Seasonal flight patterns of *Ips typographus* in southern Sweden and thermal sums required for emergence (early version)

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Abstract

1 The spruce bark beetle *Ips typographus* is the major tree-killing bark beetle in Eurasia. To increase knowledge about its seasonal flight patterns and also about the thermal sums required for emergence a field study was conducted in southern Sweden from 2006-2010.

2 Flight began on average 27 April (after 47 degree-days (dd) > 5°C). More than 50% of flight activity occurred after mid-June, and continued to mid-August.

3 Re-emergence of parental beetles after they had produced the first brood started on average 24 May (after 122 dd). Continued flight and oviposition demonstrated that sister broods were frequent. A much higher proportion of parental beetles re-emerged from trees colonized in May (95%) than in July (20%). Beetles that colonized trees late had to accumulate a much higher thermal sum before re-emerging (400 dd).

4 Filial beetles began to emerge on average 29 June (after 437 dd), and started to fly in early July, giving rise to at least a partial second generation in each year. A much higher proportion of filial beetles had emerged from trees colonized in May (75%) than in July (15%).

5 Knowledge of these region-specific flight patterns and the associated thermal sums required for emergence will facilitate efficient pest management by enabling the timely removal of fallen and standing weakened host trees. The obtained data will also be useful for parameterization of models that predict the population dynamics in a warmer climate.

Keywords degree-days, flight activity, re-emergence, pest management, phenology, phytosanitary measures, *Picea abies*, spruce bark beetle, voltinism.

Introduction

The European spruce bark beetle *Ips typographus* (Coleoptera: Curculionidae, Scolytinae) is one of the most destructive pests of Norway spruce (*Picea abies* L. Karst.) forests in Europe and Asia (Christiansen and Bakke, 1988). During outbreaks of *I. typographus* millions of Norway spruce trees have been killed. Due to salvage logging and reduced quality of the wood as a resource for timber or pulp production this has led to large economic losses (Schelhaas et al. 2003). In the 1990s, ca 30 million m^3 of spruce were killed by *I. typographus* following several severe storm-fellings in Central Europe (Grégoire and Evans, 2004). In Sweden, about 9 million m^3 of Norway spruce have been killed since 1960 (Kärvemo and Schroeder, 2010), of which the most recent outbreak in southern Sweden, between 2006 and 2010, destroyed 3.5 million m^3 (Swedish Forest Agency unpubl.). The outbreak was triggered by a storm in January 2005 that blew down 75 million m^3 of wood (Långström et al., 2009). This was the most severe storm felling in Swedish history, and necessitated a huge effort to deal with the large volumes of damaged spruce in a short space of time, in order to prevent loss of timber value and build-up of bark beetle populations (Långström et al., 2009).

Efficient control of bark beetle populations relies mainly on the well-timed removal of any potential host trees that have a reduced defence capacity, e.g. fallen or weakened trees (Christiansen et al., 1987, Christiansen and Bakke, 1988). This requires good knowledge of the regionally specific seasonal flight patterns and the temperature-dependent development of the beetle (Netherer and Pennerstorfer, 2001). The most recent outbreak in southern Sweden has highlighted the need for such knowledge.

I. typographus starts to fly in spring after a specific thermal sum is reached (Doležal and Sehnal, 2007a). During flight the beetles disperse through the forest in search of host trees suitable for breeding. After initial excavation of a nuptial gallery the male frequently attracts up to three females to create a polygamous gallery system. After mating, the females lay eggs in niches along their gallery (Bombosch, 1954). Thereafter, the parental beetles may leave the gallery and initiate one or more sister broods (Martinek, 1956). The time of re-emergence and the occurrence of sister brood flights depends upon both temperature (Anderbrant, 1986) and intra-specific competition (Anderbrant et al., 1985). When the beetles of the first brood are fully developed they may emerge and initiate a second generation within the same season (bivoltine) or they may hibernate (univoltine), depending on the thermal conditions and the photoperiod (Doležal and Sehnal, 2007b). Beetles in northern Europe are primarily univoltine whereas in Central Europe beetles are primarily bivoltine (Anderbrant, 1989, Christiansen and Bakke, 1988).

A key factor in determining the extent of any *I. typographus* outbreak is the proportion of the initial colonizing beetle population that goes on to initiate a second and a following third brood that same year (Wermelinger and Seifert, 1999); also important is the proportion of the second generation that develops fully before winter. It has been shown that the initiation of a second generation is dependent on both temperature and day length (Schopf, 1985).

Knowledge of the region-specific thermal sums required for certain developmental phases of *I. typographus* is therefore necessary for efficient pest management, as it enables planning for the timely removal of fallen and standing weakened host trees. Reproductive success in *I. typographus* tends to be higher in such trees and they are therefore generally recommended to be removed before spring flight (i.e. before they are first attacked), thus preventing pest build-up and avoiding the consequent deterioration in wood quality. However, an alternative pest management strategy, which is more efficient but risky, is to remove trees once they have already been attacked; this method requires that infected trees are removed before the new bark beetle generation emerges, and is even more effective if they are removed before the parent beetles leave the tree to establish a sister brood.

Thermal sums, or the cumulative temperature requirement for development above a lower threshold (measured in degree-days, dd), can forecast the initiation of spring flight, the time for beetle development from egg to imago and the subsequent emergence of new generations, as well as the re-emergence of parental beetles (Anderbrant, 1985; Annila, 1969). The required thermal sums for flight, development and emergence have been shown to differ between regions as an adaptation to local conditions (Netherer & Pennerstorfer 2001; Bentz et al. 2001, 2011). Thermal sums for the developmental stages of *I. typographus* in southern Sweden are, however, unavailable, and information on seasonal flight patterns here is also sparse (Trägårdh, 1939; Eidmann and Klingström, 1990).

The aims of this study were twofold; (1) to describe the flight pattern and voltinism of *I. typographus* in southern Sweden, and (2) to determine critical thermal sums to allow the prediction of life history events such as the beginning of the spring flight, re-emergence of parental beetles, and the development time of the new generation.

Material and Methods

Study sites

The flight activity and development of *I. typographus* was studied in southern Sweden (Götaland), in 2006–2010 at two research stations Asa (57°10′ N, 14°47′ E) and Tönnersjöheden (56°41′ N, 13°06′ E), and in 2008–2010 at two additional locations, Gammalstorp (56°19′ N, 15°19′ E) and Remningstorp (58°27′ N, 13°40′ E). All locations are in the area that was affected by the *I. typographus* outbreak that followed the storms of 2005 and 2007 (Anon., 2006; Bergqvist, 2009).

Seasonal flight patterns and thermal requirements

Flight activity was monitored at each location using two flight interception traps baited with a pheromone (Ipslure®) that attracts *I. typographus* from long distances (Helland et al. 1984). The traps were emptied weekly from mid-April until September. The pheromone dispensers were renewed at all sites in late June or early July depending on the annual weather situation. Trap catches were stored in a freezer (-18°C) before quantification in the laboratory. The number of beetles caught was determined either by direct counting (if less than 100) or measured by volume (100 ml corresponding to 4400 individuals, $R^2 = 0.9844$; $p < 0.001$, N = 341 (Å. Lindelöw., unpublished)). With the exception of the beetles trapped in Asa, all beetles trapped in 2009 and 2010 (45 497 in total) were categorized according to elytra colour, into parental beetles (darker) or filial beetles (lighter) (Merker and Wild, 1954).

Air temperature data (daily mean and maximum temperature recorded in a open area by a weather station at 1.7 m height) was obtained from the research stations at Asa and Tönnersjöheden. In Remningstorp and Gammalstorp, temperature data came from the Swedish Meteorological and Hydrological Institute (SMHI). A 5°C threshold was used since it has been reported as being the lower temperature threshold for preimaginal development in a study conducted with beetles originating from Finland (Annila, 1969). The 5°C threshold has also been applied in later studies (Harding and Ravn, 1985; Jönsson et al., 2011) and is also easy to obtain for foresters since it is the common temperature used to determine the growing season.

To avoid possible bias effects from single individuals flying unusually early, flight was considered to have started when the weekly trap catch consisted of more than 10 individuals. The start date was considered to be the first day, during that week, when the maximum temperature exceeded 16°C, i.e. the flight initiation threshold (Lobinger, 1994), or if there were no such days, the day with the highest daily maximum temperature during that week. The correlation between expected flight date according to thermal requirements and measured date for flight initiation was tested using regression analyses run in the Minitab 15 statistical software® (Inc., State College, PA).

The thermal sums for parental and filial beetle emergence were calculated using 5°C as the lower developmental threshold. Thermal sums expressed as degrees-days (dd) were calculated by summing up the daily mean temperature above the specified threshold starting from both 1 January and first colonization in spring. Differences in thermal sum requirements for emergence between cohorts of beetles from trees felled at different dates were tested using one-way ANOVA in Minitab. When differences were significant ($p < 0.05$), they were further examined using Tukey's test.

Development and mortality

At all four locations two Norway spruce trees were cut before the first flight of *I. typographus* in 2008, 2009, and 2010 (Table 1). All trees were initially baited with pheromone to ensure beetle colonization. This procedure may also have decreased the initial colonization time, avoiding a protracted emergence and less precision in the determination of the critical thermal sums. Each tree was inspected weekly for entrance holes made by *I. typographus*. When the tree was avoided and no additional entrance holes were observed, despite beetles being caught in the flight interception traps (thus indicating good flight weather), a tree was considered to be fully colonized, and a 70 cm stem section was cut from the middle part of the bole and suspended in an emergence bag fitted with a collection bottle, in a nearby shaded position. Emerging beetles were collected weekly, counted and categorized into parental beetles or filial beetles (Merker and Wild, 1954).

The procedure described above was repeated at the beginning of June and July (Table 1). This was done in order to follow the seasonal progress of beetle colonization and to evaluate whether the thermal sums necessary for complete development differed depending on when during the season the host tree was colonized. In June, stem sections are expected to be colonized not only by late first time flight of parental beetles, but also by re-emerging parental beetles. In July both late-flying, re-emerging parental beetles and the new generation emerging beetles are expected to colonize trees. The beetles associated with trees felled on different dates can thus be considered to roughly represent biologically distinct cohorts, and are referred to as such (e.g. May cohort) hereafter. At the end of the season, the number of exit holes, mother galleries, and adult live and dead beetles on each stem were counted. For each cohort, colonization density was measured as the number of egg galleries/m^2.

Differences in attack density were tested using one-way ANOVA in Minitab. Differences in percentage emergence and mortality were tested using a Kruskal-Wallis test (since data were not normally distributed) in Minitab. When significant differences occurred, Nemenyi's method was used to separate significantly different means.

Results

Seasonal flight patterns and thermal requirements for spring flight

Flight of *I. typographus* began, on average, 27 April when an average thermal sum of 47 ± 24 (mean ± st dev) dd (> 5°C) was exceeded (Table 2). Colonization of cut trees was found to occur one week after the first beetles were caught in pheromone traps, on average 5 May, at an average thermal sum of 82 ± 28 dd (Table 2).

In order to find the best predictor for flight initiation, different thermal factors were tested for their correspondence with the estimated first day of flight using linear regression functions (Fig. 1, see M&M for procedure). The first day of flight showed no correlation with the first day with a daily maximum temperature exceeding 16°C ($y = -0.0297x+120.92$; $R^2 = 0.0012$; $p = 0.899$), but it did significantly correlate with the critical thermal sum threshold (47 dd) ($y = 0.9186x+11.324$; $R^2 = 0.5797$; $p < 0.001$). A better prediction of first flight was in fact obtained when both the critical thermal sum of 47dd and a daily maximum temperature of 16ºC had been reached, however, it should be noted that even this model did overestimate the date of flight initiation by approximately three days.

More than 50% of the observed flight activity (trapped beetles) occurred after mid-June, and flight activity continued until mid-August (Fig. 2). Beetles from at least seven groups (defined by sister brood- or new generation flight) could be observed during the season. The first beetles flying, from the end of April until the end of May, were brood offspring beetles from the previous year (Fig. 2). On average, the first 35% of the yearly catch consisted of individuals that were flying for the first time that season, and re-emerging parental beetles started to contribute to the catch at the end of May (Table 3). Between then and the end of June, the trap catch consisted of both parental beetles flying for the first time and re-emerged parental beetles that were flying to initiate a second brood (so-called sister brood) (Table 3). The filial beetles (the new generation, lighter in colour than the parents), and also parental beetles that had re-emerged for a second time in order to lay a third brood, started to contribute to the catch in early July, by which time approximately 70% of the total catch of beetles for the year had occurred (Fig. 2). Thus, the new generation beetles and parents re-emerging for a second time together contributed less than 30% to the overall catch. In mid-July, by when approximately 80% of the beetles had been caught, beetles from the third brood may have been present together with parents re-emerging for a third time (Fig. 2). Based on the colour of the elytra at least 17% of the overall catch consisted of filial beetles from the first and second generation (Fig 3); thus, beetles re-emerging from mid-July onwards made up about 13% (100-(70+17)) of the overall catch.

Thermal sums for re-emergence of parental beetles and emergence of filial beetles

The first re-emergence of parental beetles from the May cohort was observed, on average, on 24 May, approximately three weeks after the first brood was initiated (Table 3). This occurred at a thermal sum, accumulated since colonization, of 115 ± 46 dd. After another seven weeks, on average on 10 June, 50% of the parental beetles had re-emerged, at a thermal sum since colonization of 256 ± 107 dd. The corresponding thermal sums if calculated from 1 January were 195 ± 58 dd for the start of re-emergence and 334 ± 110 dd for the time when 50% of the parental beetles had re-emerged.

The emergence of filial beetles (the new generation) from the May cohort started, on average on 29 June, approximately eight weeks after the brood was initiated (Table 3). This occurred at a thermal sum accumulated since colonization of 449 ± 107 dd. After another three weeks, on average on 20 August, 50% of the filial beetles had emerged, at a thermal sum since colonization of 1019 ± 280 dd. The corresponding thermal sums calculated from 1 January were 527 ± 100 dd for the start of emergence and 1115 ± 294 dd for the time when 50% of the new generation had emerged.

There were no differences in the thermal sum requirements of filial beetles regardless of the time of attack. A lower proportion of parental beetles had re-emerged at the end of the season from trees colonized later in the season, and they only re-emerged after accumulating a higher thermal sum (Fig. 5). The start of re-emergence by the May cohort occurred at a time when 27% of the thermal sum (449 dd) for total development of the new generation was reached. The corresponding proportions were higher for trees colonized later: 60% in June and 95% in July (Fig. 4). There was no correlation between colonization density and timing of re-emergence (data not shown),

Since the yearly thermal sum calculated from the start of the colonization was around 1420 dd for all locations and years (data not shown), subtracting the thermal requirement for filial beetle emergence, i.e. 449 dd (Table 3), gives a thermal window of 971 dd that allows time for nearly 50% of the new generation to produce a second generation, from which at least some individuals will be fully developed beetles before winter (Fig. 2).

Development and mortality

The proportion of beetles that re-emerged was significantly lower in trees colonized later in the season. Almost 95% of the parental beetles of *I. typographus* from the May cohort re-emerged from under bark before the end of the season (Fig. 2). The corresponding values for the June and July cohorts were 60% and 20%, respectively. The mortality under bark was significantly higher in trees colonized later in the season. Only 3% of the May cohort was found dead under bark (Table 4). In the June and July cohorts 40% and 60%, respectively, of the parental beetles were found dead.

In the May cohort 75% of the offspring left the trees before the end of the season, 3% were found dead under bark, and the remaining 22% stayed to overwinter underneath the bark (Table 4). In cohorts that colonized trees later a decreasing proportion of filial beetles left the trees: approximately 50% from the June cohorts and 15% from the July cohorts (Fig. 5; Table

4). Also cohorts that colonized trees later showed higher mortality: approximately 9% from the June cohorts and 22% from the July cohorts (Table. 4). The difference between cohorts was significant with respect to both proportion of emerged beetles and mortality. By the end of the season all beetles from all cohorts (May, June and July) had developed to adults except for a very small fraction of the offspring (0.03%) found as pupae under bark in the July cohort.

The colonization density (mother galleries/ m^2) did not significantly differ between cohorts (May: (mean ± st dev): 263 ± 141; June 173 ± 124; July: 132 ± 127, one-way ANOVA: F = 1.43; p = 0.255), and neither did the reproductive success (daughters/mother gallerie) (May: 4,1 ± 3,2; June 4,9 ± 5,1; July: 5,6 ± 8,1, one-way ANOVA: F = 0,36; p = 0.702).

Discussion

Seasonal flight patterns

Our study showed that *I. typographus* usually has a long period of flight activity, starting in mid-April and lasting into mid-August (Fig. 2). Over the whole study period, 10% of the flight activity occurred before the end of April and 50% after mid-June (Fig. 2). Previously, it had generally been thought that in Sweden the flight period started in mid-May and lasted until the beginning of July (Trägårdh, 1939, Eidmann and Klingström, 1990). However, the extended flight period described here is more in line with findings from Denmark, i.e. flight activity between early May and mid-August (Harding and Ravn, 1985), or the flight period in Central Europe which is even longer, i.e. between April and September (Faccoli and Stergulc, 2004, Baier et al., 2007). Such an extended flight period has also been recorded further north, (i.e. in southern Norway) but only during unusually warm summers (Bakke et al., 1977). Thus the length of the flight period seems to be explained to a large extent by temperature, and southern Sweden appears to be warm enough for an extended flight period.

We also found that the flight period consisted of the main spring flight followed by one or several, frequently occurring, sister brood flights; in addition, a second generation was initiated every year (Fig. 3). However, a completed second generation was a rare phenomenon, as will be discussed below.

Thermal sums for emergence

The spring flight of *I. typographus* was initiated when the accumulated thermal sum had reached an average of around 47 dd (Table 2; Fig. 2). The flight initiation in 2010 was later than in other studied years in terms of both date and thermal sum, but still within the range previous observations, i.e. between 20 April - 20 May (Öhrn, 2012). The thermal sum obtained in this study corresponds well with results from Denmark (Harding and Ravn, 1983) and southern Finland (Annila, 1969), where the thermal sums for first flight are around 45 dd.

It is generally believed that the first flight in spring occurs as soon as the daily maximum temperature exceeds18 - 20°C (Annila, 1969; Bakke et al., 1977). However, thermal sums for when first flight occurs have been calculated in earlier studies (Annila, 1969; Baier et al., 2007; Jönsson et al., 2007, 2009), our results show closer correlation with those figures when a combination of flight threshold and a thermal sum is used, i.e. the first day with a maximum temperature exceeding 16°C after the mean thermal sum at first flight has been exceeded (47 dd). These results require further verification however, since predictions were made using the same dataset that had been used to define flight thresholds, and we might therefore expect the flight start date to be underestimated in years when the flight threshold temperature is reached before the thermal sum has been reached.

The re-emergence of parental beetles in the current study was at a slightly lower thermal sum than reported in most previous studies (122 dd > 5°C dd)(Table 3, Fig. 2). Laboratory results which also were verified in a field experiment in southern Norway estimated the temperature sum threshold to be 168 dd > 7.5°C for mean re-emergence from exposed trees (Anderbrant, 1986). Field studies in southern Finland suggested 150-200 dd > 5°C for re-emergence (Annila, 1969). The comparisons between studies should be interpreted with caution due to the fact that these thermal sums are based on different thresholds.

In addition, our results show an increasing delay in parental re-emergence in trees colonized later in the season: the beetles in the July cohort required thermal sums almost twice as high before they re-emerged (Fig. 4). This may be due to ageing parental beetles associated with later colonization, as discussed below. Another hypothesis is that it could be due to deterioration of the under-bark environment leading to sub-optimal conditions for both parental beetles and their offspring. However this is not likely since the reproductive success did not differ between cohorts.

The thermal sum required for the emergence of filial beetles (new generation) (449 dd) of *I. typographus* in southern Sweden is similar to those from studies conducted in the Nordic countries reporting thermal sums of around 600 dd (Annila, 1969, Harding and Ravn, 1985).

Voltinism

Our analysis of the brood origin of *I. typographus* that had been caught during flight showed that beetle individuals originated from seven different beetle groups in the same season (Fig. 2). As with many insect species, *I. typographus* voltinism depends both on thermal and photoperiodic thresholds and therefore varies over latitude and altitude with regard to the number of days needed to complete development to the stage that can survive hibernation (imago). The considerable flight activity late in the season and the appearance of newly emerged individuals in July shows that sister brood flights and partial second generation flight occurs frequently (Fig 3).

Confirmed records of bivoltinism in Fennoscandia are rare and the phenomenon has only been recorded in years with unusually warm summers. In Sweden, initiation of a second generation was recorded in 1932, 1935 and 1937 (Trägårdh and Butovitsch, 1935, Butovitsch, 1938). A completed second generation has only been recorded in 1975 (in southern Norway; Austarå et al., 1977), in 2006 (in southern Sweden; Långström et al., 2009) and in 2010 (in southern Finland; Pouttu and Annila, 2010). A completed second generation was also recorded in 2010 following an additional (unplanned) felling on 5 August of a non-attacked tree in Asa. Presumable filial beetles that had already emerged from other trees attacked, and by the end of the season more than 90% of their offspring had reached the adult stage and more than 10% of them had emerged from the tree. A fully developed second generation the same year was also developed in southern Finland (Pouttu and Annila, 2010). Nonetheless, our study showed that the thermal conditions in southern Sweden during each of the study years would have allowed the development of a second generation. This is in accordance with calculations by Jönsson et al. (2009), which indicated that even with the current climate; a fully developed second generation can be expected in some years each decade. With global warming, we can expect a second generation of *I. typographus* to occur more frequently in Fennoscandia (Lange et al., 2006; Schlyter et al., 2006; Jönsson et al., 2007, 2009). The thermal sums that we have presented here could be used to improve parameterization of simulation models in southern Sweden, since they are both more region specific and based on a higher number of replicates of localities and years than previous data sets that had been used for simulations of bark beetle population dynamics in this region (Harding and Ravn, 1985; Jönsson et al 2007, 2011).

Development and mortality

More than 90% of the parental beetles re-emerged at least once before the end of the season (Fig. 2), but the potential for this to happen was significantly reduced the later in the season a colonization occurred (Table 4). The proportion of parental beetles in southern Sweden that re-emerge and go on to produce a sister brood is unclear. Both laboratory studies (Anderbrant, 1988) and field studies (Bakke, 1983) have indicated that around 60% of beetles re-emerge, but in calculations based on the number of attacked trees and estimated re-emergence in a south Norway forest, Anderbrant (1989) showed that only one third of the beetles actually produced a second brood. In the southern Alps the long summers allow the beetles to re-emerge several times and produce more than one sister brood (Faccoli and Stergulc, 2004), and in the Czech Republic, the proportion of beetles re-emerging at least once was 91%, while 38% were reported to re-emerge a second time (Martinek, 1956).

We found some evidence that several sister broods were produced during the study period. In trees colonized later in the season there was increased parental mortality (Table 4) and increased time before parental beetles re-emerged (Fig. 4). As a large proportion of these late colonizing beetles were probably flying for a second or third time, it is likely that increased mortality was due to their energy supplies becoming exhausted after repeated oviposition. Shorter day length can induce diapause to prevent untimely emergence of beetles (Doležal and Sehnal, 2007b). However, filial beetles emerged at the same thermal sum regardless of when the tree was colonized and the brood was initated. Many of the parental beetles colonizing logs in early June were doing so to produce a first sister brood, and they started to re-emerge at the beginning of July (Fig. 2). The considerable flight activity recorded at this time indicates a substantial number of parental beetles flying to establish a second sister brood (i.e. third brood overall).

Conclusions

Considerable flight activity of *I. typographus* in July, almost complete re-emergence of parental beetles from trees colonized during spring flight, and newly emerged beetles that fly in early July indicate that sister broods and at least partially developed second generation broods are frequent. The occurrence of sister broods may, under current climatic conditions with limited bivoltinism, be one of the most important factors for the propagation of *I. typographus* in southern Sweden.

The thermal sum thresholds and correlations found in our study can be used, in conjunction with information on colonization dates, to predict roughly (1) when parental beetles and filial beetles will start to emerge, (2) the proportion of beetles that will re-emerge, and (3) the extent of mortality by the end of the season. This information should be useful for pest management purposes since it allow timely removal of colonized trees prior to sister brood and new generation flights. The results should also be useful to parameterize simulation models of the propagation potential for *I. typographus* in a warmer climate.

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Table 1. Dates when trees were felled and stem sections placed in emergence bags at different locations in southern Sweden from 2008-2010. In all years stems were removed from the emergence bags for examination at the end of the season (Oct-Dec).

			2008		2009		2010	
Location	Felling	Cohort	Felled	Bagged	Felled	Bagged	Felled	Bagged
Asa	1st	May	winter	20 May	14 Mar	8 May	11 Mar	1 Jun
	2nd	June	30 May	25 Jun	28 May	29 Jun	28 May	29 Jun
	3rd	July	1 Jul	*	29 Jun	30 Jul	8 Jul	27 Jul
Tönnersjöheden	1st	May	winter	20 May	winter	12 May	23 Apr	1 Jun
	2nd	June	4 Jun	25 Jun	25 May	*	1 Jun	23 Jun
	3rd	July	1 Jul	30 Jul	23 Jun	7 Jul	*	27 Jul
Remningstorp	1st	May	14 Apr	19 May	6 Apr	11 May	6 Apr	2 Jun
	2nd	June	2 Jun	16 Jun	1 Jun	29 Jun	3 Jun	21 Jun
	3rd	July	27 Jun	4 Aug	29 Jun	27 Jul	12 Jul	2 Aug
Gammalstorp	1st	May	21 Apr	21 May	27 Apr	11 May	*	*
	2nd	June	5 Jun	12 Jul	26 May	13 Jul	*	*
	3rd	July	12 Jul	*	13 Jul	27 Jul	*	*

* Data missing

Table 2. The recorded dates and thermal sums (dd > 5°C) at flight initiation at the four locations in 2006–2010. Flight was considered to have started when the weekly pheromone trap catch consisted of more than 10 beetles. The start date of first trap catch was considered to be the first day, during that week, when the maximum temperature exceeded 16°C. The onset of colonization was considered to occur when the first mother galleries could be observed.

		First pheromone trap catch		Onset of colonization of cut trees	
Location	Year	Date	Thermal sum	Date	Thermal sum
Asa	2006	4 May	32	*	*
	2007	13 Apr	34	*	*
	2008	21 Apr	10	28 Apr	33
	2009	23 Apr	35	28 Apr	65
	2010	19 May	91	20 May	103
Tönnersjöheden	2006	3 May	36	*	*
	2007	13 Apr	62	*	*
	2008	23 Apr	28	28 Apr	55
	2009	10 Apr	19	28 Apr	103
	2010	14 May	68	20 May	113
Gammalstorp**	2008	25 Apr	38	28 Apr	55
	2009	24 Apr	53	27 Apr	71
	2010	18 May	101	20 May	125
Remningstorp**	2008	23 Apr	26	28 Apr	58
	2009	23 Apr	59	27 Apr	92
	2010	7 May***	52	19 May	108
Average (Julian day number)		27 Apr (118)	47	5 May	82
	st dev	12	24	10	28

*Data missing

**Data missing 2006-2007.

***First beetles were trapped at 13°C.

Table 3. The recorded dates and thermal sums (dd > 5°C) at the start, when 50% of the parental beetles had re-emerged, and when the filial beetles had emerged from stem sections (May cohort) that were colonized during the first swarming in spring and then put into emergence bags (cf Table 2 for a definition of start date).

		Re-emergence of parental beetles				Emergence of filial beetles			
Location	Year	Date		Thermal sum		Date		Thermal sum	
		Start	50%	Start	50%	Start	50%	Start	50%
Asa	2008	17 May	31 May	130	201	25 June	27 July	436	766
	2009	8 May	26 May	43	127	25 June	9 Aug	360	870
	2010	2 June	24 June	95	256	7 July	29 July	427	721
Tönnersjöheden	2008	22 May	29 May	148	207	9 July	24 Oct	616	1482
	2009	14 May	31 May	83	197	1 July	28 Aug	489	1154
	2010	21 June	29 June	218	291	1 July	< 50%	318	1315*
Gammalstorp	2008	**	17 June	**	394	19 June	18 July	407	711
	2009	12 May	23 May	78	148	30 June	19 July	489	726
	2010	**	**	**	**	**	**	**	**
Remningstorp	2008	22 May	10 June	157	382	1 July	19 Aug	553	1126
	2009	19 May	28 June	111	442	7 July	15 Aug	573	1010
	2010	31 May	17 June	91	176	22 June	< 50%	278	1333*
Date (Julian day number)/ Thermal sum from colonization	Average	23 May (143)	10 June (161)	115	256	29 June (180)	20 Aug (232)	449	1019
	st dev	13	14	46	107	6	N/A	107	280
Thermal .sum from 1 Jan	Average	N/A	N/A	195	334	N/A	N/A	527	1115
	st dev	N/A	N/A	58	110	N/A	N/A	100	294

* The thermal sum at the end of the season was used since less than 50% of the beetles had emerged by the end of the season. This was done in order to not obtain an underestimated average value.

** Data missing

Table 4. Percentage emergence and mortality of parental and filial beetles (mean ± st dev) from emergence logs in Asa, Tönnersjöheden, Remningstorp (2008–2010) and Gammalstorp (2008–2009).

	May (n=11)	June (n=10)	July (n=10)	*Kruskal-Wallis* H	*Kruskal-Wallis* P
Parental - re-emerged	94.8 ± 9.7^{a}	57.9 ± 33.3^{b}	20.1 ± 21.5^{b}	18.9	<0.001
Parental - alive under bark	2.7 ± 8.8^{a}	3.8 ± 12.1^{a}	20.4 ± 21.2^{b}	9.2	0.01
Parental - dead under bark	2.6 ± 3.9^{a}	38.3 ± 31.5^{b}	59.6 ± 22.6^{c}	18.4	<0.001
Total number of trapped parental beetles	6130	1556	1269		
Filial - emerged	75.3 ± 26.8^{a}	46.4 ± 27.9^{ab}	14.7 ± 11.5^{b}	16.6	<0.001
Filial -alive under bark	21.6 ± 2.9^{a}	44.7 ± 29.0^{ab}	63.9 ± 31.9^{b}	8.3	0.016
Filial - dead under bark	3.1 ± 4.2^{a}	8.9 ± 8.5^{b}	21.5 ± 28.0^{c}	8.8	0.012
Total number of trapped filial beetles	24925	15121	6046		

Means followed by a different superscript letter within a row are significantly different ($\alpha = 0.05$)

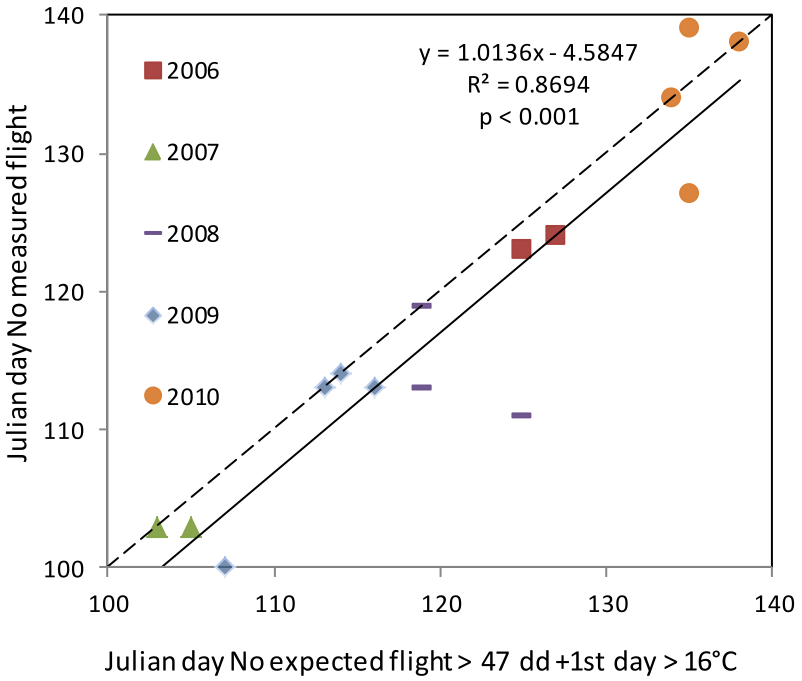

Figure 1. Correlation between Julian day number of measured first flight of *Ips typographus* in spring and Julian day number of expected first flight according to average thermal sum and the first day with temperature exceeding 16°C (solid line) recorded 2006–2010 in Asa and Tönnersjöheden and 2008–2010 in Gammalstorp and Remningstorp (n=16) (cf table 2 for a definition of start date). Dashed line shows 1:1 ratio.

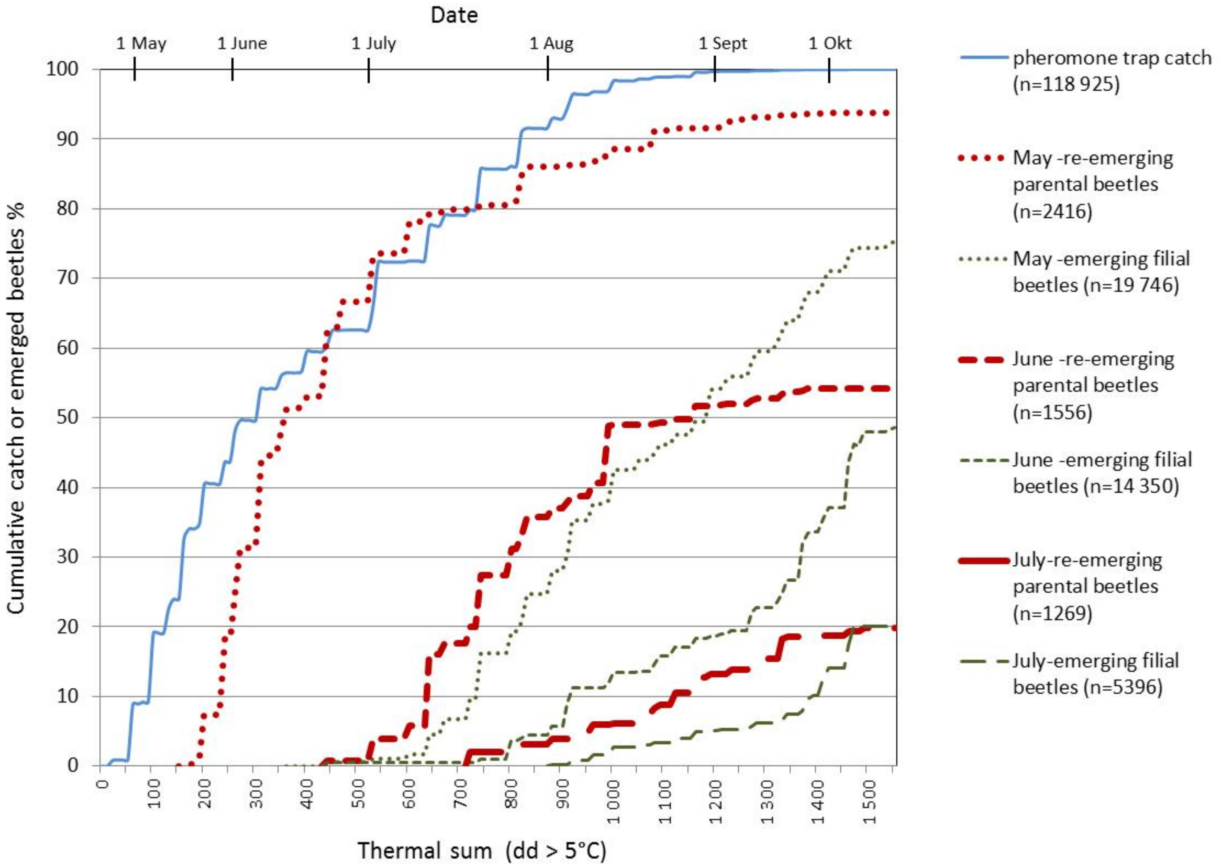

Figure 2. Cumulative catch from pheromone traps and from all emergence logs in relation to thermal sum accumulated from 1 January (lower x-axis). Also an estimation of approximately when these thermal sums occur is provided (upper x-axis) in Asa, Tönnersjöheden, Remningstorp (2008-2010) and Gammalstorp (2008-2009). Numbers (n) in the legend represent the total number of trapped or emerged beetles.

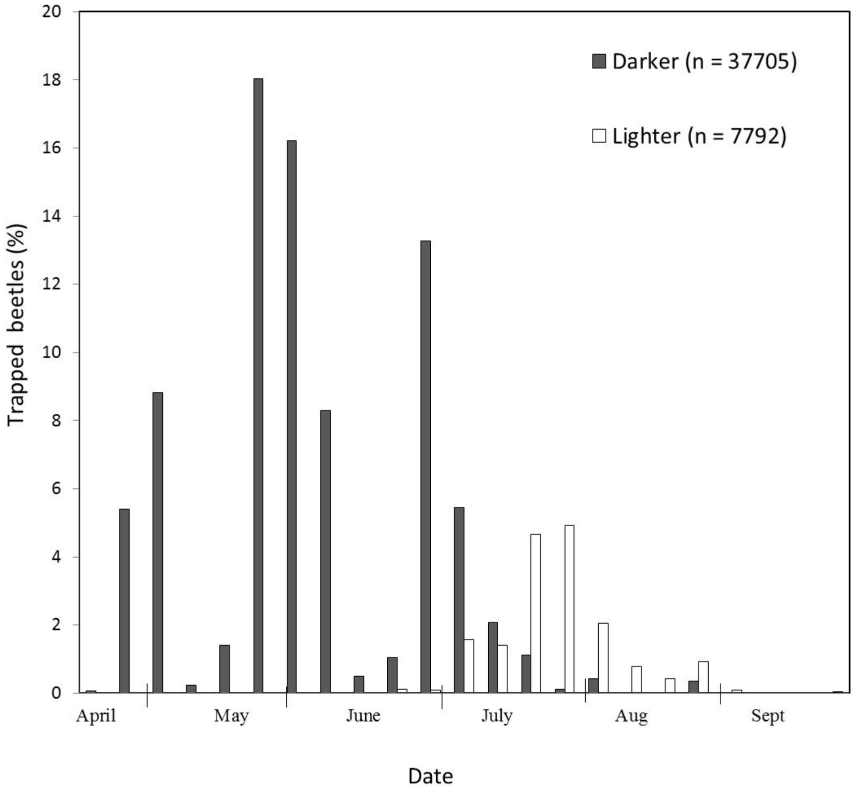

Figure 3. Frequency of recently emerged beetles during the season expressed as the average percentage of beetles cought weekly in pheromone traps categorized according to elytral colour (darker and lighter) in Tönnersjöheden, Remningstorp and Gammalstorp (2009 - 2010). Numbers (n) in the legend represent the total number of trapped beetles.

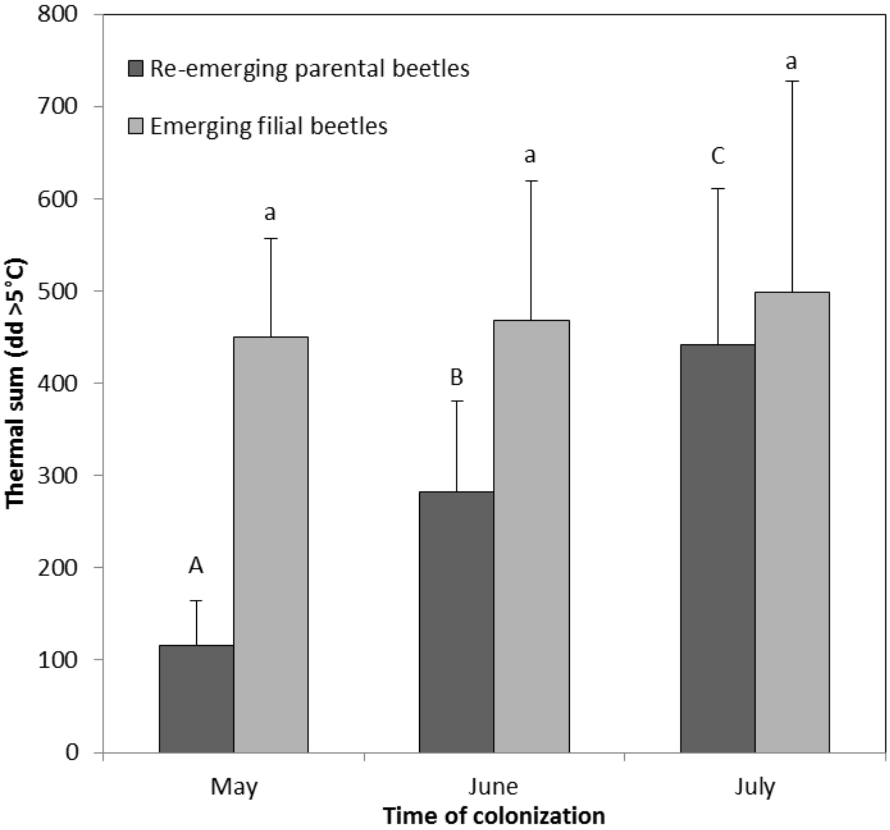

Figure 4. The start of parental beetle re-emergence (F = 19,25; $p < 0.001$) and filial beetle emergence (F = 0.22; p = 0.807) expressed as the thermal sum > 5 °C accumulated since colonization of the tree (mean ± st dev) for different cohorts (month) in Asa, Tönnersjöheden, Remningstorp (2008–2010) and Gammalstorp (2008–2009). Cohorts with different letters are significantly different (α = 0.05).

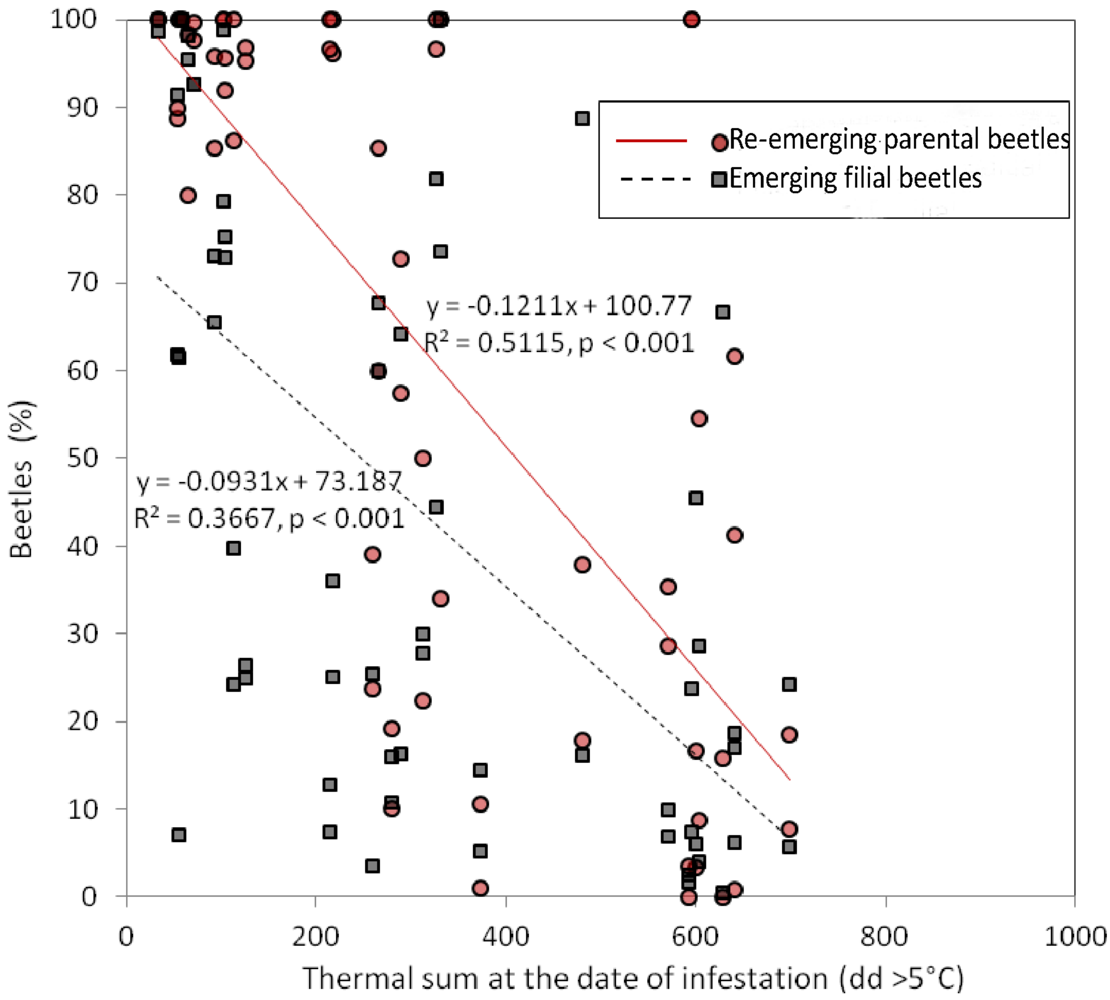

Figure 5. Correlation between the thermal sum at colonization and the percentage of re-emerged parental (solid line) and emerged filial (dotted line) *Ips typographus* collected from emergence bags at the end of the season in Asa, Tönnersjöheden, Remningstorp (2008–2010) and Gammalstorp (2008–2009) (n = 61).