Seasonal flight patterns of the Spruce Bark Beetle (*Ips typographus*) in Sweden

-Phenology, Voltinism and Development

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Cover: Bark piece with maternal galleries of the Spruce bark beetle
(photo: Petter Öhrn)

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Abstract

The major bark beetle threat to Norway spruce (*Picea abies* (L.) Karst.) in Eurasia is the spruce bark beetle *Ips typographus*. Beetles cause damage after population build-up in defenseless trees. To minimize attacks, timely removal of these trees is important. This is practiced by clearing of wind throws and sanitation felling. Thus, knowledge about the region-specific flight pattern and voltinism of *I. typographus* is necessary for efficient pest management.

This thesis focuses on the flight initiation and the variation in flight pattern of *I. typographus* over the season, which we have studied using pheromone traps during a seven year period in Sweden. Additionally, logs, that became colonized, were used to determine thermal sums required for the re-emergence of parental beetles and the emergence of filial beetles in southern Sweden.

Swarming began in the end of April (51 degree-days (dd) >5°C; daytime temp. >18°C). More than 50% of the flight activity occurred after mid-June and it continued until mid-August. That is a longer flight period than has been recorded previously. At least partly, this discrepancy with previous observations may be explained by our results that the temperature requirement for flight commencement is fulfilled more than two weeks earlier now than 30 years ago.

Re-emergence of parental beetles from the first brood started in the end of May (122 dd >5°C). A much higher proportion of parental beetles had re-emerged from trees colonized in May (95%) compared to in June (60%) or July (20%). This verifies that sister broods is an important part of the beetles' reproductive biology. The high proportion of beetles that re-emerged together with a significant continued beetle flight and oviposition showed that a high proportion of the beetles initate at least one sister brood.

Filial beetles began to emerge in the end of June (437 dd >5°C) and were caught in flight traps in early July and at least a partial second generation was started in each year. A much higher proportion of filial beetles had emerged from trees colonized in May (75%) than in June (50%) and July (15%).

We have shown that the temperature requirement for flight initiation are met earlier in the present climate which gives more time for the development of several sister broods and a potential second generation. This together with an expected increase in severe storm fellings indicates that the need for efficient pest management will increase with time. Timely removal of wind-felled trees is the main pest management option and in this thesis I present results of when the critical time periods occurs.

Keywords: callow adults, climate change. Day-degrees, flight activity, pest management, phenology, re-emergence, second generation , spruce bark beetle

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Granbarkborrens flygaktivitet i Sverige– huvudsvärmning, syskonkullar och ny generation

Granbarkborren är en av våra värsta skadegörare på levande skog. På den europeiska kontinenten har den dödat mer än 30 miljoner m^3 av gran efter flera omfattande stormfällningar under 1990-talet. Under det senaste utbrottet i Sverige dödades mer än 3,5 miljoner m^3 gran (2006-2010). Utbrottet utlöstes av stormen Gudrun som i januari 2005 blåste ner närmare 75 miljoner m^3 skog. Stormen som var den värsta i modern tid kvarlämnade stora mängder vindfällen och brutna träd. Det krävdes omfattande insatser för att förhindra förluster i virkesvärde och minska risken för skador orsakade av granbarkborrar.

För att effektivt kunna förebygga och bekämpa skador av granbarkborrar krävs kunskap om vilka regionspecifika temperatursummor som fordras för svärmning och uppkomst av en ny generation. Granbarkborren börjar svärma på våren. Enligt mina resultat sker detta efter en uppvärmningsperiod på 50 daggrader (dd) > 5°C och när dagstemperaturen når över 18°C. Under svärmningen flyger baggarna på jakt efter lämpligt yngelmaterial såsom vindfällen eller stående granar med nedsatt försvar. Mer än 50 % av svärmningen i södra Sverige ägde rum efter mitten av juni och den pågick en bra bit in i augusti, vilket är längre än vad man tidigare har trott.

De senaste 30 åren har första dag med temperaturförhållanden lämpliga för granbarkborrens svärmning tidigarelagts ca två veckor i Sverige, vilket innebär svärmning i slutet av april istället för mitten av maj i södra Sverige.

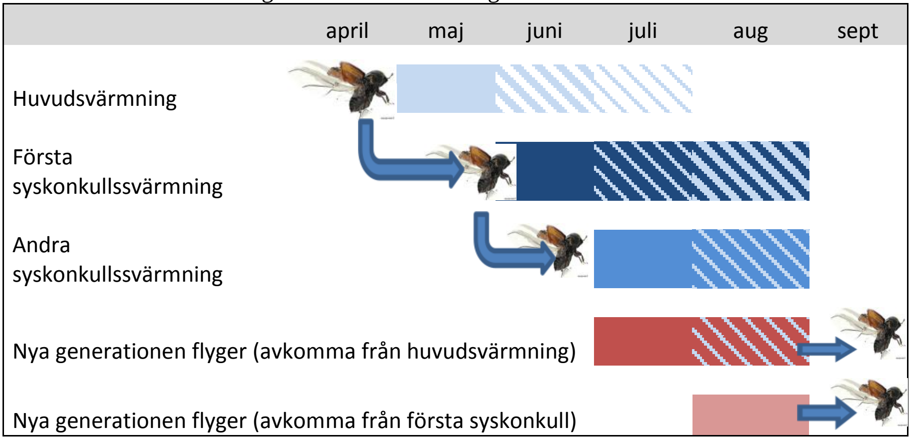
Efter parning och äggläggning lämnar föräldradjuren värdträdet för att svärma en andra gång och anlägga en eller flera syskonkullar. Den första syskonkullssvärmningen skedde i slutet av maj vid en temperatursumma av 122 dd > 5°C, knappt en månad efter första svärmning i södra Sverige (se figur). Andelen föräldradjur som hann lämna träden innan säsongens slut var lägre i träd som angripits senare på säsongen. I stort sett alla föräldradjur lämnade träden som angrips vid första svärmningen i maj. I sena angrepp som skedde i början av juli lämnade endast en femtedel av föräldradjuren träden. Dessutom, i de värdträd som angripits sent lämnade föräldradjuren träden vid en anmärkningsvärt högre temperatursumma (400 dd > 5 °C).

Den nya generationen baggar började lämna sina värdträd redan i slutet av juni, ca två månader efter första svärmning (se figur), vid en temperatursumma av 437 dd > 5°C. Vid slutet av säsongen hade en högre andel av den nya generationen lämnat träd som angripits vid den första svärmningen i maj (75 %) i jämförelse med träd angripna i början av juli (15 %).

Den höga andelen föräldradjur som lämnar sina värdträd och en omfattande flygaktivitet i juli som inkluderade ljusfärgade baggar från den nya generationen, visar att syskonkullar och en påbörjad andra generation är vanligt förekommande, även under rådande klimat i södra Sverige.

Med vetskapen om när angreppen av granbarkborrarna skett och med hjälp av ovan nämnda temperatursummor är det möjligt att förutsäga ungefär när och hur stor andel av föräldradjuren som går ut för att anlägga en syskonkull och när och hur stor andel av den nya generationen som lämnat värdträdet. Detta är viktigt för skogsbrukaren att veta, för att i rätt tid innan syskonkull och den nya generationen kryper ut, kunna forsla bort angripet virke och oskadliggöra barkborrarna.

Granbarkborrens svärmningsmönster i södra Sverige.



Dedication

Till Elis och Alvilda

Om man väntar på något gott så är det bara härligt!
Fredrik Lindström alias ”HD-knuttewannabe”

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Öhrn, P., Björklund, N., Lindelöw, Å. and Långström, B. 'Seasonal flight patterns and thermal sums required for swarming and emergence of *Ips typographus* in southern Sweden' (submitted)

II. Öhrn, P., Björklund, N., Lindelöw, Å. and Långström, B. 'Earlier spring flight of two bark beetles (*Tomicus piniperda* and *Ips typographus*) in Sweden' (manusscript)

Not included in this thesis:

Öhrn, P., Lindelöw, Å. and Långström, B. (2012) 'Flight activity of the ambrosia beetles *Trypodendron laaeve* and *Trypodendron lineatum* in relation to temperature in southern Sweden', in Delb, H. and Pontuali, S., eds., *Biotic risks and climate change, 10th IUFRO Workshop of WP 7.03.10 "Methodology of Forest Insect and Disease Survey in Central Europe"*, Freiburg, Germany, September 20-23, 2010, Fakultät für Forst- und Umweltwissenschaften der Albert-Ludwigs-Universität Freiburg, Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg, 86-90.

Långström, B., Lindelöw, Å., Schroeder, M., Björklund, N. and Öhrn, P. (2009) 'The spruce bark beetle outbreak in Sweden following the January-storms in 2005 and 2007', in Kunca, A. and Zubrik, M., eds., *Insects and Fungi in Storm Areas, Methodology of Forest Insect and Disease Survey in Central Europe, workshop of IUFRO Working Party 7.03.10*, Štrbské Pleso, Slovakia, September 15 to 19, 2008, p.13-19.

Persson, Y., Vasaitis, R., Långström, B., Öhrn, P., Ihrmark, K. and Stenlid, J. (2009) 'Fungi vectored by the bark beetle *Ips typographus* following hibernation under the bark of standing trees and in the forest litter', *Microbial ecology*, 58(3), 651-659.

Öhrn, P., Klingenberg, M., Hopkins, G. and Björklund, N. (2008) 'Two non-destructive techniques for sex determination of live adult *Hylobius warreni*', *The Canadian Entomologist*, 140, 617-620.

The contribution of Petter Öhrn to the papers included in this thesis was as follows:

I Main author, field and lab work, and analysis. Idea and design together with Bo Långström.

II Main author and analyses. Idea and design together with Bo Långström.

Introduction

Tree-killing bark beetles

Around 6000 species of bark beetles (Coleoptera; Scolytinae) are described, but only a few species are sometimes able to kill healthy trees (Raffa et al. 2008). Among these are *Dendroctonus* species in North America and especially Mountain pine beetle *Dendroctonus ponderosae* is a big threat to the forestry (Amman 1977). In Europe, the spruce bark beetle *Ips typographus* is the most economically important forest pest (Christiansen and Bakke 1988). Nevertheless, in absence of human exploitation bark beetles participate in the decomposition of dead wood material and thus be a part of the nutrient cycling and long term productive capacity of the ecosystem and a regeneration of climax forest (Christiansen et al. 1987).

Tree killing bark beetles are characterized by their use of chemical communication, involving aggregation pheromones, and by their association with blue stain fungi which participate in exhausting the defense of the host tree (Christiansen et al. 1987, Raffa and Berryman 1983). Both aggregation and anti- aggregation pheromones have been identified. In *I. typographus* and other *Ips* species, but unlike *Dendroctonus* bark beetles, males are the major producers of pheromones (Christiansen and Bakke 1988). After releasing attracting aggregation pheromones when females entered the gallery anti-aggregation pheromones are released and they seem to regulate attack density and shift the attack to neighboring bark surface or tree (Christiansen and Bakke 1988).

Secondly all these species are associated with virulent fungi (Paine et al. 1997). *I. typographus* carry at least four species of blue-stain fungi of the genus *Ophiostoma*, *Grossmania and Ceratocytis* of which *C. polonica* is able to kill healthy trees (Christiansen and Bakke 1988, Persson et al. 2009). The fungi are inoculated by the beetle to the phloem and may help in strangling the water transport in the xylem (Paine et al. 1997). The importance of the fungi for the actual “tree-killing” are however under debate (Six and Wingfield 2011).

The third characteristic for the aggressive bark beetle species is a high resistance to high resin flow and other chemical tree defense reactions (Christiansen and Bakke 1988).

Biology and ecological relevance of the spruce bark beetle

The spruce bark beetle (*Ips typographus)* is one of the most destructive pests to spruce forest in Europe and Asia (Christiansen and Bakke 1988). *I. typographus* starts to fly in the spring have experienced a thermal sum high enough for ovarian development to be completed (Doležal and Sehnal 2007b). The beetles disperse in the forest in search for suitable breeding material. Under endemic (non-outbreak) low population levels they breed underneath the bark of newly dead or dying Norway spruce trees *Picea abies* and unbarked timber, starting decomposition of wood and bark. The male initiates gallery construction by excavating a nuptial chamber in the phloem, whilst doing this the male also emits aggregation pheromones attracting conspecifics of both sexes to the site (Christiansen and Bakke 1988). The male attracts 1- 4 females to create the polygamous gallery system. After mating each female lay their eggs in niches along their gallery (Bombosch 1954). Thereafter, the parental beetles may leave their first brood to initiate one or several sister broods. After more than three weeks time the parental beetles leave their first brood to initiate a sister brood on a different tree. Hatched larvae feed under the bark and then pupate. When beetles of the first brood, i.e. the filial beetles, are fully developed they may emerge and initiate a second generation, or hibernate, depending on the thermal conditions and the photoperiod (Doležal and Sehnal 2007a). Beetles in central Europe are primarily bivoltine whereas in northern Europe beetles are primarily univoltine and they (Anderbrant 1989, Christiansen and Bakke 1988). An Outbreak (epidemics) of *I. typographus* shows a drastic change in population levels when the beetle is able to colonize and kill growing trees. Outbreaks are frequently either initiated by storm felling (abundance of defenseless breeding substrate) or triggered by drought (weakened host) or a combination of both.

Pest management of the spruce bark beetle

Outbreaks of *I. typographus* have lead to millions of killed Norway spruce trees and to large economic losses due to salvage logging and reduced quality of the wood as resource for timber or pulp production. In the 1990s, ca 30 million m^3 of spruce was killed by the spruce bark beetle following several severe storm-fellings in Central Europe (Grégoire and Evans 2004). In Sweden, ca 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 has killed 3.5 million m^3 (2006-2010) (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). Methods used to minimize attacks on healthy spruce trees are sanitation felling of colonized trees, clearing of wind throws or use of pheromone traps. Hence, efficient pest management to reduce bark beetle populations relies on well-timed removal of host trees with reduced defense capacity, e.g. wind felled trees (Christiansen et al. 1987, Christiansen and Bakke 1988). This requires good knowledge of the regional population specific requirements for seasonal flight patterns and its temperature dependent development. The most recent outbreak in southern Sweden has raised a need for such knowledge. In addition, increased mean temperatures and frequency of storms and drought is likely to increase in the future (Cubasch et al. 2001), which will increase the risk for bark beetle outbreaks (Schlyter et al. 2006).

Thesis aim

The main aim of this study was to better understand the regional population specific requirements for seasonal flight patterns of *I. typographus* and its temperature dependent development. Specifically I addressed the following questions:

1. How can flight pattern and voltinism of the spruce bark beetle *I. typographus* be better described in southern Sweden (Paper I)?
2. What are the thermal sums that may predict important life history events like the start of the spring flight, re-emergence of parental beetles, and the development time of the new generation of *I. typographus* in southern Sweden (Paper I)?
3. Have the first possible date for flight commencement of *Ips typographus* changed over time and is there a corresponding change in documented flight observations (Paper II)?

Methods

A more detailed description of material and methods used can be found in the two papers enclosed in the thesis.

Study sites

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 stations are located in the area that was affected by the *I. typographus* outbreak that followed the storms of 2005 and 2007 (Anon. 2006, Långström et al. 2009, Bergqvist 2009) (Paper I).

Flight commencement of *I. typographus* was studied in 2005-2011, in Asa and Tönnersjöheden in the southern parts of Sweden, Siljansfors (60°53 N, 14°23 E) in the middle of Sweden, and Svartberget (64°16 N, 19°47 E) in the northern part (Paper II).

Temperature data

Air temperature data (daily mean and max temperature) was obtained from the research stations in Asa and Tönnersjöheden (Paper I and II). In Remningstorp and Gammalstorp temperature data came from SMHI (Swedish Meteorological and Hydrological Institute) (Paper I).

In Asa and Svartberget temperature data is lacking from the 1970s, thus, air temperature data from this decade was obtained from nearby SMHI–stations in Växjö and Umeå, respectively (Paper II).

Seasonal flight patterns and thermal requirements for spring flight (Paper I and II)

The flight activity of *I. typographus* was monitored using two traps baited with pheromone (Ipslure®) at each location. Traps were emptied weekly from the mid-April through September. Trap catches were stored in freezer (-18°C) before quantification in laboratory. The number of beetles' caught was determined either by direct counting or measured by volume (100 ml corresponding to 4000 individuals).

Thermal sums for re-emergence of parental beetles and emergence of filial beetles (Paper I)

The thermal sums for parental- and filial beetle emergence were calculated using the 5°C threshold, since it's the common temperature to calculate threshold for vegetation period and consequently easy to obtain for the forest practice. Thermal sums expressed as degrees-days (dd) was calculated by accumulating the daily mean temperature above a certain threshold (e.g. 10°C daily mean temp. will add 5 dd above a 5°C threshold).

Development and mortality (Paper I)

At all four locations two Norway spruce trees (*Picea abies* L. Karst.) were cut before the first swarming of *I. typographus* in 2008, 2009, and 2010 (Table 1). All trees were baited with pheromone to ensure beetle colonization. Each trunk was inspected weekly for entrance holes created by *I. typographus*. When no more new entrance holes were seen, despite good flight weather, a trunk was considered as fully colonized and a 70 cm stem section from it were suspended in an emergence bag fitted with a collection bottle, in a nearby shaded position. Emerging beetles were collected weekly, counted and categorized, according to elytra colour (Merker and Wild 1954), into parental beetles (darker) or filial beetles (brighter).

In order to follow the seasonal progress of beetle attacks and to evaluate whether the thermal sums necessary for complete development differed depending on when during the season the host tree was colonized, the procedure described above was repeated at the beginning of June and July

(Table 1). In June, stem sections would have been colonized not only by parental beetles swarming late for the first time, but also by re-emerging parental beetles (swarming for the second time). In July some of the late-flying, re-emerging parental beetles and the new (first) generation emerging beetles should infest trees. The beetles from trees felled on different dates can thus be considered to represent different cohorts, and are referred to as such (e.g. May cohort) hereafter. At the end of the season, each stem was removed from the emergence bag and analysed to determine beetle attacks, i.e. exit holes, mother galleries, and adult live and dead beetles were counted.

Results and discussion

Seasonal flight patterns (Paper I)

Our study showed that *I. typographus* usually has a long period of flight activity, starting in mid-April and lasting into September (Fig 1), 10% of the flight activity, during the studied years occurred before 1 May and 50 % after 1 June (Fig 1). The common knowledge for Sweden has been that flight period starts in mid May and lasts until the beginning of July (Eidmann and Klingström 1990, Trägårdh 1939). The extended flight period described here is more in line with Danish (Harding and Ravn 1985) and Central European (Baier et al. 2007, Faccoli and Stergulc 2004) findings. Flight activity between early May and mid-August is the common in Denmark (Harding and Ravn 1985). In central Europe the flight period is even longer occurring between April and September (Faccoli and Stergulc 2004).

We also found that the flight period consists of the main spring flight followed by one or several sister brood flights. In addition, a second generation is initiated every year. However, a completed second generation is a rare phenomenon.

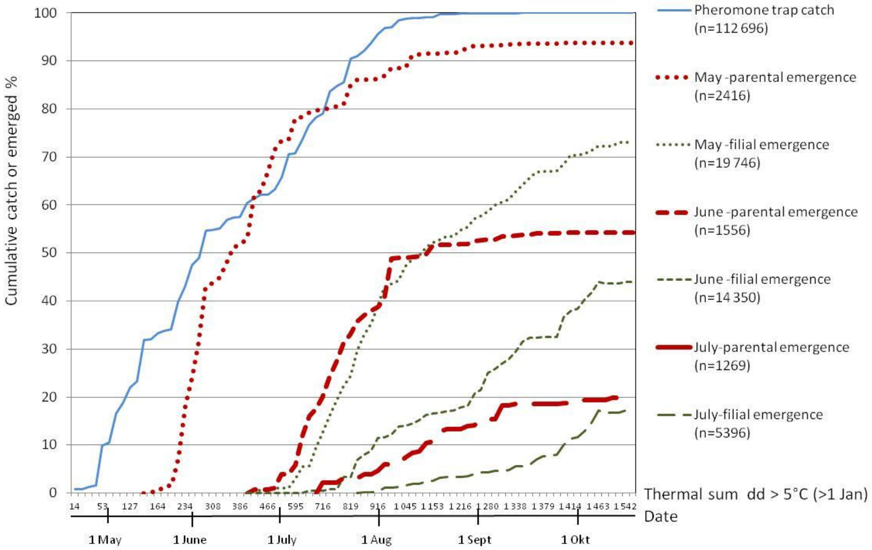


Figure 1. Cumulative catch from pheromone traps and from all emergence logs in relation to thermal sum in Asa, Tönnersjöheden, Remningstorp (2008-2010) and Gammalstorp (2008-2009). Numbers (n) in the legend represent the total number of trapped or emerged beetles.

Thermal requirements for spring flight (Paper I & II)

The initiation of spring flight of *I. typographus* started when the accumulated thermal sum had reached an average of around 50 dd > 5°C (Fig. 1), which is more close to what has been reported from Denmark (Harding and Ravn 1983) and southern Finland (Annila 1969), than lowland Austria (Baier et al. 2007).

It is generally believed that the first flight in spring occurs on the first day with a temperature exceeding 18-20°C. To find the best predictor for flight commencement (Paper I), different thermal factors were tested for their correspondence with the recorded first day of flight (Table 1). The tests showed that the first flight is more closely correlated with the first day with maximum temperature exceeding 18°C after the mean thermal sum at first flight have been exceeded (51 dd > 5°C), than only using a daily maximum temperature exceeding 18°C or 20°C. The predictive value of these correlations were further tested on flight data from locations in mid- and northern Sweden (Paper II), showing that the first day with temperatures exceeding 20°C may predict spring flight of *I. typographus* in southern Sweden but not in mid- and northern Sweden (Fig. 2a), first when adding day degrees (dd) to the function the regression lines shifts (Fig. 2b). This indicates that *I. typographus* must accumulate a certain thermal sum before flight initiation in spring (Annila 1969). This may be due to different conditions at overwintering sites; primarily in the soil in the northern Europe (Annila 1969) and primarily under the bark in central Europe (Faccoli 2002).

Table 1. Regression functions for the first day of recorded flight and expected flight date based on different thermal factors in Asa and Tönnersjöheden (2006–2010), Remningstorp (2008–2010) and Gammalstorp (2008–2009), (n=16).

y = first day of recorded flight (Julian Day No)	x = expected flight (Julian Day No) according to first day with:	y = f(x)	R^2	p -value
	>20°C	y = 41.4 + 0.629x	0.3717	0.012
	>18°C	y = 57.0 + 0.542x	0.4459	0.005
	>51 dd >5°C	y = - 17.4 + 1.15x	0.6472	<0.001
	>10 dd >8°C	y = 1.0491x - 4.917	0.6687	<0.001
	>51 dd >5°C and >18°C *	y = 1.0511x - 9.0913	0.8546	<0.001
	>10 dd >8°C and >18°C	y = 1.1314x -18.499	0.8931	<0.001

*Regression plot presented in figure 1 where the 5°C threshold was chosen since it is most commonly used elsewhere (e.g. in determining growing season).

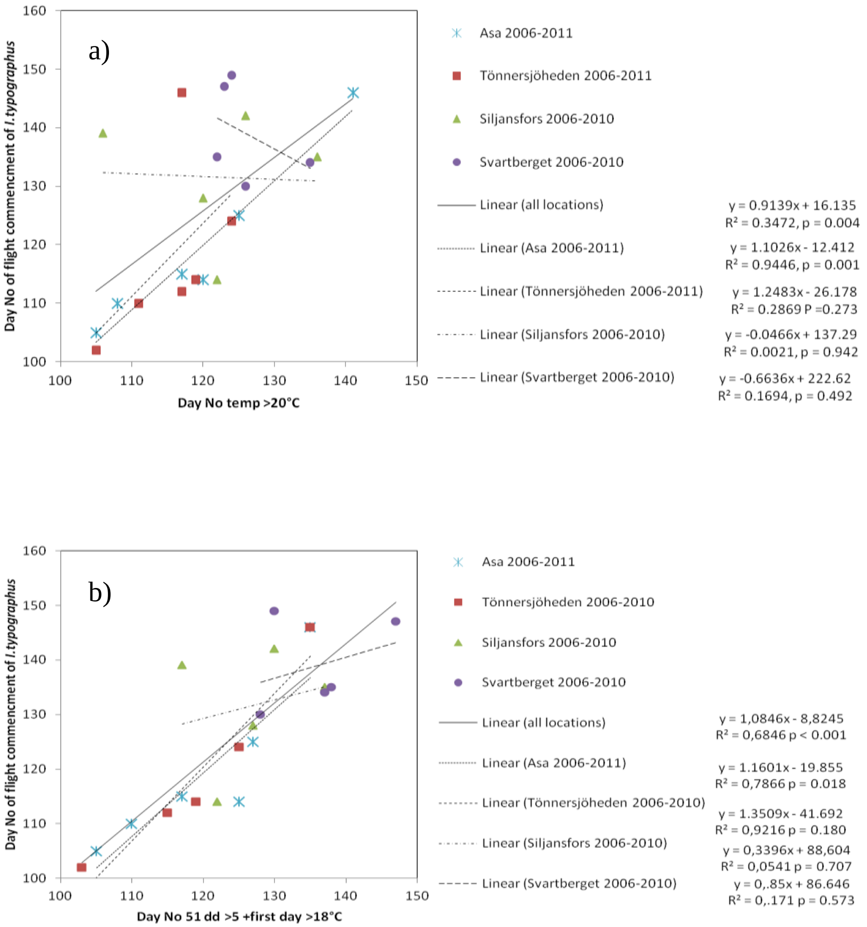


Figure 2. Correlation between Julian day number of recorded first flight of *I. typographus* and first day with daily maximum temperature exceeding 20°C (a) or first day with daily maximum temperature exceeding 18°C after a thermal sum of 51 dd > 5°C (b). The swarming was considered to have started when the weekly trap catch consisted of > 0.5% of the yearly trap catch. The start date was considered to be the first day, during that week, when the maximum temperature exceeded 18^{o}C, or if there were no such days, the day with highest maximum temperature during that week.

Records of daily maximum temperature (Paper II)

Our study (Paper II) showed that the flight commencement of *I. typographus* may start about two weeks earlier now than 30 years ago since the first flight of *I. typographus* is significantly correlated to the first day with maximum temperature exceeding 20°C (Fig. 2a) and due to increasing spring temperatures and earlier occurrence of first day with a daily maximum temperature suitable for flight (Fig. 4). The advancement of the first day with maximum temperature exceeding the critical 20°C is between 5 to 7 days per decade according to the slope of linear trends of the first day with temperatures exceeding 20°C (Fig. 4). This is consistent with quantitative analysis of phenological responses giving estimates of 5.1 days per decade for the subset of species showing substantive change (> 1 day per decade) (Root et al. 2003).

More specific, among bark beetles, Faccoli (2009) has shown a 20 day advancement of spring flight of *I. typographus* in the southeastern Alps during a 10 year period (1996-2005). Studies on bark beetle spring phenology are sparse; anyhow there is some evidence of changes in voltinism (Jönsson and Bärring 2010, Lange et al. 2006) and spread in latitude (Nilsson 1976) and altitude (Logan and Powell 2001). The general pattern supported by many studies on plant- and animal phenology is a strong evidence of onset of spring is starting earlier across the whole northern hemisphere (Wolkovich et al. 2012, Schwartz et al. 2006, Parmesan 2006).

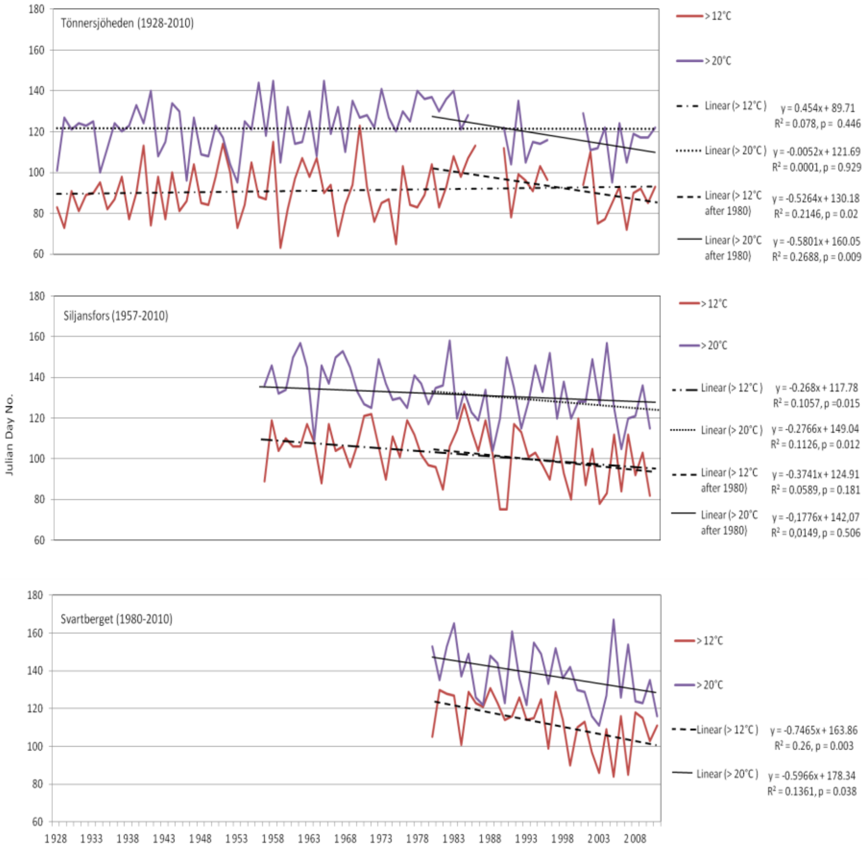


Figure 4. First day (Julian Day No.) with daily maximum temperature exceeding 12°C and 20°C and the linear trend since temperature measurements started and from 1980 in Tönnersjöheden, Siljansfors and Svartberget.

Thermal sums for re-emergence of parental beetles and emergence of filial beetles (Paper I)

The first re-emergence of parental beetles from the May cohort were observed on average on 24 May, approximately three weeks after the first brood was initiated (Fig. 1). This occurred at a thermal sum, accumulated from infestation, of 122 ± 46 dd > 5°C. After another seven weeks, on average on 10 June, 50% of the parental beetles had re-emerged, at a thermal sum of 256 ± 107 dd > 5°C. The first re-emergence of parental beetles in the current study was at a slightly lower thermal sum than reported in most previous studies. Laboratory results verified in the field in southern Norway estimated the temperature sum threshold to 168 dd > 7.5°C for mean re-emergence in exposed trees (Anderbrant 1986). Field studies in southern Finland suggested 150-200 dd > 5°C for re-emergence (Annila 1969). The required thermal sum reported from Austria is, however, much higher, 278 dd > 8.3°C for re-emergence of parental beetles (Baier et al. 2007).

The emergence of filial beetles (new generation) from the May cohort started, on average, on 29 June, approximately eight weeks after the brood was initiated (Fig. 1). This occurred at a thermal sum accumulated from infestation of 449 ± 104 dd > 5°C. After another three weeks, on average on 20 Aug, 50% of the filial beetles had emerged, at a thermal sum of 1019 ± 280 dd > 5°C.

A contributing factor to the variation in reported thermal sums for different phenological events of *I. typographus* could be due to a region-specific thermal requirement (Netherer and Pennerstorfer 2001). Which may be due to variation in selection pressures between geographical regions, and thus different cues may operate in different parts of the distribution area of *I. typographus* (Jönsson et al. 2011). Two different cues which may differ regionally is the lower threshold temperature for development and the thermal sum requirement of different developmental stages.

In addition, our results show an increasing delay in parental re-emergence in later infestations: the beetles in the July cohort required thermal sums almost twice as high before they emerged (Fig. 3). This may be due to ageing parental beetles associated with later infestation, as further discussed below.

A difference in lower temperature limit has been calculated for two populations in central Europe: the lower developmental threshold for *I. typographus* larvae of High Tatras, Slovakia (1200 m.a.s.l.) was 4°C but in Nasswald, Austria (750 m.a.s.l.) it was 7°C (Netherer and Pennerstorfer 2001). In Finland beetles showed some activity from 5°C (Annila 1969) and in Switzerland the lower threshold for total preimaginal development from egg to pupae was 8.3°C (Wermelinger and Seifert 1998). Supporting this hypothesis is the earlier flight (as already discussed) and following infestation in spring in southern Sweden compared to what has been reported from lowland Austria (Baier et al. 2007).

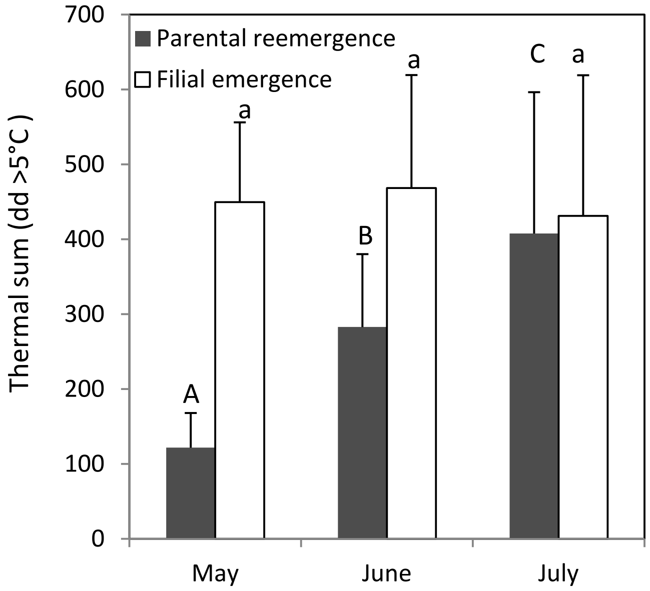


Figure 3. The start of parental beetle re-emergence (F = 17.37; $p < 0.001$) and filial beetle emergence (F = 0.15; p = 0.863) expressed as the thermal sum >5 °C accumulated since infestation of the tree (mean ± st dev) for different cohorts (month) in Asa, Tönnersjöheden, Remningstorp (2008–2010) and Gammalstorp (2008–2009). Cohorts with different letters are significantly different ($\alpha = 0.05$).

Shorter duration to complete egg stage, larval stage and preimaginal development has been found in populations of mountain areas in Slovakia compared to lowland Austria when bred under different constant temperatures (Netherer and Pennerstorfer 2001). The thermal sums for emergence of filial beetles (new generation) (449 dd > 5°C) of *I. typographus* in southern Sweden is in better agreement with the results from studies from the Nordic countries (Annila 1969, Harding and Ravn 1985) than central Europe (Baier et al. 2007). The first filial beetles in the current study (emerging from May cohort) were observed after 278 dd > 5°C (Fig 1). This is in rather good agreement with observations made in Finland (Annila 1969) and Denmark (Harding and Ravn 1985). The thermal sums reported from central Europe is much higher; 334 dd > 8°C for callow beetles to develop under bark and 557 dd for the complete development (including maturation feeding) (Baier et al. 2007, Wermelinger and Seifert 1998). Consequently, as earlier suggested by Netherer and Pennerstorfer (2001), regional variations in the development time of bark beetle populations may result from differences in voltinism or in specific lower developmental thresholds.

Development and mortality (Paper I)

More than 90% of the parental beetles re-emerged at least once from under bark before the end of the season (Fig. 1) but the potential for this to happen was significantly reduced the later in the season an infestation occurred (Table 2). It is not clear what proportion of the re-emerging parental beetles in southern Sweden does actually swarm for a second time and produces a sister brood. It has been reported that the proportion of re-emerging parental beetles is around 60% from both laboratory- (Anderbrant 1988) and field studies (Bakke 1983).

We found some evidence that several sister broods were produced during the study period. An increasing parental beetle mortality (Table 2) and a delayed parental re-emergence (Fig. 3) from trees colonized later in the season indicates that the trees studied were colonized with a large proportion of beetles that swarmed for a second or third time, and an increasing number of beetles that after repeated oviposition, exhausted their energy supplies and died. Parental beetles from logs colonized in early June, partly by the first sister brood, started to emerge at the beginning of July (Fig. 2). At this time the flight activity was considerable and consequently one can assume the existence of a second sister brood (third brood).

From trees colonized during the first swarming 75% of the filial beetles had left the trees at the end of the season (Table 2). In later infestations a decreasing proportion (~50% in June and ~15% in July) left the trees. The average of these values (45%) is in good agreement with earlier studies, which repoted that roughly 50 % of a population in southern Sweden (Komonen et al. 2011) and a univoltine population in Switzerland (Wermelinger et al. 2011) emerged to overwinter in soil. An explanation for the slightly higher proportion leaving the trees in our experiment could be due to faster drying of the wood and the phloem inside the emergence bag. The filial beetle mortality increased in latter infestations, nearly 30% in July - compared to less than 5% in May cohort. A possible explanation is that pathogens, such as viruses and microsporidia is more frequent in late emerging *I. typographus* than those that early (Wegensteiner et al. 2007). Another explanation may be, faster drying of wood and phloem due to higher temperatures during the peak of the summer in July.

Table 2. 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	June	July	*Kruskal-Wallis*	
	(n=11)	(n=10)	(n=10)	H	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
n_{total} parental	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
n_{total} filial	24925	15121	6046		

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

Voltinism (Paper I & II)

There was a large flight activity late in the season and newly emerged beetles occurred in July. This verifies the importance of sister brood flight and indicates a partial second generation flight. As for many other insect species, *I. typographus* voltinism depends both on thermal and photoperiodic thresholds and varies over latitude and altitude with regard to the number of days needed to complete development to the stage suitable for surviving hibernation (imago).

Confirmed records of bivoltinism in Fennoscandia are rare and the phenomenon has only been recorded under unusually warm summers. In Sweden, in the 1930s, initiations of a second generation was recorded (Butovitsch 1938, Trägårdh and Butovitsch 1935). A completed second generation has only been recorded in 1975 in southern Norway (Austarå et al. 1977), 2006 in southern Sweden (Långström et al. 2009) and 2010 in Finland (Pouttu and Annila 2010).

Since the yearly thermal sum during all studied years in southern Sweden was around 1500 dd > 5°C (data not shown), subtracting the thermal requirement for filial beetle emergence - 449 dd > 5°C, will give a thermal window of 1051 > dd 5°C allowing time for more than 40% of the new generation to produce a second generation where at least some beetles will be fully developed before winter (Fig. 2). This was further verified in 2010 by an additional non-planned felling that was undertaken on 5 August, after many filial beetles had emerged. In the tree more than 90% of the offspring had reached the adult stage and according to the number of exit holes more than 10% had already left the tree at the end of the season. No large peak in flight activity or any attacks on standing trees was recorded in late summer 2010 (Lindelöw 2010) in contrast to Finland, which experienced a second peak during the flight period and a fully developed second generation the same year (Pouttu and Annila 2010).

Nevertheless, there is still evidence that the thermal conditions in southern Sweden during all study years would have allowed the development of a second generation. This is in accordance with earlier occurrence of thermal conditions suitable for spring flight (Fig. 3). Since, increased temperatures in early spring allowing earlier flight could be more crucial for the bivoltinistic potential than increased temperatures during the end of the vegetation period due to limited day length, at least in the absence of evolutionary change in the responses to photoperiodic cues that mediate diapause induction. This has also been hypothesized for other insects, e.g. the grape berry moth *Paralobesia viteana* (Tobin et al. 2008).

In addition, it has been indicated that even with the current climate, a fully developed second generation can be expected in some years each decade (Jönsson et al. 2009). Hence, with global warming, the bivoltine potential will increase and we can expect a second generation of *I. typographus* to occur more frequently in Fennoscandia (Lange et al. 2006, Jönsson et al. 2009). A second generation gives rise to a higher potential population increase that must be taken into consideration when choosing pest management strategies.

Conclusion and implications for forest management

Almost complete re-emergence of parental *I. typographus* from trees colonized during first swarming and large flight activity in July shows that sister brood- and second generation flight occurs frequently. It has been suggested by Wermelinger and Seifert (1999) that in areas where beetles only produce one generation per year and experiencing possible fatal winter mortality of immature stages, sister broods is suggested to contribute substantially to the propagation of *I. typographus*. Anyhow this is probably already changing, since bivoltinism of *I. typographus* has been observed at even higher elevations (Baier et al. 2007) and a northward movement is predicted in the future (Lange et al. 2006).

To avoid population build-up of *I. typographus*, forest managers need to remove colonized trees prior to sister brood- and new generation flight and in case of a second generation flight forest managers may also need to search for newly attacked trees later in the season. For timely removal it is essential to know when trees were colonized with *I. typographus*, then it is possible to apply the presented thermal sums, to roughly predict when parental beetles and filial beetles start to emerge, how large proportions of beetles that will emerge, and how large the mortality will be in the end of the season. These results will also be useful to parameterize simulation models of *I. typographus* propagation potential in a warmer climate (Jönsson et al. 2007).

There is consensus in the scientific community that global warming already has an effect on our environment (Parmesan 2006). However, not all species respond to changes in environments experiencing warming trends, up to 70% of all species at a given location show no response at all, hence experiencing stable phenological patterns (Parmesan and Yohe 2003). Anyhow, insects are ectothermic organisms with their physiological processes showing a high degree of sensitivity to ambient temperature (Beck 1983). The major responses of climate change to insect are an earlier spring flight, enhanced winter survival, acceleration of development rate and more generations per season

(Robinet and Roques 2010, Jönsson et al. 2009). In accordance, this thesis shows that suitable conditions for flight commencement of *I. typographus* occur more than two weeks earlier now than 30 years ago and that a second generation is frequently initiated and occasionally completed in southern Sweden. However, if it's not warm enough the second generation will be unfinished and all immature stages (egg-larvae) will die during winter, having negative effects on the population growth rate(Wermelinger and Seifert 1999).

The first flight of *I. typographus* is best predicted using a thermal sum (50 dd >5°C) combined with a daily maximum temperature (>18°C). However, the first day with maximum temperatures exceeding 20°C is reasonable well correlated with the flight initiation in southern Sweden. Even though, the first day with maximum temperatures exceeding 20°C is sufficient enough to predict flight in southern Sweden. This latitudinal difference may be due to different conditions at overwintering sites, i.e. in the soil in the north and under the bark in the south. This further verifies the importance of knowledge of region-specific thermal requirements of *I. typographus.*

In the future, there are predictions of more stormy weather (Nilsson et al. 2004), and we may see even more damages such as large storm fellings that serves as breeding material for bark beetles. Thus, in a future warmer climate we may expect higher populations of *I. typographus* doing more damage. It seems to me as if the size of storm-fellings is more important than frequency of them since it is only after large storm- fellings that we don't have the capacity to take care of all the wind-thrown trees before they are colonized by the beetles. For a future climate, forest management does not only have to be planned and adapted for increased wind damage risks and more severe droughts but also, as a consequence of these changes, potentially higher population levels of tree-killing bark beetles species. Hopefully, the results presented in this thesis will be helpful for forest managers to deal with the threat of *I. typographus*.

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