

Flight initiation and survival in the bark beetle *Ips typographus* (Coleoptera: Scolytidae) during the spring dispersal

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Temperatures in the forest litter of Norway spruce *Picea abies* were recorded throughout the day to obtain environmental parameters that could be used to design realistic flight-activity experiments in the laboratory. Flight activity and survival were monitored electronically in plastic chambers where the conditions were controlled by an environmental chamber. Flight attempts of the bark beetle *Ips typographus* were initially lower in chambers with forest duff but were prolonged compared with those of beetles in chambers with a metal screen substrate. Small bark slabs and spruce twigs in the duff were utilized as food and extended the period of flight and survival. A thermal gradient in duff from 25° at the surface down to 13.8°C at a depth of 4 cm also slightly increased the survival of beetles compared with a constant 25°. A daily ambient temperature cycle as well as the duff thermal gradient increased the survival from about 3 d to more than 8 d. The latter length in the laboratory agreed with survival rates of caged beetles in a clearcut forest area, while beetles caged in the forest survival for more than 14 d. Temperatures were monitored at the duff surface of the caged beetles and compared with the catches of beetles that were attracted to a pheromone trap and collected with an electronic fraction collector. Information on flight and survival during the dispersal period is necessary to the design of ecologically sound management programs for control of bark beetles.

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Introduction

The spruce bark beetle *Ips typographus* is an important pest of Norway spruce throughout Scandinavia, Central Europe and across Russia to Japan. In Scandinavia, the life cycle of *I. typographus* begins in the spring with the colonization of the host-tree phloem by dispersing adults that have overwintered in the forest litter. Their larvae develop into callow adults by late summer. Usually both old and callow adults are induced to leave the brood tree by cold temperatures in the autumn. They crawl down to the forest litter or duff (also called moss layer) and burrow a few centimeters deep to where they are insulated, especially after the first snows, from the subzero winter. Annila (1969) found that the mortality during the winter for those adults hibernating in the duff was quite low (<7%) due to the average temperature of

duff with snow cover ($0\pm 1^\circ\text{C}$) and the beetles' cold hardiness (in December they froze at -24 to -32°C).

After leaving the brood tree, beetles in the duff starve as little or no food is available and temperatures are too cold for feeding (Merker 1957, Annila 1969). During the warming in early spring, a period of thermal-time for maturation is required, as influenced by hibernation time and conditions, which effectively synchronizes most of the population so they are ready for flight on the appropriate "swarming days" of spring (Annila 1969). According to Annila (1969), *I. typographus* leave their "hibernacula" as soon as the duff temperature rises above 7°C and "seek nearby objects which can serve as food, such as pieces of bark, branches, (and) scales of cones" shortly before swarming. However, it seems unlikely that such food sources are available to most overwintering beetles, and his observation has not

been substantiated by subsequent research (Lindelöw and Weslien 1986). Many previous studies seem to agree that *I. typographus* will take flight and disperse when the duff temperature (<10 cm) is at least 9 to 12°C and the air temperature rises above 20°C (cf. Annala 1969). Certainly other environmental parameters such as wind, humidity, and light intensity influence the degree of flight initiation on a particular day.

Once beetles take flight, our knowledge of their survival and flight activity during the dispersal and host-seeking period is limited (Forsse and Solbreck 1985). However, adult mortality is assumed to be at its greatest then, so it may be that treatment strategies using behavioral chemicals (pheromones and semiochemicals) could be designed to exploit this vulnerable period of the life history. In the present study, temperatures were electronically recorded in forest litter during the dispersal period so that flight activity experiments in the laboratory could be designed that either manipulated temperature in a realistic way or simulated natural conditions. The effects of duff, spruce parts as food, and temperature on the beetles' longevity and on their ability/willingness to initiate flight during extended periods were electronically monitored in flight activity chambers inside an environmentally controlled room. In order to gain a better understanding of the beetles' ecology during the critical dispersal period, observations were made in the forest on the survival of caged beetles over two weeks as well as the number attempting to fly at various times during the day as correlated with temperature. These observations were also correlated with 30-min collections of beetles attracted to pheromone throughout one day, or daily collections over the two week period.

Materials and methods

Forest litter temperatures during the spring dispersal

A four-probe electronic scanning thermometer (Byers 1984) was used to measure temperatures in Norway spruce *Picea abies* litter during the spring dispersal (swarming) period of *I. typographus*. The monitoring site was 2 m from the nearest tree on the outside of nearly pure spruce forest (50–70 yr old) about 15 km NNE of Skien, Norway. The integrated circuit probes (3×4×5 mm) were placed in the spruce needle duff at the depths shown in Figs 1A and B. The surface-probe rested on the needles and was exposed to the sun, but the air-probe (1 m height) was shielded with aluminum foil that surrounded the sensor like a "bell". A one-pen chart recorder was used to record the temperatures by scanning each probe for 116 s.

Flight initiation and survival in the laboratory

Flight initiation or take-off attempts were monitored electronically in cylindrical transparent plastic chambers

(14 cm diam × 18 cm high) with a phono-pickup and amplification trigger-circuit that actuated a multi-channel event recorder (Byers and Löfqvist, unpubl.). The flight chamber floor was made from a plastic petri-dish bottom (14 cm) on four foam rubber legs (1.5 cm). In the chamber floor a metal-screen covered hole (8 cm diam.) allowed ventilation, and 15 small take-off platforms (6×6×6 mm) were glued to the screen floor (for flight without duff). Plastic photocopy transparencies were formed into a tube and taped to form the chamber sides. Eight fine-screen covered holes (1.5 cm diam) on the chamber sides also allowed ventilation and equilibration of environmental conditions which were programmed by a walk-in environmental chamber (12.6 m³; Karl Weiss, Giessen, Germany). The plastic petri-dish tops covered the top of the flight chambers and each had a mono phono-pickup appressed to the top outside center of the dish. Vibrations from flying beetles striking the top and sides were usually detected by the system (>90% of flights were detected), although pickup sensitivity differences make comparisons between chambers less accurate than comparisons over time within a chamber.

Duff (down to the soil layer) was collected from a spruce forest near Veberöd, Sweden, and stored up to three months at 4°C in a plastic bag until placed at the beginning of each experiment in the flight chambers. Six dried spruce twigs were pressed into the duff so that they stood 3–4 cm high to serve as take-off points. Just above the duff layer a thin film of sebaceous oil was smeared around the inside chamber sides to prevent walking beetles from climbing up the sides and possibly triggering the recorder when later falling to the floor. Temperatures were measured inside the flight chambers with the electronic thermometer (without scanner) and a thermistor thermometer. Beetles in all the laboratory experiments were obtained from a laboratory culture (Sweden/Norway beetle mixture maintained on spruce logs) and used one to two days after emergence.

Effect of duff

Males and females were placed in flight chambers with or without duff to see whether duff has an effect on the ability/willingness of beetles to initiate flight (28 October 1983). Four chambers, two with a 4 to 5 cm layer of duff and 30 males or 30 females and two with the screen floor and 30 males or 30 females were tested beginning at 1900 hours on a 19:5, L:D photoperiod (dark at 2200 hours) at 700 lux, 80±5% r.h. and 25±0.2°C. Flight attempts were recorded continuously for each chamber for 3.5 d until most beetles were dead at which time survivors were counted.

Effect of food in duff

The effect of food (five 2.5×3×1 cm thick bark slabs) on flight initiation and survival was tested in two chambers (6 November 1983). The bark slabs were buried 1–2 cm deep in a 5 cm thick duff layer in each chamber.

Since sexual differences in flight survival were not observed in the 28 Oct. experiment, each chamber had an even mixture of 25 males and 25 females. The environmental conditions were identical except that the test was run for 13 d. During the test, the number of beetles walking on the surface was recorded each day between 1100 and 1500 hours. At the end of the test, the bark slabs were dissected to determine if feeding had occurred.

Since the duff appeared quite dry after 13 days in the above experiment, a 0.5 cm layer of tissue paper on the bottom above the screen was soaked with water at the beginning of all subsequent tests. Each day 5 ml of water were injected with a syringe and tube extending to the center of the upper surface of the paper to insure high moisture conditions at the bottom of the duff layer. On 23 November 1983, two chambers each containing a 4–5 cm layer of duff with 25 males and 25 females were monitored for flight initiation activity under the same environmental conditions as above for 8 d. The only difference between the chambers was that one had six freshly cut spruce twigs (about 4 mm diam. \times 7 cm, with needles) buried just under the duff surface. On 2 December 1983, this experiment was repeated with eight spruce twigs. During both tests the numbers of beetles walking on the surface each day were counted, and at the end of the tests the extent of twig feeding was observed.

Effect of thermal gradient in duff

Beetles may be able to take advantage of the thermal gradient in forest duff (Fig. 1A and B) and survive longer by burrowing down to the cooler depths if heat/moisture-stressed during flight dispersal. To test for this possibility, the plastic petri-dish bottoms were removed and two chambers were set directly on either an aluminum plate with underlying peltier element (electronic cooler) or on a plastic sheet. The 4 \times 4 cm Peltier element (15 VDC, 3.6 A, Elfa Corp., Solna, Sweden) was heat-sunked and fan cooled with cooling controlled by adjustment of voltage to 8.7 VDC at 1.8 A. The environmental conditions were as described above except that the humidity was reduced to 40% to inhibit dew accumulation on the cold plate. The temperature at the center of the tissue paper surface (bottom of 4–5 cm of duff) was 13.8°C. The experiment was performed for about 7 d (5–12 January 1984) until no beetles were seen alive on the surface and flight activity had ceased.

Simulated natural environment

The environmental conditions in the flight chambers were programmed to simulate natural conditions in order to see if survival rates would be similar to those in nature (4 February 1984). The flight chambers were set up as in the experiment with the Peltier element except that both the environmental chamber and the Peltier element were programmed. The temperatures of the air/duff surface and the bottom of the duff layer are

shown in Fig. 6. The Peltier element was turned on or off at the times indicated to maintain a relatively constant temperature at the bottom of between 8 and 15°C (usually either 11 or 14°C). The humidity was influenced by the temperature and so it ranged from 37 \pm 3% r.h. at 25°C up to 67 \pm 2% at 11°C. The number of beetles walking on the surface was recorded on certain days, and at the end the duff was dissected to determine the location of dead beetles.

Correlation of survival, attraction to pheromone, and temperatures in the forest

The field studies were conducted daily in Esrum forest district, Grib skov, northern Shælland, Denmark, from 20 May through 5 June 1984. The catch of beetles attracted to a pheromone trap, indicating the general level of flight activity in the area, was compared with the relative numbers of caged beetles walking on the duff surface, indicating the general level of take-off activity. A black plastic pipe trap (1.36 m long \times 0.12 m diam.) with 900, 3.5 mm, holes (Bakke and Riege 1982) with a large plastic funnel (40 cm diam.) releasing the pheromone components 2-methyl-3-buten-2-ol at 50 mg d⁻¹ and *cis*-verbenol at 1 mg d⁻¹ (Bakke et al. 1977, Schlyter et al. 1987) was used to catch attracted beetles. An electronic fraction collector (Byers 1983) was used to make half-hour collections of the trapped beetles as shown in Fig. 8 and summarized in Fig. 9. The pipe trap and fraction collector were located about 30 m from spruce forest in a clearcut. About 10 m away, three "bubble-like" window screen cages over the duff surface were constructed by digging a 30 cm square trench through the litter layer to 3–4 cm below the soil surface and then driving small stakes through the periphery of a flat screen into the trenches. The forest duff was replaced in the trenches and a small hole for inserting beetles was cut in the dome-forming screen cage. Another set of identical cages was placed about 100 m away and about 40 m inside a spruce forest with >90% shading.

On 20 May 1984, several hundred beetles were collected in pheromone pipe traps and separated by sex that evening. At 0900 hours the next day, 50 males, 50 females, and 150 unsexed (but about 70% females) beetles were placed in the three cages in each of the two areas. Temperatures in the cages at the clearcut were recorded on the duff surface and in the air (0.7 m) with the multiprobe scanning thermometer and pen recorder (Byers 1984) and on the duff surface in the forest with a mercury thermometer. Counts of beetles on the duff surface and screens (combined) were made at all cages during several times each day from 21 May to 5 June (except 25 May due to heavy rains).

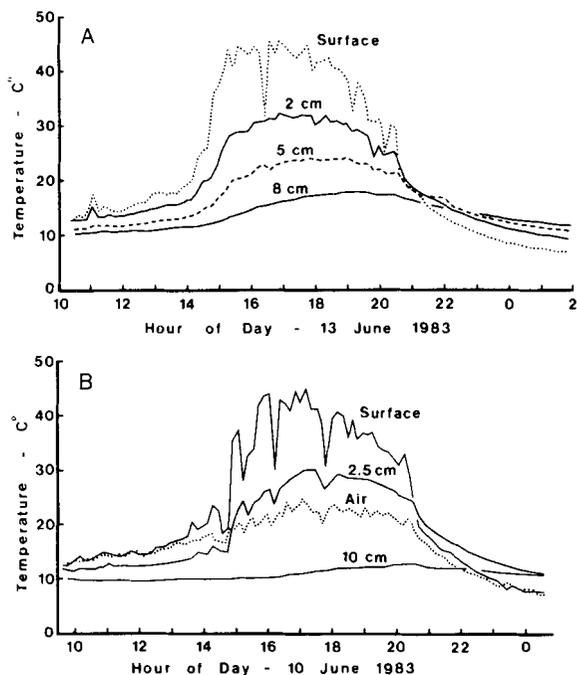


Fig. 1 A and B. Temperatures of forest litter of Norway spruce at the surface and various depths (A, B) and in the air (B) throughout the day during the latter part of the spring swarming flight of *Ips typographus* (10 and 13 June 1983) near Skien, southern Norway. The sharp daily rise and fall in surface temperature was due to shading of the sun by trees and mountains while the briefer temperature changes were due to shading by occasional clouds.

Results and discussion

Forest litter temperatures during the spring dispersal

The temperatures of forest duff at various depths as compared to air temperatures at 1 m are shown in Fig. 1, A and B. The steep rise and fall in the duff temperature was due to the sun passing over the trees and then setting behind the opposite mountain. Fluctuations during the intervening period were due to occasional clouds blocking the sunlight.

The steep thermal gradients of spruce duff (Fig. 1, A and B) indicate that beetles could seek their preferred temperature with a vertical movement of only a few cm. The thermal diffusivity (insulative property) of spruce duff, $K = 0.06 \text{ mm}^2 \text{ s}^{-1}$ (Byers 1984), indicates that duff is an ideal hibernation substrate as well as resting place preparatory to flight dispersal. The temperatures recorded at the site (Fig. 1) indicate that any beetles attempting to fly away would not be able to do so until 1400–1500 hours due to shading. Furthermore, flight attempts between 1530 and about 1900 hours would need to be performed for only a few minutes at one time, otherwise the heat/low moisture at the surface would kill them.

Flight initiation and survival in the laboratory

Effect of duff

The rate of take-off attempts by males and females from forest duff were only 31% and 43%, respectively, that of males and females from the screen floor (Tab. 1). The survival of both sexes appeared to be reduced in the screen-floor chambers compared with duff-filled chambers (Tab. 1). This was corroborated by observations on the third test day when no females and only two males were alive in the chambers without duff while ten males and four females were alive on the surface of the duff-containing chambers.

Beetles survived longer when placed in spruce duff than in the screen-floored chamber (Tab. 1) probably because of the higher moisture conditions (even free water for the first day) in the duff. It is also possible that beetles in the "bare" chamber attempted to fly continuously (more than twice as many flights initially) as there were no hiding places and so became exhausted sooner compared with those in the chamber with duff (many beetles in the duff experiments were resting under the surface, Tab. 2).

Effect of food in duff

The chamber in which the small bark slabs were available as food had a reduced take-off rate during the first few days compared with the control without food (Fig. 2). This was probably due to most beetles feeding as few were observed on the duff surface at this time (Tab. 2, Fig. 3). The beetles without food died while beetles with food continued to attempt flight for a considerable number of days (Figs 2, 3). The hourly flight rate recordings indicate that beetles without food continuously fly during the "daylight hours" and only fatigue and/or mortality decreased the flights taken (Fig. 3). The flights beetle⁻¹ d⁻¹ in Figs 2 and 3 assume that the initial numbers of beetles were alive throughout the experiment (these rates rather than the absolute amounts are shown so comparisons between experiments can readily be done). However, a closer approximation of the true flight initiation rate per beetle, at least during the later part of the test, can be obtained by dividing the total flights by the number observed on the duff surface (Tab. 2). This should partially account for the mortality later in the

Tab. 1. Flight rates (number of flights beetle⁻¹ d⁻¹) of *Ips typographus* (30 males or 30 females) in chambers with either forest duff or bare floor at 25°C, 19:5 L:D photoperiod, and 80% r.h. (28–30 Oct., 1983).

Day	No Duff		Duff	
	Male	Female	Male	Female
1	63.7	58.6	19.6	25.3
2	2.9	10.1	17.2	15.0
3	0	0	2.5	0.8

Tab. 2. Comparison of survival and flight rates (adjusted for apparent number flying) of *Ips typographus* in chambers (each 25 males + 25 females) with fresh spruce tissue (bark slabs or twigs) or without food at 25°C, 19:5 L:D photoperiod, and 80% r.h.

	Day							
	1	2	3	4	5	6	7	8
6 November 1983								
<i>Food: five bark slabs</i>								
Number flying	0	0	2	5	6	6	5	3
Flights beetle ⁻¹ d ⁻¹	-	-	45	56	56	61	35	38
<i>No Food</i>								
Number flying	44	27	6	1	0	0	0	0
Flights beetle ⁻¹ d ⁻¹	34	24	18	17	0	0	0	0
23 November 1983								
<i>Food: 6 twigs</i>								
Number flying	10	12	12	6	3	0	1	0
Flights beetle ⁻¹ d ⁻¹	32	29	12	5	3	-	0	0
<i>No Food</i>								
Number flying	27	3	1	0	0	0	0	0
Flights beetle ⁻¹ d ⁻¹	14	18	16	0	0	0	0	0
2 December 1983								
<i>Food: eight twigs</i>								
Number flying	11	14	7	5	2	1	0	0
Flights beetle ⁻¹ d ⁻¹	36	11	8	3	4	0	0	0
<i>No food</i>								
Number flying	36	12	3	0	0	0	0	0
Flights beetle ⁻¹ d ⁻¹	29	27	8	0	0	0	0	0

tests. The dissection of the bark slabs revealed that the phloem of all five was eaten, two completely, and three healthy pupae were found in another. In the five bark slabs, a total of 15 dead beetles and one living male were found (16 d after the test start).

Beetles did not usually attempt a possible dispersal flight while the bark slabs were suitable as food and apparently also as breeding substrates (three pupae found in one slab). It is surprising that these buried slabs could preoccupy the 50 beetles under crowded conditions for the first three days. The beetles without food mostly died after only 2.5 d and exhibited no diel flight periodicity, nor did beetles in any other tests under constant temperature.

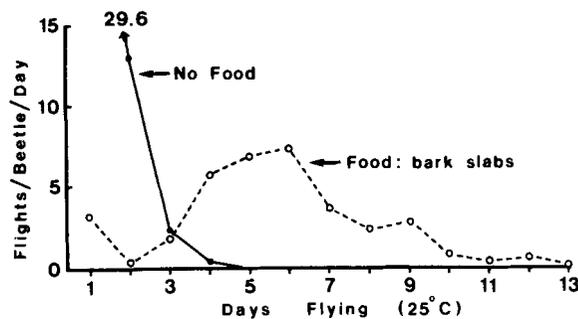


Fig. 2. Flight rates per day of *Ips typographus* at 25°C in chambers (each 25 males + 25 females) with forest duff and either five bark slabs as food or without food over a 13-d period (6-19 Nov. 1983).

In the experiments on 23 November and 2 December 1984, beetles fed on the bark/phloem of twigs while avoiding the green needles and woody xylem. Four of the six twigs were eaten (each 20 to 80% of the bark) in one experiment, while only two of the eight twigs were eaten (20 and 80%) in the other experiment. The twigs did seem to prolong the flight period and survival (Fig. 4 and Tab. 2) but not as much as the bark slabs. The tissue paper soaked with water at the bottom of the duff control without food did not appear to significantly affect survival when compared with the duff control without soaked paper in either the 6 November experiment (Fig. 3) or in the first experiment (Tabs 1 and 2).

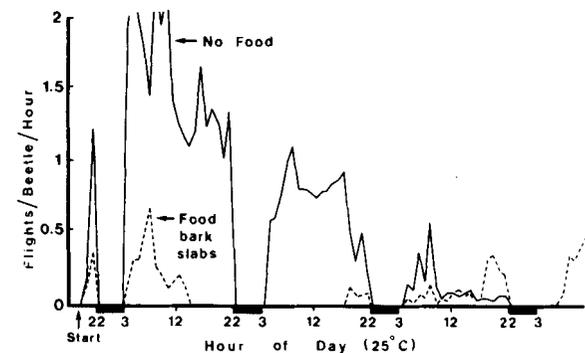


Fig. 3. Flight rates per hour of *Ips typographus* at 25°C in chambers (each 25 males + 25 females) with forest duff and either five bark slabs as food or without food over the first four days of the test (6-19 Nov. 1983). Black bars on abscissa indicate period when flight ceased.

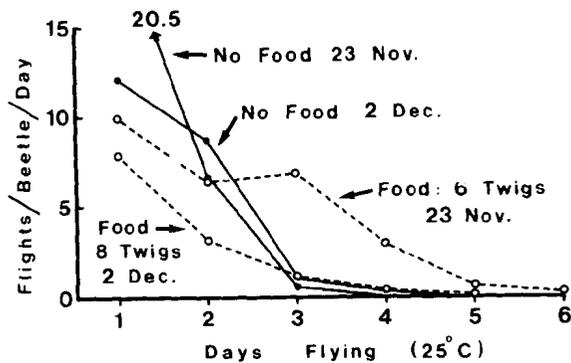


Fig. 4. Flight rates per day of *Ips typographus* at 25°C in chambers (each 25 males + 25 females) with forest duff and either fresh spruce twigs as food or without food.

The feeding of beetles in twigs was less pronounced or prolonged and their survival was increased only slightly over unfed beetles (Fig. 4). Annala (1969) states that "the majority of beetles overwinter in the moss layer, where no food is available" but he also claims that beetles may eat pieces of bark, branches, and scales of cones just before swarming. It appears from our study that even starving beetles will eat only fresh phloem, and that if this is present in the duff then beetles could feed upon it. However, since fresh phloem in the duff is a rare incident, except at the base of stumps, it seems that the majority of beetles must take flight and find host trees without the benefits of feeding. Subsistence feeding on twigs in trees or in bark of trees (without intending to reproduce) has not been reported and our observations have provided no evidence for beetles feeding in this way. Of course "pioneer" attacks by males may be compelled by starvation, but then one should find female pioneer attacks also, and we do not find them.

Effect of thermal gradient in duff

The Peltier cooling plate produced a 13.8°C temperature at the bottom of the duff but this caused very little

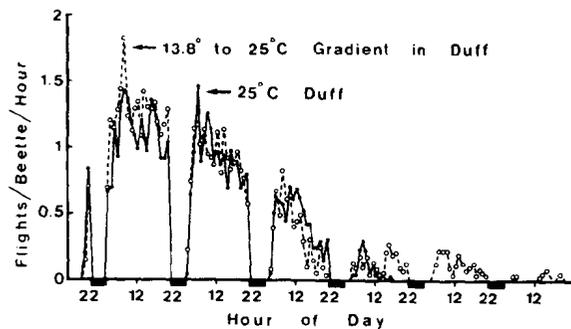


Fig. 5. Flight rates per hour of *Ips typographus* at 25°C in chambers (each 25 males + 25 females) with forest duff either uncooled or cooled from below (13.8°C at 4–5 cm depth) over a 6-d period (5–11 Jan. 1984). Photoperiod indicated by black bars on abscissa.

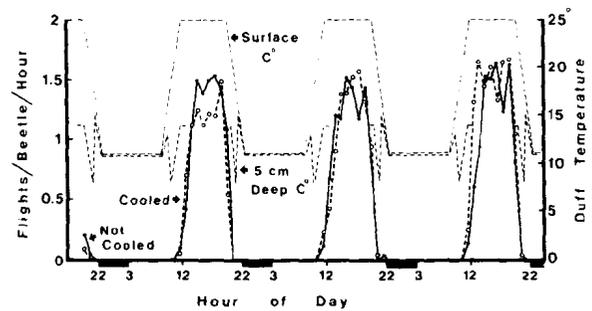


Fig. 6. Flight rates per hour of *Ips typographus* on a diel temperature cycle in chambers (each 25 males + 25 females) with forest duff either uncooled or cooled from below (11–14°C at 4–5 cm depth) over the first three days of the test (4–13 Feb. 1984). Photoperiod indicated by black bars on abscissa.

difference in the flight initiation rate for the first three days compared with no cooling (Fig. 5). The hourly rates again indicate that beetles fly throughout the daylight hours (as in Fig. 3 also) and fatigue and/or mortality caused a gradual decline in the flights taken. However, on the latter part of the fourth full day and subsequent two days there was a prolonging of flight activity in the cooled chamber (Fig. 5). The number of walking beetles on the duff surface (3 and 2) on the fifth and sixth full days of the cooled duff, while none were seen on the control, also indicates that survival was slightly longer due to the lower temperature deeper in the duff. No evidence of a diel periodicity of flight was found for repeated flights in any of the laboratory experiments, although there may be a "first-attempt" flight rhythm (emerging from duff) as found for emergence of adults from logs (Byers 1983). It appears that beetles emerge from the overwintering duff and try to fly continuously until they find a brood source, or until environmental conditions such as temperature or dark temporarily prohibit flight. Survival benefits of cooling could probably be increased by lengthening the dark period when beetles were observed to burrow into the duff.

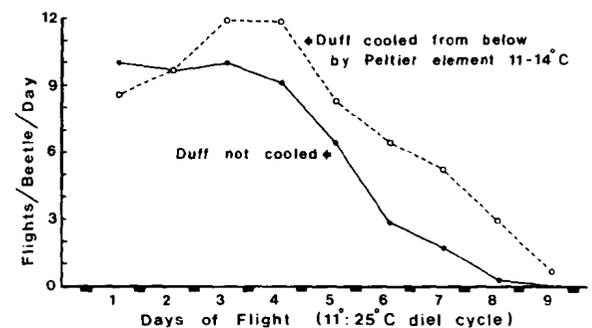


Fig. 7. Flight rates per day of *Ips typographus* on a diel temperature cycle (11 to 25°C, Fig. 6) in chambers (each 25 males + 25 females) with forest duff either uncooled or cooled from below over a 9 d period (4–13 Feb. 1984).

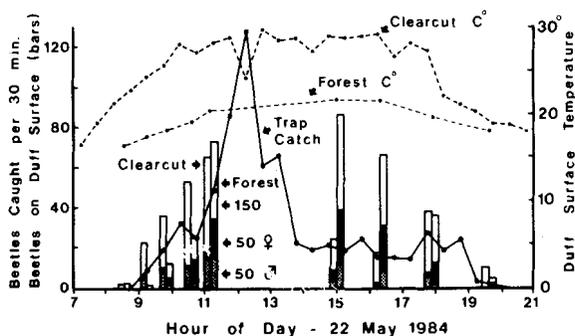


Fig. 8. Comparison of catches of *Ips typographus* at a pheromone trap in a clearcut with temperatures on the duff and the numbers of beetles visible in screen cages on the duff in the clearcut and forest during 22 May 1984 in Denmark. Fifty males, 50 females, and 150 unsexed beetles were placed in each of three cages in each area on 21 May.

Simulated natural environment

Based on the temperature regimes in nature (Fig. 1), flight chambers were tested with or without a thermal gradient in the duff under a "natural" temperature program to estimate how long and when beetles may attempt flight in nature. The beetles in both chambers only flew when the temperatures were above the threshold (20°C) which compressed their flight activity period. No apparent differences in activity during the first three days could be observed between the chambers where the duff was either cooled or not from below (Fig. 6). However, as the experiment progressed there were significantly more flights in the chamber with the bottom-cooled duff (Fig. 7). In this chamber which simulated nature the most closely, beetles survived and flew at significant rates for eight days and walked about for 12 d, while none were alive on the surface of the other chamber after 9 d. After 17 days the duff from both chambers was dissected and four beetles were found alive at the bottom of the cooled duff.

The survival was longer in the chamber where duff was cooled from below during the warmer "day" (25°C) probably because some beetles remained cool for longer periods before returning to the warmer surface where their "ageing" processes were speeded up. The peaks of flight activity are not symmetrical with the peaks of daily temperature probably because of a time-lag in "wake-up" of beetles and warming of the surrounding duff at intermediate depths (Fig. 6).

Correlation of survival, attraction to pheromone, and temperatures in the forest

On 22 May, the caged beetles emerged from the duff and began to attempt flight around 0800 or 0900 hours which corresponds to the earliest catches of beetles in the pheromone trap (Fig. 8). During the morning, the

numbers emerging from the duff increased as the trap catch increased, while the prolonged high surface temperatures in the clearcut during the afternoon may have forced the caged beetles there to seek cooler temperatures in the duff and also were correlated with decreased trap catch (Fig. 8). The beetles caged in the cooler forest emerged later in the morning and were still attempting flight in the afternoon because temperatures were still favorable. It is interesting that only a small proportion (up to 1/3) of the total were ever attempting flight at any particular time (Figs 8, 9) – as was found in the laboratory experiments. Both sexes seem to behave similarly.

The survival time of caged beetles in the clearcut area was shorter than that of caged beetles in the forest (about 9–10 d versus 16 d). The numbers of beetles visible in the cages correlate reasonably well with the trap catches and temperatures throughout the period tested except on 24, 26 and 27 May for the clearcut cage (Fig. 9). The forest cage had few beetles visible on these days and few beetles were caught in the pheromone trap because rains occurred on 23 and 25 May. Higher temperatures and sun in the morning and early afternoon of 24 and 27 May can explain the numbers in the clearcut cage. However, on 26 May it was cloudy and cooler with rain droplets in the screen but relatively large numbers of beetles were attempting to fly anyway. Later in the period (after 29 May for the clearcut cage and after 3 June for the forest cage) correlations are inappropriate due to the mortality of beetles (Fig. 9). Again, both sexes had apparently similar survival rates and behavior.

The proportions of beetles in the forest cage during the day of 22 May are similar to the results of Annala (1969) for emergence of beetles from duff. However, the beetles in the clearcut cage seemed to escape the high afternoon temperature by burrowing into the duff. The method of Annala (1969) for monitoring the emer-

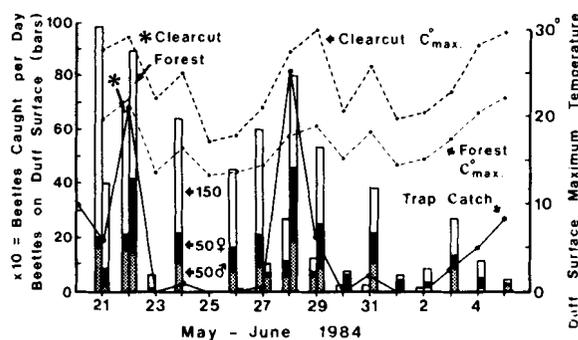


Fig. 9. Comparison of catches of *Ips typographus* at a pheromone trap in a clearcut with maximum temperatures on the duff and the maximum number of beetles visible each day in screen cages on the duff in the clearcut and forest from 21 May to 5 June 1984 in Denmark. Fifty males, 50 females, and 150 unsexed beetles were placed in each of three cages in each area on 21 May. Heavy rains occurred on 23 and 25 May.

gence of *I. typographus* from duff differed from ours since we caused beetles to return to the duff. The laboratory results of survival in the "natural" environment were similar to the field results in the clearcut where beetles survived for about 8 d in both cases (Figs 7, 9). Beetles may have lived longer in the forest because the mid-day temperatures therein rarely exceeded 20°C while the laboratory temperatures were 25°C, and clearcut temperatures sometimes higher than those in the laboratory.

Previous studies with the American bark beetle *Dendroctonus ponderosae* at 1–2°C showed they could survive for 1–2 months (Watson 1971, Safranyik 1976). Wagner et al. (1984) reared *D. frontalis* at 10 constant temperatures; at 10 and 12.5°C the average longevity was 18 d while at higher temperatures the survival times decreased exponentially. In both these "monogamous" species, the females survived several days longer than males, but the differences were only about a day at temperatures above 25°C. Our experiments are the first to be done with thermal gradients present in natural duff, or under varying daily temperatures to simulate nature.

Our laboratory-reared beetles appeared to be in the same behavioral and physiological condition as wild-dispersing populations since both are non-diapausing and are not winter-dormant any longer. Probably the major disadvantage of experiments where beetles are caged with duff in order to observe longevity and flight initiation is that this is unnaturally confining. This introduces an artifact whose importance is difficult to estimate. The fact that most beetles fly for at least several meters before landing and presumably may fly usually for several minutes would either increase or decrease their survival time compared with the conditions devised here. More continuous flying would require more energy so one could argue that survival time for wild beetles would be shorter than that of caged beetles which fly repeatedly for very short periods. On the other hand, wild beetles could live longer because they may land in areas of lower thermal stress (in the forest) when unable to locate breeding trees. Of course, in many cases beetles find host trees and feed to replenish their energy reserves for a possible second flight.

Lindelöw and Weslien (1986) showed that some duff-emerging individuals of *I. typographus*, without prior feeding, can find pheromone (colonized trees) over several hundred meters within 30 min of flight initiation. Forse and Solbreck (1985) found that laboratory-reared beetles can fly for several hours before landing, and no differences were found between the sexes or for different sized beetles. Aside from exhaustion/starvation, beetles could certainly die after landing in very hot clearcuts (Byers and Löfqvist 1985, and unpubl.), lakes, or spider webs (observed by J. A. Byers), and can be eaten by various predators or killed by the tree's defensive system of resinosis.

While several studies have observed the daily flight

periodicity of bark beetles in response to pheromones (Gara 1963, Gara and Vité 1962, Vité and Gara 1962), our study is the first on *I. typographus* and it provides objective data from fraction collectors and electronic temperature recording. We also know of no other studies on bark beetles which have followed the survival of beetles in the forest (in hot clearcuts and cool shaded forest) over several weeks. The results of our longevity tests may be useful when considering a control program with pheromones/allomones that would be used to disrupt or "confuse" the beetles' orientation to suitable host trees. If beetles can be induced to continually land in duff after exhaustive searches during dispersal/host-seeking flights by the use of behavioral chemicals, then we have a reasonable approximation of how long this treatment must continue to cause significant mortality of the beetles (about 2–3 wk).

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References

- Annala, E. 1969. Influence of temperature upon the development and voltinism of *Ips typographus* L. (Coleoptera, Scolytidae). – *Ann. Zool. Fennici* 6: 161–207.
- Bakke, A. and Riege, L. 1982. The pheromone of the spruce bark beetle *Ips typographus* and its potential use in the suppression of beetle populations. – In: Kydonieus, A. F. and Beroza, M. (eds). *Insect suppression with controlled release pheromone systems*, Vol. II. CRC Press Inc., Boca Raton, Florida, pp. 3–15.
- , Frøyen, P. and Skattebøl, L. 1977. Field response to a new pheromonal compound isolated from *Ips typographus*. – *Naturwissenschaften* 64: 98.
- Byers, J. A. 1983. Electronic fraction collector used for insect sampling in the photoperiod-induced diel emergence of bark beetles. – *Physiol. Entomol.* 8: 133–138.
- 1984. Electronic multiprobe thermometer and multiplexer for recording temperatures of microenvironments in the forest litter habitat of bark beetles (Coleoptera: Scolytidae). – *Environ. Entomol.* 13: 863–867.
- Forse, E. and Solbreck, C. 1985. Migration in the bark beetle *Ips typographus* L.: Duration, timing and height of flight. – *Z. Angew. Entomol.* 100: 47–57.
- Gara, R. I. 1963. Studies on the flight behavior of *Ips confusus* (LeC.) (Coleoptera: Scolytidae) in response to attractive material. – *Contrib. Boyce Thompson Inst.* 22: 51–66.
- and Vité, J. P. 1962. Studies on the flight patterns of bark beetles (Coleoptera: Scolytidae) in second growth ponderosa pine forest. – *Contrib. Boyce Thompson Inst.* 21: 275–290.
- Lindelöw, A. and Weslien, J. 1986. Sex-specific emergence of *Ips typographus* L. (Coleoptera: Scolytidae) and flight behaviour in response to pheromone sources following hibernation. – *Can. Entomol.* 118: 59–67.
- Merker, E. 1957. Die ökologischen Ursachen der Massenvermehrung des grossen Fichtenborkenkäfers in Südwestdeutschland während der Jahre 1941 bis 1951. Freiburg.

- Safranyik, I. 1976. Size- and sex-related emergence, and survival in cold storage, of mountain pine beetle adults. - *Can. Entomol.* 108: 209-212.
- Schlyter, F., Löfqvist, J. and Byers, J. A. 1987. Behavioral sequence in the attraction of the bark beetle *Ips typographus* to pheromone sources. - *Physiol. Entomol.* 12: 185-196.
- Vité, J. P. and Gara, R. I. 1962. Volatile attractants from ponderosa pine attacked by bark beetles (Coleoptera: Scolytidae). - *Contrib. Boyce Thompson Inst.* 21: 251-274.
- Wagner, T. L., Gagne, J. A., Sharpe, J. H. and Coulson, R. N. 1984. Effects of constant temperature on longevity of adult Southern pine beetles (Coleoptera: Scolytidae). - *Environ. Entomol.* 13: 1225-1230.
- Watson, J. A. 1971. Survival and fecundity of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) after laboratory storage. - *Can. Entomol.* 103: 1381-1385.