were trapped at the emptying on 16 July 2018 (altogether 17%). In Vindeln 2020, no beetles were trapped for

1 month starting from 20 July 2020 when intermediate brown beetles constituted 7% of the catch. On 18 August 2020, when beetles were trapped again, both light brown and intermediate brown beetles occurred and constituted 50% of the catch. In two cases (Tönnersjöheden 2018, Vindeln 2016), the period without light brown and intermediate brown beetles was only 1 week. In all other cases, this period lasted at least 2 weeks. In two cases, Siljansfors 2018 and 2019, the start of new-generation flight may have occurred 1 week earlier because the trapped beetles from this week were missing.

The beetles did not change colour during storage. When comparing the proportion of beetles classified into the five colours among years for the three main regions, there was no trend of change in proportions over time (Table S1).

Thermal sum required from start of flight in spring until onset of new-generation flight in summer

Among the three regions, the average thermal sum required from start of *I. typographus* flight in spring until onset of new-generation flight in summer (i.e. ≥5% light brown and intermediate brown beetles) was highest for Tönnersjöheden in southern Sweden [LDT 5°C = 744 dd ± 38 (± always denotes SE in the following); LDT 8.3°C = 467 dd ± 24] and about the same for Siljansfors (LDT 5°C = 666 dd ± 28; LDT 8.3°C = 420 dd ± 18) and Vindeln (LDT 5°C = 668 dd ± 16; LDT 8.3°C = 418 dd ± 2). For the ≥10% level of new-generation beetles, the thermal sum was highest for Tönnersjöheden (LDT 5°C = 835 dd ± 62; LDT 8.3°C = 531 dd ± 37), intermediate for Siljansfors (LDT 5°C = 748 dd ± 57; LDT 8.3°C = 482 dd ± 51) and lowest for Vindeln (LDT 5°C = 668 dd ± 16; LDT 8.3°C = 418 dd ± 2). The difference between Tönnersjöheden and Vindeln (Siljansfors not included in the statistical test) was not significant for the 5% level but significant at the 10% level in both the 5°C LDT (5%: $t = 4.643$, $p = 0.118$; 10%: $\chi^2 = 4.86$, $p = 0.027$) and the 8.3°C LDT (5%: $t = 4.251$, $p = 0.118$; 10%: $\chi^2 = 3.84$, $p = 0.05$). Data for individual years are given in Table S2.

In 2020, when seven extra localities were included (but Vindeln excluded), there was a clear pattern with somewhat higher thermal sums in the southern locations compared with the two northernmost locations (Nordmaling and Siljansfors) and the northwestern location Åmål (Figure 8a,b and Table S3).

The mean number of days ± SE between the start of flight in spring until ≥5% of the catch consisted of new-generation beetles was 89 ± 6.08 in Tönnersjöheden (mean date = 20 July/21 July), 80 ± 7.12 in Siljansfors (mean date = 31 July/1 August) and 79 ± 5.12 in Vindeln (mean date = 31 July/1 August) (Table S2).

Proportion of total seasonal trap catch constituted by new-generation beetles

When estimating the proportion of total seasonal flight activity constituted by the new-generation beetles, the change in colour over time of the new-generation beetles should be taken into account. Thus, to include only light brown and intermediate brown beetles would result in an underestimate. In all years in the three regions
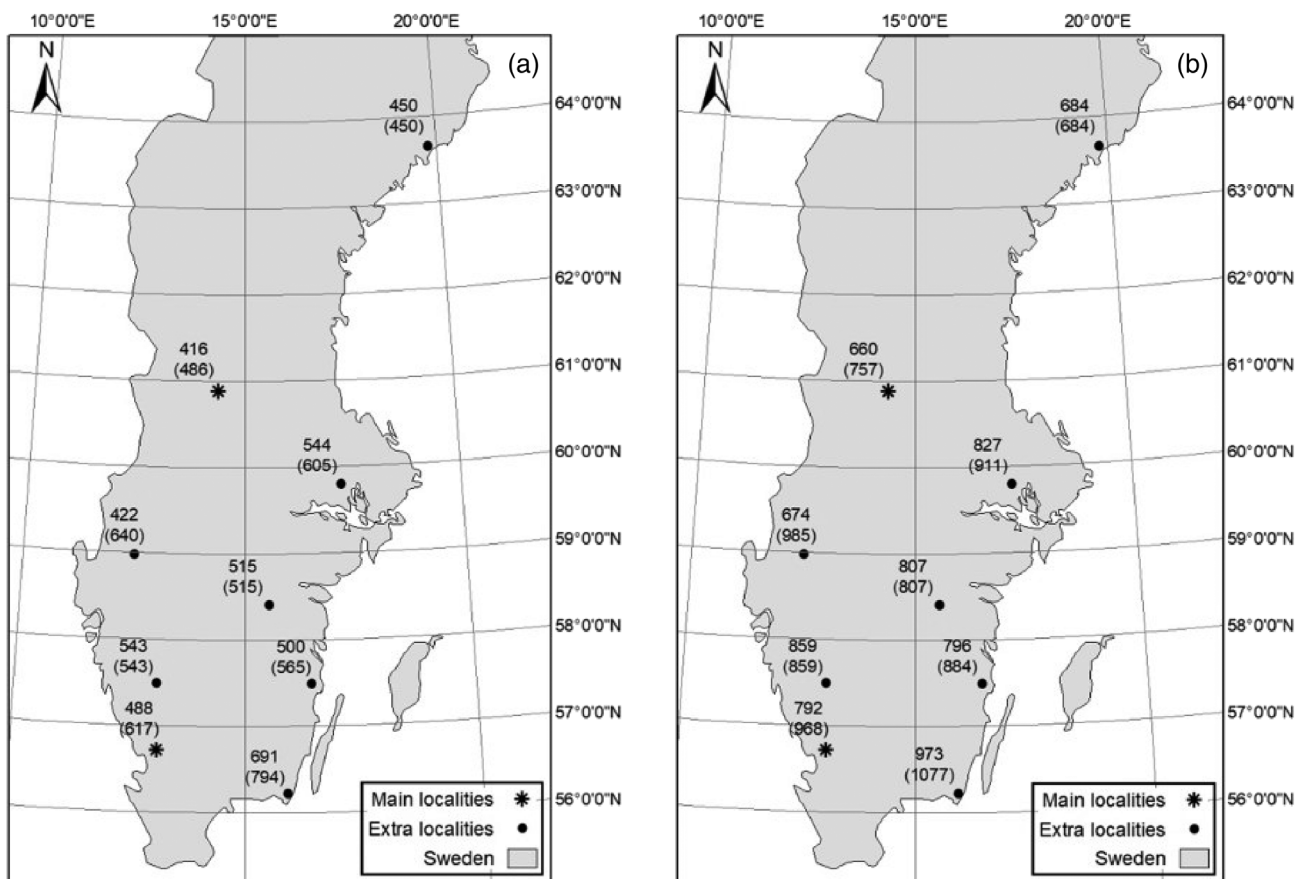

FIGURE 8 Thermal sum in degree-days from start of *Ips typographus* flight in spring until the first week at least 5% and 10% (in brackets) of trap catches were colour-classified as new-generation beetles in different localities in Sweden in 2020. Main localities represent the three regions in which several years of trapping were conducted, while beetles were trapped in the extra localities in 2020 only. The 8.3°C (a) and 5°C (b) lower developmental threshold

(Vindeln 2020 excluded), the proportion of red brown beetles started to increase after the weeks without light brown and intermediate brown individuals. This indicates that most of the red brown beetles also belong to the new generation (Figures 5–7). The same proved to be true for all extra localities in 2020 (data not shown). Thus, when estimating the proportion of seasonal catch constituted by new-generation beetles also red brown beetles were included.

The percentage of total seasonal beetle catch constituted by new-generation beetles (as defined above), collected from the week when new-generation flight started until the end of the season, varied between 0.05% and 17.7% for the three regions (Table 1). The mean percentage was 9.6% ± 2.0% for Tönnersjöheden, 4.0% ± 3.2% for Siljansfors and 1.6% ± 2.4% for Vindeln. A comparison between Tönnersjöheden and Vindeln showed a significant difference in mean proportions ($p = 0.045$). In the two more northern regions, 2018 was an outstanding year with much higher proportions compared with the other years. For all three regions, the proportions were much higher when new-generation flight started at earlier dates (Figure 9). In 2020, with the seven extra localities included but Vindeln excluded, the percentage varied between 0.4% and 8.8% (Table 1). The northernmost localities had the lowest percentage while there was no clear geographical pattern for southern Sweden.

The remaining seasonal thermal sum, accumulated from the start of new-generation flight (i.e. ≥5% new generation in trap catches), was considerably higher for Tönnersjöheden (LDT 5°C = 885 ± 17 dd; LDT 8.3°C = 527 ± 95 dd) than for Siljansfors (LDT 5°C = 502 ± 113 dd; LDT 8.3°C = 238 ± 103 dd) and Vindeln (LDT 5°C = 440 ± 91 dd; LDT 8.3°C = 246 ± 70 dd). Between Vindeln and Tönnersjöheden, the difference in remaining seasonal thermal sum was significant (LDT 5°C: $t = 3.003$, $p = 0.02$; LDT 8.3°C: $t = 2.384$, $p = 0.049$). Data for individual years are given in Tables S2 and S3.
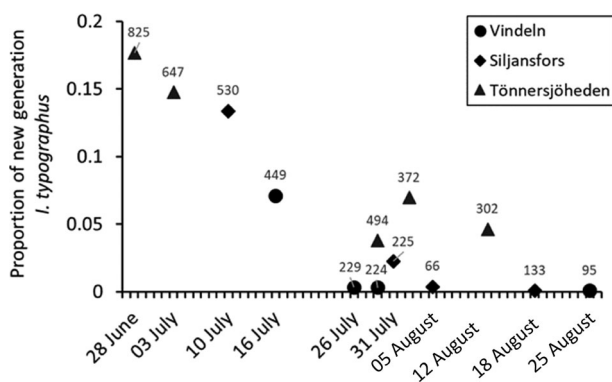

FIGURE 9 Proportion of total *Ips typographus* seasonal trap catch being made up by new-generation beetles plotted against the date when the new-generation flight started (defined as the first trap emptying when new generation constituted at least 5% of total catch) in Tönnersjöheden (south), Siljansfors (central) and Vindeln (north). The numbers above symbols give the remaining seasonal thermal sum at lower developmental threshold of 8.3°C

Proportion of trapped beetles that were attracted by pheromone bait per se

Not a single *I. typographus* was caught in the unbaited traps while an average of 939 ± 504 beetles were caught in the pheromone-baited traps.

DISCUSSION

I. typographus adults gradually get darker throughout their lifetime as demonstrated by the sampling of beetles in breeding substrate. Being light brown when newly moulted, the beetles darken until they become dark brown or black when they colonize new trees the following summer. It is unlikely that the colour change we observed was a result of higher mortality rates among more light-coloured beetles, because we did not find many dead adults when sampling adults from their brood trees in 2019/2020 or from newly-colonized trees in summer 2020. We are not aware of any earlier study demonstrating gradual changes in colour of a bark beetle, or any other insect species, over such a long time span as the 13 months in the present study. A short-term experimental study (longest survival 21 days) demonstrated that both light brown and dark brown pre-emergent *Ips paraconfusus* adults got darker when incubated separately with and without food (McNee et al., 2000). The underlying mechanism explaining the long-term gradual darkening of *I. typographus* and its potential adaptive value is not clear. Melanization has been connected to increased immunity and to increased body temperature when exposed to solar radiation in earlier insect studies (Fedorka et al., 2013; Krams et al., 2016).

Average thermal sums required from initiation of *I. typographus* flight in spring until start of the new-generation flight in summer were 10% higher at the 5% level and 20% higher at the 10% level for the southernmost region (Tönnersjöheden) than for the northernmost region (Vindeln). One factor that could explain the lower thermal sum required in the north compared with in the south is that *I. typographus* may be more constrained to sun-exposed breeding material, and thus exposed to higher temperatures during development than recorded by climate stations, in the north. Two empirical studies suggest that this could be the case: in southern Sweden wind-felled trees in both sun-exposed and shaded conditions were colonized even though sun-exposed were preferred (Göthlin et al., 2000), while in the north only up-rooted trees in sun-exposed conditions were colonized (Schroeder & Lindelöw, 2003). Another possibility could be local adaptations with faster developmental rates in the north. A difference in developmental rate between northern and southern populations has been demonstrated for the bark beetle *Dendroctonus ponderosae* in North America (McManis et al., 2019). Further studies are required to sort out the relevance of the two factors for explaining the difference in required thermal sum between south and north for *I. typographus*.

There is only one previous study about thermal sum requirements for development of a new generation of *I. typographus* in Sweden

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TABLE 2 Summary of this and earlier studies on the thermal sums required from flight/colonization by parent beetles in spring to emergence/flight of new-generation *Ips typographus*.

Location	Thermal sum (degree-days)		Description	Ref.
	LDT = 5°C	LDT = 8.3°C		
Southern, Central and Northern Sweden	744 ± 38 (SE) (south) 666 ± 28 (central) 668 ± 16 (north)	467 ± 24 (SE)(south) 420 ± 18 (central) 418 ± 2 (north)	• Field study • Colour classification of 100 beetles in weekly trap catches, 2015–2020, three regions: southern, central and northern Sweden • Period: first 100 beetles trapped in spring until first new-generation beetles were caught (5% of total catch) • Air temperature, thermal sums based on daily mean temperatures	Present study
North Zealand, Denmark	573 (sun-exposed) 685 (shaded)		• Field study • Pheromone-baited stem sections that after colonization were hung in emergence traps, beetles classified as new generation based on colour and bristles, 1980–1981, one sun-exposed and one shaded locality each year • Period: start colonization until first emergence • Air temperature, thermal sum based on hourly mean temperature	Harding and Ravn (1985)
Southern Sweden	449 ± 107 (SD)		• Field study • Cut pheromone-baited trees, stem sections hung in emergence traps in shade, weekly emptyings, beetles classified as new generation based on colour, 2006–2010, four locations • Period: start colonization until emergence of first new-generation beetles • Air temperature, thermal sum based on daily mean temperature	Öhrn et al. (2014)
Austria		573 ± 56 (SD) (trap trees) 562 ± 43 (photoeclectors)	• Field study • Trap trees felled in spring and inspected weekly for start of colonization and brood development, when the pupal or teneral adult stage was reached a stem section was cut from each tree and placed in outdoor photoeclectors, 2001–2003, 4–6 altitudes (trees) per year • Period: start of tree colonization until first emergence holes (trap trees) or start of emergence of new-generation beetles (photoeclectors) • Air temperature, thermal sums based on daily maximum temperature	Baier et al. (2007)
Switzerland		334 ± 12 (SE) (adults) 239 ± 91 (maturation feeding) 573 (sum)	• Laboratory study • Rearing experiment (sandwich technique) under 6 different temperatures, teneral new-generation adults provided with fresh bark for maturation feeding, determination of developmental threshold (8.3°C) • Period: (1) development into adults, construction of maternal gallery until development of new-generation adults; (2) maturation feeding, from boring into bark piece until emergence from bark piece (and capable of reproduction) • Air temperature	Wermelinger and Seifert (1998)

(Continues)

TABLE 2 (Continued)

Location	Thermal sum (degree-days)		Description	Ref.
	LDT = 5°C	LDT = 8.3°C		
Slovenia		550 ± 75 (SD) (30 min) 557 ± 62 (daily)	• Field and laboratory study • Trap trees felled in spring, inspected weekly for start of colonization and brood development; when pupal or teneral adult stage was reached, two stem sections were cut from each tree and placed in climate chambers with 16 h light and 23°C, respectively, 28°C, 2017 and 2018, 1–4 trees per year, shaded conditions • Period: start of tree colonization until first emergence of new-generation beetles in climate chambers • Bark temperature, thermal sums based on half-hourly and daily maximum temperatures	Ogris et al. (2019)

Note: Results presented for the two most commonly used lower developmental thresholds (LDT), LDT = 5°C and LDT = 8.3°C.

(Öhrn et al., 2014). The study was based on the timing of emergence of new generation from stem sections in shaded conditions with known colonization dates (Table 2). The average thermal sum was 40% lower than our results for Tönnersjöheden in southern Sweden. In contrast, a study using the same methods as Öhrn et al. (2014) but conducted in Denmark, showed results similar to our study for shaded conditions (Harding & Ravn, 1985, Table 2). We have no explanation for the discrepancy in results between our and the Danish study on one hand and the study by Öhrn et al. (2014) on the other hand. Studies conducted in Austria, Switzerland and Slovenia all reported slightly higher thermals sums, 18% to 23%, compared with our results for Tönnersjöheden in southern Sweden (Table 2).

For a better understanding of *I. typographus* population dynamics, the proportion of the new generation that chose to reproduce before hibernation is of large interest. Even though we cannot directly calculate this proportion, our data offer an opportunity to roughly estimate how large part of the total seasonal flight activity (as measured by pheromone-baited traps) that is constituted by new-generation flight in different parts of Sweden. Obviously, some new-generation *I. typographus* tried to reproduce in all regions and years. However, their contribution to total seasonal flight activity was generally small in northern (Vindeln) and central (Siljansfors) Sweden but somewhat higher in southern Sweden (Tönnersjöheden). For all three regions, the proportions were higher in years with an early start of flight of the new generation. This is expected as day length determines how large proportion of new-generation *I. typographus* that will be reproductive, respectively, be in reproductive diapause (Doležal & Sehnal, 2007; Schebeck et al., 2022; Schroeder & Dalin, 2017). In addition, the proportions of new-generation flight activity decreased with latitude in agreement with Schroeder and Dalin (2017) demonstrating that the proportion of reproductive new-generation *I. typographus* decreased with latitude for a given day length.

In Sweden, there are no observations of larvae and pupae of *I. typographus* surviving winter and in central and southern Europe mortality is high (Dworschak et al., 2014; Faccoli, 2002). Thus, it is very important that the remaining seasonal thermal sum is high enough for the offspring of the new-generation adults to reach adult stage before winter. According to Baier et al. (2007), 60% of the total thermal sum required for complete development of *I. typographus* (including maturation feeding of adults) is needed for development into adults. In the present study, the average remaining thermal sum for the southernmost region (Tönnersjöheden) was about twice as high as this requirement at the start of new-generation flight, and in 3 out of 5 individual years this criteria was met. For the central (Siljansfors) and northern (Vindeln) regions, the averages were just at the limits for adult development, and in only the exceptionally warm summer of 2018 the criteria was fulfilled. Thus, our results indicate that bivoltinism is currently of marginal importance to the population dynamics of *I. typographus* in central and northern Sweden while in some years, it may be a factor to consider in southern Sweden.

As our results demonstrate, it is challenging to differentiate between parent and new-generation *I. typographus* in trap catches based on colour. The main reasons are the gradual change from light brown to dark brown or black coloration extended over a long time and the presence of all colours from light brown to black beetles in the first weeks of flight in spring. The latter is most probably a result of beetles originating from substrates colonized during different times in the previous summer (i.e. darker beetles originate from early colonizations and lighter beetles from late colonizations). Nevertheless, in most cases we were able to determine when the new generation started to occur in the traps based on the following: First, there was a period of at least 1 week in the summer when no light brown and intermediate brown beetles were caught in the pheromone-baited traps. This occurred in 19 out of 21 studied

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trapping materials, including the extra localities in 2020. The first week after this period, when at least 5% of the trapped beetles were light brown or intermediate brown was interpreted as the start of new-generation flight. Second, only light brown and intermediate brown individuals were present in colonized wind-felled trees when emergence holes first occurred. In addition, the presence of the first emergence holes in wind-felled trees coincided with the first catches in summer of light brown and intermediate brown beetles in a pheromone-baited trap in the same region. Thus, we conclude that our method, utilizing a five-colour scale to classify the ventral side of the thorax of trapped *I. typographus*, works for determining when the new generation initiates flight in summer under Nordic conditions.

Almost all *I. typographus* caught in the pheromone-baited traps are assumed to have been attracted by the pheromone (i.e. not trapped by chance or only visually responding to the silhouette of the trap) and thus to be in reproductive state (i.e. not in reproductive diapause). Two field experiments support this assumption. In the experiment with unbaited and pheromone-baited funnel traps not a single *I. typographus* was caught in the unbaited traps while on average 939 individuals were caught in the baited traps. In an earlier study with transparent flight barrier traps, unbaited traps caught on average 1.9 *I. typographus* compared with 6264 individuals in pheromone-baited (Pheroprax) traps (Schroeder, 2003).

From a management perspective, our study demonstrates that currently attacks and reproduction by new-generation *I. typographus* in summer are not a problem in northern Sweden. In 3 out of 4 years, less than 1% of total flight activity could be attributed to new-generation beetles and even in the extremely warm summer of 2018 the proportion was only 7%. In southern and central Sweden, the situation was somewhat different with 13%–18% of new-generation flight activity in years with an early start of new-generation flight. Thus, it is important to provide forest owners from these regions with predictions about when attacks by the new generation can be expected.

In monitoring programs, it may be tempting to assess beetle colour directly in the field. However, this is not an easy task to conduct with accuracy without good light conditions, magnification and reference colours. The light brown individuals that should be recognizable under field conditions generally constituted a very small proportion of the catch (in several cases none found of the 100 beetles checked per week). Neither was it possible to infer the start of new-generation flight from trap catch patterns because there was no evident peak in catches correlated with the start of the new-generation flight. Thus, we recommend that the main strategy should be to provide forest owners with real-time predictions about when attacks by new-generation beetles can be expected based on start of *I. typographus* flight in spring and thermal sums required. If predictions show an early start, forest owners should carefully check their forests for newly-attacked trees, in particular during dry summers when tree vitality will be compromised by drought stress.

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

TABLE S1 Proportions *Ips typographus* beetles classified into the five different colours in the different years in Tönnersjöheden, Siljansfors and Vindeln, and the total number of beetles classified for each year

TABLE S2 General data and results for individual years for Tönnersjöheden (southern Sweden), Siljansfors (central Sweden) and Vindeln (northern Sweden). Baiting date: date of pheromone baiting of traps. Start spring flight: the first day with a maximum temperature of ≥16.5°C in the first week when an accumulated catch of ≥100 *Ips typographus* was caught (including previous weeks), in total in the 15 traps. Start new-generation flight: first date when light brown and intermediate brown beetles constituted ≥5% and 10% of total catch. Percentage new generation: actual percentage constituted by light brown and intermediate brown beetles when the 5% and 10% levels were reached. Thermal sum 8.3°C and 5°C LDT (dd): thermal sum from start of spring flight until ≥5% and 10% of the catch was constituted by light brown and intermediate brown beetles. Number of days to start new-generation flight: number of days from start of spring flight until start of new-generation flight. Remaining thermal sum 8.3°C and 5°C LDT (dd): remaining thermal sum from start of new-generation flight at the 5% level until the end of the year

TABLE S3 General data and results for the extra localities in 2020 arranged from south to north (see Figure 2 for geographic locations). Baiting date: date of pheromone baiting of traps. Start spring flight: the first day with a maximum temperature of ≥16.5°C in the first week when an accumulated catch of ≥100 *Ips typographus* was caught (including previous weeks) in total in the 15 traps. Start new-generation flight: first date when light brown and intermediate brown beetles constituted ≥5% and 10% of total catch. Percentage new generation: actual percentage constituted by light brown and intermediate brown beetles when the 5% and 10% levels were reached. Thermal sum 8.3°C and 5°C LDT (dd): thermal sum from start of spring flight until ≥5% and 10% of the catch was constituted by light brown and intermediate brown beetles. Number days to start new-generation flight: number of days from start of spring flight until start of new-generation flight. Remaining thermal sum 8.3°C and 5°C LDT (dd): remaining seasonal thermal sum from start of new-generation flight at the 5% level until the end of the year

FIGURE S1 Number of trapped *Ips typographus* each week (bars) and daily maximum air temperature (line) in Tönnersjöheden from 5 years. Number of trapped beetles represent the total catch in 15 traps distributed on 5 fresh clear-cuts. Observe that the *Y*-axis is log-transformed. The vertical dotted line indicates when trapping started. The stars indicate when the first new-generation beetles were caught and constituted at least 5% (*) and 10% (**) of the inspected beetles. The arrow indicates the defined start of spring flight. The dates when the traps were emptied are given at the *X*-axis

FIGURE S2 Number of trapped *Ips typographus* each week (bars) and daily maximum air temperature (line) in Siljansfors from 4 years.

Number of trapped beetles represent the total catch in 15 traps distributed on 5 fresh clear-cuts. Observe that the *Y*-axis is log-transformed. The vertical dotted line indicates when trapping started. The stars indicate when the first new-generation beetles were caught and constituted at least 5% (*) and 10% (**) of the inspected beetles. The arrow indicates the defined start of spring flight. The dates when the traps were emptied are given at the *X*-axis. In a few cases in 2015 and 2018 traps were emptied after 2 weeks instead of 1 week.

FIGURE S3 Number of trapped *Ips typographus* each week (bars) and daily maximum air temperature (line) in Vindeln for 5 years. Number of trapped beetles represent the total catch in 15 traps distributed on five fresh clear-cuts. Observe that the *Y*-axis is log-transformed. The vertical dotted line indicates when trapping started. The stars indicate when the first new-generation beetles were caught and constituted at least 5% (*) and 10% (**) of the inspected beetles. The arrow indicates

the defined start of spring flight. In one case in 2015, the traps were emptied after 2 weeks instead of 1 week. The dates when the traps were emptied are given at the *X*-axis

FIGURE S4 Proportions of Ips typographus of different colours at different trapping dates in 2019 in the pheromone-baited trap in Uppsala. The number of beetles checked for each date is given at the top of the bars. The dates when the traps were emptied are given at the *X*-axis