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Pystynävertäjän (Blastophagus piniperda L., Col., Scolytidae) elämänkierrosta, erityisesti sen lisääntymisbiologiasta

Kalervo Salonen

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ON THE LIFE CYCLE, ESPECIALLY ON THE REPRODUCTION BIOLOGY OF *BLASTOPHAGUS PINIPERDA* L. (*COL., SCOLYTIDAE*)

KALERVO SALONEN

SELOSTE

PYSTYNÄVERTÄJÄN (BLASTOPHAGUS PINIPERDA L., COL., SCOLYTIDAE) ELÄMÄNKIERROSTA, ERITYISESTI SEN LISÄÄNTYMISBIOLOGIASTA

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FOREWORD

During the present investigation I have received valuable support and assistance from several persons. Dr. Esko Kangas, Professor and Head of the Department of Agricultural and Forest Zoology of the University of Helsinki, has closely followed the progress of my work and has given a lot of valuable advice during the study. With his permission, I have been able to continue my study in the facilities of his department in 1966—1967, even after I transferred to a new job at Kemira Ltd. Dr. Kangas has also read the final manuscript.

During the study, a great deal of valuable advice has been given by Dr. Matti Nuorteva and Dr. Erkki Pulliainen. They have also read the final manuscript.

In the field work, my wife Eeva Salonen has continuously assisted me during many years. In 1968, Miss Mirjam Nieminen, M.Sc., carried out rearing of insects for the project in the biological laboratory of Kemira Ltd in Vaasa. Mr. Pentti Salonen, Agr. Tech., has assisted in the 1970 field work at the Kotkaniemi experimental farm of Kemira Ltd in Vihti. Mr. Mikko Ylänen, M.Agr., has helped in the statistical analysis of the data. During the preparation of the manuscript, valuable advice has been given by Dr. Erkki Annila and Dr. Kari Löyttyniemi.

For the study, I received a grant from the Emil Aaltonen Foundation in 1962.The manuscript has been translated and edited by Dr. Kari Mustanoja.

I wish to thank for valuable assistance that I have received from the persons and institutions mentioned above, and many others. I also want to thank the directors of Kemira Ltd for the opportunity to complete the study.

I am grateful for the Society of Forestry in Finland for publishing the study in Acta Forestalia Fennica.

Helsinki, October 1972

Kalervo Salonen

TABLE OF CONTENTS

1. INTRODUCTION

With the increasing economic significance of forests, it has been necessary to also give increasing attention to the attacks on living trees and unbarked timber by noxious insects. In order to estimate the extent and quality of their damage, and to plan their control efficiently, it is important to know, as well as possible, the life history of these noxious species and the factors affecting their reproduction.

Blastophagus piniperda L. is one of the most important noxious insects in Finland (Saalas 1949), and causes many kinds of damage to its host plant, influencing its development and its utilization. In many other regions, also, it is one of the most common noxious forest insects. It occurs throughout practically all of Europe, and in Siberia, China and Japan. It is also found in Caucasia, and in North America around New York City (cf. Schwerdtfeger 1957, Chararas 1962). Reports of its occurrence in Algeria and elsewhere in the Mediterranean countries, Madeira and the Canary Islands, probably actually refer to the species *B. destruens* Woll. (Lekander 1971).

The favorite host of the species is Scotch pine (*Pinus silvestris* L.), but it commonly attacks also other *Pinus* species (e.g. Escherich 1923, Saalas 1923, 1949). Occasionally it also attacks the *Larix* species and Norway spruce, *Picea abies* Karst. (e.g. Altum 1881, Escherich 1923, Löyttyniemi 1967, Nuorteva and Nuorteva 1968, Bakke 1968 a).

The life history of *B. piniperda* has interested scientists especially in Central Europe already in the 19th century (Ratzeburg 1839, 1856, Holmgren 1867, Eichhoff 1881, Altum 1881, 1887, Bos 1891, Judeich and Nitsche 1895, Boas 1898). Studies in the life history of the insect were still numerous in the early 1900's (e.g. Knoche 1904, 1906, 1907, Hennings 1908, Trägårdh 1911, 1921, Saalas 1919, Krausse 1920, 1922 a, 1922 b, Wolff 1920, Butowitsch 1925, 1954, Kangas 1934 a, 1934 b, Hanson, 1937, 1940, 1941). The significance of the species in reducing tree growth has been studied by, for instance, Mattson Mårn (1921), Michalski and Witkowski (1960), Vorontsov (1960), Andersson (1961) and Turĉek (1964). Bakke (1968 a) has studied the effect of temperature on its swarming and brood development.

B. piniperda has been the object of numerous studies also in Finland (e.g. Saalas 1919, Kangas 1934 b, 1934 c, 1950 a, 1950 b, 1953, 1954, 1968 a, Nuorteva 1950, 1954, 1964, Eidmann and Nuorteva 1968). Its light and flight responses have been treated in several of these (Perttunen 1958, 1959, 1960, Perttunen and Boman 1965, Perttunen and Häyrinen 1969, 1970). The cold resistance of the species has been studied by Annila and Perttunen (1964). The attraction of the insects to their host trees has been studied at the Department of Agricultural and Forest Zoology of the University of Helsinki, and several reports have been published from this study, which is still in progress (e.g. Kangas *et al.* 1965, 1967 a, 1967 b, 1970, 1971, Oksanen *et al.* 1968, 1970, Perttunen *et al.* 1968, 1970).

The present study has been started during test-insect collections for the *B. piniperda* attraction study mentioned above. At that phase of the studies it was found that many questions connected with the life history and reproduction biology required additional study. Connected with the present report, a paper has been previously published on changes in the sexual index of the species during the various stages of its life history (Salonen *et al.* 1968).

The purpose of this project is to examine questions which have previously received little attention or have not been studied, and which are primarily connected with the reproduction biology of *B. piniperda*. In the study, the life cycle of the insect has been followed around the year. Special attention has been given to the effect of temperature on swarming, progeny development, movement into overwintering sites and to mortality during the winter. An attempt has also been made to provide additional information on some factors affecting the selection of breeding sites, pair formation and progeny size.

In connection with this study, several questions have been treated on the basis of fairly limited data. This has, however, been considered justified, since studying these questions has been considered useful for completing the picture of the reproduction biology and the life cycle of *B. piniperda*.

2. PROCEDURES OF STUDY

21. Study areas and period of study

The study areas are shown in figure 1. All studies carried out in the laboratory have been done at the Department of Agricultural and Forest Zoology of the University of Helsinki in the years 1961—1967. Outdoor rearing of beetles was carried out in 1962—1965 at the Viikki Experimental Farm in Helsinki and in 1968 in Vaasa at the experimental field of the biological laboratory of Kemira Ltd.

Osbervations and studies concerning swarming and egg gallery establishment were made in 1961—1965 in the area of the City of Helsinki, and at the Ruotsinkylä Experimental Area of the Forest Research Institute in Tuusula. In 1961—1962 and in 1964, swarming and egg gallery establishment were under observation in the Rural Commune of Rovaniemi. In the spring of 1970, the progress in swarming was observed in Vihti, about 50 km northwest of Helsinki.

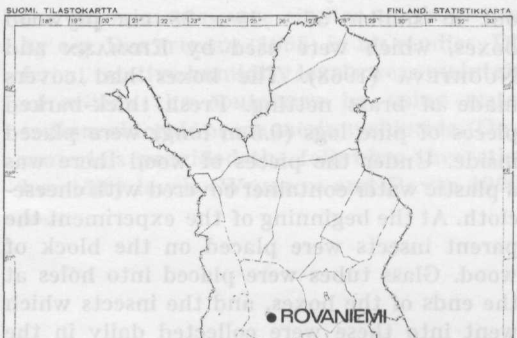


Figure 1. Study areas.

Kuva 1. Tutkimusalueet.

The development of the egg galleries was studied in the field in the area of the City of Helsinki in 1962—1965.

In 1962—1965, egg gallery lengths were measured, and the numbers of larval galleries and the exit holes of adults of the new generation were counted in various breeding materials, in Helsinki, Tuusula, Pusula, Ruovesi, Kuorevesi and Lammi. In Lammi, in summer 1963, *B. piniperda* populations were also studied in various parts of the crowns of standing pine trees.

The studies concerning overwintering have primarily been carried out in the forests in the area of the City of Helsinki. The numbers and mortality of *B. piniperda* adults overwintering in the bases of trees were studied in the area of the City of Helsinki during the winter seasons 1961/1962 and 1962/1963 on the basis of specimen collections. The movement of these beetles into their overwintering sites was under observation in autumn 1968 in Jakomäki, Helsinki, and in autumn 1970 in Vihti, in the area where the progress of swarming had been studied in the spring. In 1962—1967, somewhat more irregular observations were made of movement into the overwintering sites, in different parts of the City of Helsinki.

22. General methods

The nature of the study has made it necessary to use several different methods, which are described in more detail in connection with each area of study; the quantity of data is also given in that context. A brief description of the most commonly used methods follows.

Field studies. The author was in the field daily in 1961—1965 at the times when the beginning of *B. piniperda* swarming was to be expected. After swarming started, insect collections were continued through the swarming period. During these collections, observations were made of insect behavior on the tree surface after the flight. Swarming collections were made in timber storage areas which were selected as suitable collection sites for this purpose when snow still covered the ground.

In spring 1970, *B. piniperda* swarming was observed in Vihti, using similar collection traps as for instance CHAPMAN and KINGHORN (1955, 1958), BAKKE (1968 a) and SUBANSENEE (1971) have used in their studies. The method used gives a good picture of the progress of swarming, even though it does not provide an accurate record of the actual number of adults which fly in the area (CHAPMAN and KINGHORN 1958). The research method has been described in more detail on page 14.

The development of egg galleries and broods was followed in several years of the study by exposing egg galleries from various breeding materials with a sharp knife. This was done from the beginning of the swarming period until all the parent adults had left the feeding galleries. In some tree cutting areas, in addition to the egg galleries, also the numbers of exit holes for new adults in the bark were counted from the stumps.

In Helsinki, the attack of *B. piniperda* on tree shoots was observed in 1965, 1969 and 1970 already in the spring. The observations were made by the author, who examined in the study areas, during each visit, all shoots that could be reached from the ground on approximately one hundred pines. The height of the trees was 3—6 meters. The distribution of the insects, in various parts of the tree crowns in late summer, was studied by felling the trees and counting the number of insect entrance holes in the various branches.

Two methods have mostly been used in the studies concerning overwintering. Movement to the overwintering sites was recorded by digging out, from marked sample trees, the insects which had gone into the bases of trees, with a sharp-tipped knife at intervals of one or more days. The following method was used to determine the effect of tree size and location on the number and winter mortality of the overwintering insects. During early winter, trees which had numerous *B. piniperda* entrance holes in the bases were felled. The stumps were dug out of the ground and taken into the laboratory, where they were kept for some days at 1° C. From there they were taken to room temperature (22—24° C), and the insects that emerged were collected. About 24 hours after they were taken to room temperature, the stumps were debarked and the living and dead insects that were found were counted. If the insides of the dead insects oozed out under pressure between the fingers, they were considered to have died during the previous winter.

Controlled development methods. Except for pupal development experiments (see page 29), both the development experiments in the laboratory and outdoors were carried out in similar 57 × 28 × 28 cm plywood boxes, which were used by EIDMANN and NUORTEVA (1968). The boxes had covers made of brass netting. Fresh thick-barked pieces of pine logs (0.5 m long) were placed inside. Under the pieces of wood there was a plastic water container covered with cheesecloth. At the beginning of the experiment the parent insects were placed on the block of wood. Glass tubes were placed into holes at the ends of the boxes, and the insects which went into these were collected daily in the laboratory. In the outdoor development experiments, the lower end of the glass tubes was filled with glycerine, and the insects that were caught in these were not collected before autumn.

Sex identification. The sex of the *B. piniperda* specimens was identified on the basis of the differences in the last segment of their abdomen (see SALONEN *et al.* 1968). Males could be distinguished from females also by the sound they made by rubbing the last segments of their abdomen against the wing sheaths; this sound was audible when the insect was held close to the ear (see also BARR 1969).

Temperature and relative air humidity measurements. During controlled development experiments in the laboratory, temperature and relative air humidity were generally measured with a Lambrecht thermo-hygrograph. In some cases, however, temperatures were measured with a maximum and a minimum thermometer. In using the Lambrecht thermo-hygrograph, the sensor of the instrument was kept in a similar controlled-development box as the ones in which the development experiments were carried out. This box also contained a fresh piece of pine log of the same size. Temperatures and moisture within the bark were thus not measured. Temperature in laboratory conditions is, however, about the same within the bark and outside the bark (see Annila 1969). No attempt was made to study the significance of the wood moisture content on brood development during this work. The significance of moisture in pupal development was studied at various temperatures in development experiments which were carried out in glass selection containers. The containers used for the experiments were similar to those used by e.g. Perttunen (1958) in his studies. Different relative humidity levels were maintained within the containers by using water, sodium chloride or magnesium chloride. These materials provided the following theoretical humidity levels (Winston and Bates 1960):

	Temperature and moisture			
	15° C	20° C	25° C	30° C
H_2O	100 %	100 %	100 %	100 %
NaCl	76 %	76 %	75.5 %	75.5 %
$MgCl_2$	34 %	33 %	32.5 %	32.5 %

In connection with the swarming collection in spring 1970 in Vihti, temperature was measured with a Lambrecht thermo-hygrograph placed into the experimental stand at two meters above ground level. The instrument was protected from the sun. In the same way, temperature was measured in the fall, when the movement of *B. piniperda* beetles into the bases of pines was being observed. In other study years, the temperatures reported for the field experiments were recorded at the meteorological observation stations closest to the study areas. In the field studies in the area of Helsinki, the temperatures measured at the Ilmala, Viikki and Malmi Airport meteorological observation stations were used. In the area of Rovaniemi, the measurements made at the Hirvas and Rovaniemi Airport meteorological observation stations were used.

3. SWARMING AND CONSTRUCTION OF GALLERIES

31. General

It is typical of bark beetles that in the spring they leave their overwintering sites in large numbers to find suitable breeding sites. Each species has its own minimum temperature at which swarming begins. According to BAKKE (1968 a), the swarming of *B. piniperda* starts at the temperature of 10—12° C, that of *Blastophagus minor* Hart. at the temperature of 12—14° C and of *Ips acuminatus* Gyll. at 14—16° C. ANNILA (1969) reports that *Ips typographus* L.. does not start swarming before the temperature reaches 18—20° C.

It is also typical of bark beetles that each species has its own requirements for the breeding material (e.g. KANGAS 1954). For instance, some species favor spruce, others pine. Some attack thin-barked, others thick-barked trees. *B. piniperda* is among the species breeding in thick-barked areas of trees (see e.g. TRÄGÅRDH 1911, SAALAS 1949, SALONEN 1966). The physiological condition of the tree affects its suitability as a breeding site for various species. The so-called primary species are able to attack more vigorously growing trees than the so-called secondary species. However, according to some Russian scientists (see e.g. RAFES 1964) bark beetles can not be clearly classified into primary and secondary species.

An important role in directing the attack of bark beetles to their breeding material seems to be played by odors emitted from the tree and by the insects themselves (pheromones; e.g. CHAPMAN 1967). According to PERTTUNEN (1957), α-pinene attracts *Hylastes ater* Payk. in low concentrations, but in large concentrations it repels it. KANGAS (1968 b) and OKSANEN *et al.* (1968) have found that α-terpineol attracts *B. piniperda*. The attraction effect is still greater if this is mixed in a suitable ratio with trans- and cis-carveol. Observations concerning the attraction effect of bark beetles which have entered the tree on other insects of the same species have been made already by WATSON (1928). Recently, this question has been discussed in several studies (e.g. WOOD and BUSHING 1963, RUDINSKY 1966, BORDEN 1967, CHAPMAN 1967, MCCAMBRIDGE 1967, HERTEL *et al.* 1969, PITMAN and VITÉ 1969, RUDINSKY and SCHNEIDER 1969, RUDINSKY et al. 1972).

Bark beetles can be classified into monogamous and polygamous species. It has been found that the female of the monogamous species starts cutting the egg gallery, whereas in polygamous species, the male starts the cutting into the tree (see the review by ANNILA 1971).

Copulation of bark beetles can already take place at the overwintering site, on the surface of the breeding material after swarming and before starting the cutting into the tree, at the beginning of cutting into the tree, or in the egg gallery.

In the present study the effect of temperature on the exit of the insect from the overwintering site and on swarming has been studied. The attack on various sides of felled trees and on various-sized pine stumps and growing trees has also been studied.

In connection with test-insect collections for the continuing study of *B. piniperda* attraction at the Department of Agricultural and Forest Zoology of the University of Helsinki it seemed that debarked trap trees and light colors (for instance a white shirt) attracted *B. piniperda* more than unbarked trap trees and dark colors. Whether this is the case has also been examined in connection with this study.

In connection with the swarming collections, observations have also been made about the penetration of the species into the bark and copulation. This chapter also deals with feeding in pine shoots immediately following swarming.

32. Emergence from overwintering sites

Method of study. A pine tree was felled in Helsinki on April 5, 1964, in the base of which there seemed to be numerous overwintering *B. piniperda* beetles. The stump was excavated from the ground and covered with snow. Two days later it was taken to the laboratory and placed into a similar development box as the ones used for controlled development experiments in connection with this study. The container was then put into a 250-liter temperature chamber. Glass tubes were inserted into the holes at the ends of the container, and a maximum and a minimum thermometer was placed on top of the stump inside the container. A 25-Watt electric bulb was lit within the temperature chamber outside of the controlled development container. The container was covered so that light entered only through the glass tubes. During the two first days the stump was kept at a temperature of 3—5° C, on the third and fourth day the temperature was 4—6° C, on the fifth, 6—8° C, on the sixth, 7—8° C, on the seventh, 10—11° C, on the eighth, 13—14° C and on the ninth and tenth, 21—23° C. After ten days had passed from the start of the experiment, the stump was debarked and the insects encountered were collected.

Results. The results are summarized in table 1. Six adults had left their overwintering sites already during the first day of the experiment, at a temperature of 3—5° C. They had all, however, probably reacted photonegatively, since none of them had gone toward light into the glass tubes. During the second day at the same temperature, one of the two beetles found was in the glass tube on the side of the light. With a temperature higher by one degree on the next day, there were four insects in the glass tubes in light, and three on the bottom of the container in the dark. With a temperature of 6—8° C or higher, all insects which had left the stumps had gone into the glass tubes. The largest number (12) of insects was found in the glass tubes seven days after the experiment had been started, after the temperature had been raised from 7—8° C to 10—11° C.

Table 1. The numbers of *B. piniperda* specimens found daily in the development chamber and in the glass tubes in increasing temperatures (for details, see text).

Taulukko 1. Kasvatuslaatikkoon pannusta kannosta talvehtimiskäytävistään liikkeelle lähteneiden pystynävertäjien lukumäärä kasvatuslaatikon sisällä pimeässä ja sen päässä valossa olleissa lasiputkissa eri vuorokausina kokeen alkamisesta. Lämpötilaa nostettiin jatkuvasti 1—2 vuorokauden kuluttua.

Days from beginning of experiment *Vuorokausia kokeen alkamisesta*	Temperature *Lämpötila* °C	Number of beetles *Hyönteisten lukumäärä kpl*		
		In development chamber *Kasvatuslaatikossa*	In glass tubes *Lasiputkissa*	Total *Yhteensä*
1	3—5	6	0	6
2	3—5	1	1	2
3	4—6	3	4	7
4	4—6	0	0	0
5	6—8	0	3	3
6	7—8	0	1	1
7	10—11	0	12	12
8	13—14	0	8	8
9	21—23	0	6	6
10	21—23	0	1	1
Total *Yhteensä*		10	36	46

Discussion. According to this study, *B. piniperda* can leave its overwintering site already at a temperature of 3—5° C. This result also supports the observations of PERTTUNEN and HÄYRINEN (1969) indicating that the species can already move at a temperature of 1° C, but that movement at this temperature is slow. RUDINSKY and VITÉ (1956) have found that *Dendroctonus pseudotsugae* Hopk. also starts controlled movement at a temperature of 3—4° C. According to the results now obtained, the insects which started moving at 3—5° C responded negatively to light, with the exception of one specimen. Only after the temperature was 6—8° C or more, all reacted photopositively. This seems to indicate that about 6° C is the temperature threshold, above which the response of insects starting from their overwintering sites changes into a photopositive response. There may, however, be differences among individual insects. This conclusion is supported by previous results indicating that in the spring, *B. piniperda* exhibits a photonegative response at 5° C, but a photopositive one at 10° C (see PERTTUNEN 1960).

According to the results of this study, the largest number of insects had come from the overwintering sites into the glass tubes after the temperature had risen from 7—8° C to 10—11° C. At this temperature, *B. piniperda* does not fly, however (PERTTUNEN 1960, Perttunen and Boman 1965). It is probable that also in natural conditions, a large part of the insects leave their overwintering sites long before the temperature rises to a level high enough for the beginning of swarming. Majewski (1965) has found that this is actually the case. Nuorteva (1962 a) found the first *B. piniperda* egg galleries in the stumps of trees that had been felled in the winter, already on March 11, 1961. In the same year, the author found at the end of March several egg galleries which already had eggs in the stumps of trees felled in the winter, on a sunny slope facing south. In this area, swarming did not start before April 17. M. Koponen (pers. comm.) found numerous *B. piniperda* egg galleries in the stumps of pines felled in the previous winter, in a felling area in the Commune of Nurmijärvi, 40 km north from Helsinki, on April 15, 1965, five days before swarming started in the area. In these cases, the egg galleries can only have been established by insects which had overwintered in the same stumps. Thus *B. piniperda* can establish an egg gallery even without the swarming flight, if the temperature is high enough for the insect to start moving. In the field, this may already happen in March or April, when temperatures at the bases of trees may, in the sun, rise considerably above that at two meters above ground level (see Haarløv and Beier Petersen 1952, p. 49, Bakke 1968 a, Annila 1969).

33. Swarming

Data collected in 1961—1965. The swarming collections of *B. piniperda* in the region of Helsinki were started on the follow ing dates in 1961—1965:

Helsinki, Kaarela	17 April 1961
» Haaga	17 April 1962
» Fazerila	20 April 1963
Tuusula, Ruotsinkylä	18 April 1964
Helsinki, Myllypuro	20 April 1965

In the Rovaniemi area, swarming collections were started in the years of the study on the following dates:

Hanhivaara	19 May 1961
Hirvas	10 May 1962
Muurola	9 May 1964

This indicates that swarming has started at Rovaniemi 3 ½—4 ½ weeks later than in the Helsinki region. In spring 1963, the difference was apparently smaller, since S. Lilja

Table 2. Daily mean and maximum temperatures in Helsinki, during the period April 10—22, according to measurements in Ilmala in 1961—1964 and in Viikki in 1965.

Taulukko 2. Vuorokausien keski- ja maksimilämpötilat 10.—22. IV vuosina 1961—1964 Ilmalassa ja vuonna 1965 Viikissä suoritettujen mittausten mukaan.

Date *Päivämäärä*	Temperature °C *Lämpötila* 1961 Mean *Keskilämpö*	1961 Maximum *Maksimi*	1962 Mean *Keskilämpö*	1962 Maximum *Maksimi*	1963 Mean *Keskilämpö*	1963 Maximum *Maksimi*	1964 Mean *Keskilämpö*	1964 Maximum *Maksimi*	1965 Mean *Keskilämpö*	1965 Maximum *Maksimi*
10. IV	−0.2	3.9	1.8	5.9	2.2	5.1	−0.8	2.0	−1.6	1.6
11. IV	−0.2	3.2	0.1	4.2	2.7	5.8	0.6	1.4	1.3	4.5
12. IV	−1.4	2.5	3.1	6.4	3.7	6.6	1.8	3.3	2.0	4.8
13. IV	0.1	1.0	3.2	7.0	3.0	5.8	2.6	3.9	3.3	7.5
14. IV	2.3	4.7	3.5	9.0	2.9	8.4	1.9	5.0	3.5	8.2
15. IV	4.0	4.7	2.4	7.7	2.6	7.6	0.1	2.0	2.4	5.9
16. IV	5.9	11.4	5.5	11.2	3.2	7.8	1.8	6.0	4.8	6.9
17. IV	5.9	12.1*	6.8	12.4*	2.4	6.3	4.3	7.2	5.5	8.9
18. IV	6.6	11.8	7.3	11.1	3.0	4.7	6.7	11.1*	5.6	8.3
19. IV	4.9	9.5	4.4	8.9	8.5	14.0	6.8	12.3**	5.5	9.0
20. IV	2.5	7.0	5.5	9.8	9.3	15.3**	9.0	16.5	7.5	11.5*
21. IV	3.2	7.0	7.0	12.8**	9.8	16.7	3.7	11.3	7.7	11.5
22. IV	3.6	8.6	6.2	9.2	6.8	13.8	4.7	8.0	7.7	12.0**

*B. *piniperda* swarming collections started **swarming maxima
**parveilukeräys aloitettiin* ***parveilun huippu*

Table 3. Daily mean and maximum temperatures during the period May 5 – 20, in 1961, 1962 and 1964, according to measurements at Rovaniemi Airport.

Taulukko 3. Vuorokausien keski- ja maksimilämpötilat 5. – 20. IV. vuosina 1961, 1962 ja 1964 Rovaniemen lentoasemalla suoritettujen mittausten mukaan.

Date *Päivämäärä*	Temperature °C *Lämpötila °C* 1961		1962		1964	
	Mean *Keskilämpö*	Maximum *Maksimi*	Mean *Keskilämpö*	Maximum *Maksimi*	Mean *Keskilämpö*	Maximum *Maksimi*
5. V	1.0	3.5	1.3	4.1	1.1	4.6
6. V	0.2	2.6	1.3	2.9	0.2	1.7
7. V	−0.2	1.4	1.5	5.4	0.6	2.7
8. V	1.4	3.0	2.8	6.6	6.0	10.9
9. V	2.4	5.2	3.6	7.5	4.1	8.9*
10. V	1.8	3.5	2.6	7.0*	6.0	10.2
11. V	1.3	2.7	5.6	8.9	9.1	13.2**
12. V	3.7	7.2	2.7	7.7	4.5	12.2
13. V	1.6	6.5	1.1	4.6	6.8	11.9
14. V	3.1	6.5	3.1	7.5	6.4	8.2
15. V	4.4	7.1	6.2	11.7**	5.8	9.9
16. V	5.0	8.6	7.7	11.1	3.1	7.0
17. V	6.4	9.7	8.2	13.0	4.7	8.8
18. V	5.3	7.8	9.2	13.1	4.3	7.7
19. V	5.4	8.3*	9.7	15.5	5.9	11.5
20. V	5.6	9.4	9.5	14.3	7.0	10.1

**B. piniperda* swarming collections started **swarming maxima
**parveilukeräys aloitettiin* ***parveilun huippu*

(pers. comm.) found large numbers of *B. piniperda* beetles from various breeding materials on May 7—8, 1963, in Laanila, about 300 km north of Rovaniemi. Since swarming started in the Helsinki region in 1963 on April 19, the time difference between the swarming periods in the Rovaniemi and Helsinki regions has probably been under two weeks. The temperature records from meteorological observation stations close to the collection sites, are shown in tables 2 and 3 for the swarming periods. Table 2 shows that swarming collections have been started in the Helsinki region after the first time the daily mean temperature has risen to 6° C, and the maximum to at least 11° C. In 1963, however, swarming collections were started a day late, probably because of the surprisingly quick rise in temperature. In the Helsinki region, the best swarming days in 1962—1965 were the ones with a maximum day temperature of at least 12° C (in 1961, the best swarming day was not recorded in either region).

The author was in the field in the Rural Commune of Rovaniemi, in 1962 and 1964, continuously for several days before the beginning of swarming. In 1961, however, the first insects could have been in flight already before May 19 (cf. table 3), when the author came to Rovaniemi. Table 3 shows that the daily temperature maxima at Rovaniemi Airport, about 20 km north of the collection sites, were 7—9° C at the beginning of the swarming collections. Maximum swarming took place in 1962 at a maximum temperature of 11.7° C (the value recorded at Rovaniemi Airport), and of 13.2° C in 1964.

Figure 2 shows the numbers of *B. piniperda* beetles collected on each day after swarming started, and the cloud cover and temperature observations at the Hirvas meteorological observation station, a few kilometers from the collection site. The figure shows that on May 10, 1962, when there was hardly any cloud cover and the temperature at 15.00 hrs was 7.7° C at Hirvas, the first 117 insects were collected. The following day, with an almost complete cloud cover and a corresponding temperature of 10.5° C, 510 insects were collected. The three next days had afternoon temperatures of 9.5° C, 5.5° C and 8.5° C, and 28, 36 and 296 *B. piniperda*

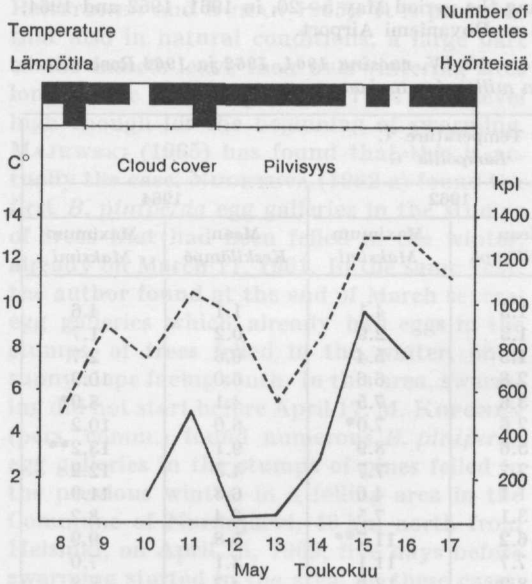


Figure 2. Numbers of *B. piniperda* beetles collected on various days in May 1962 in Rural Commune of Rovaniemi (continuous line) and temperature at the Hirvas meteorological observation station at 15.00 hours (broken line).

Kuva 2. Toukokuussa 1962 Rovaniemen maalaiskunnassa eri päivinä kerättyjen pystynävertäjien lukumäärä (yhtenäinen viiva) sekä lämpötila Hirvaan säähavaintoasemalla klo 15.00 (katkoviiva).

beetles were collected. The peak (966 beetles) was reached on May 15, with 13.0° C at Hirvas at 15.00 hrs and an almost cloudless sky. In the same temperature and cloud-cover conditions on the following day, the number of insects collected had dropped to 755.

Data from Vihti, 1970. In spring 1970, similar swarming collection traps were installed in Vihti as the ones used in several studies concerning bark beetles (e.g. Chapman and Kinghorn 1955, Bakke 1968 a, Subansenee 1971). A vertical 50 × 60 cm, 5 mm acrylic sheet was placed above a 60 cm long water container. A little detergent was added to the water containers to remove surface tension. The acrylic sheets in eight traps were painted white, and in the next eight ones black. Eight sheets were kept transparent. Six traps were installed with no trap trees. Around the other traps, four 2-meter long trap logs were placed in the direction of the main compass points. At nine sites,

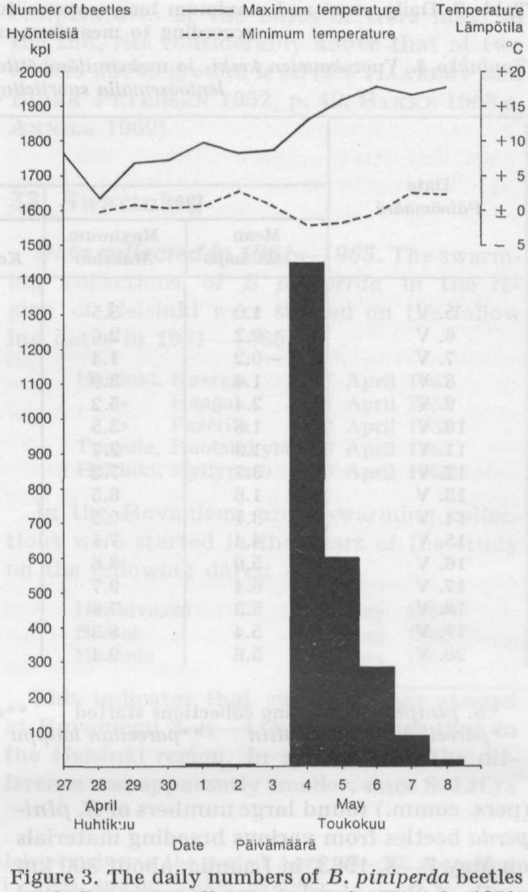


Figure 3. The daily numbers of *B. piniperda* beetles which flew into collection traps in Vihti in 1970.

Kuva 3. Eri päivinä keräilypyydyksiin lentäneiden pystynävertäjien lukumäärä Vihdissä keväällä 1970.

debarked trap logs were used, and the bark was left intact at the other nine. Also the acrylic sheets of the traps were oriented so that every other sheet was in the north-south and every other in the east-west direction. The traps were examined daily from April 27 to May 8. After this period, the traps were only examined on May 22 and 30. The traps were examined at 8.00 hrs on each day, except May 5 and 6 when they were examined hourly until 19.00 hrs. Wind velocity was estimated as calm, gentle breeze, moderate wind, and strong wind, mainly on the basis of the movement of tree branches (see Lehtinen 1965, p. 235). Strong wind on the scale corresponds to 17—21 m per second.

The results from Vihti for spring 1970 are shown in figure 3. It shows that the first

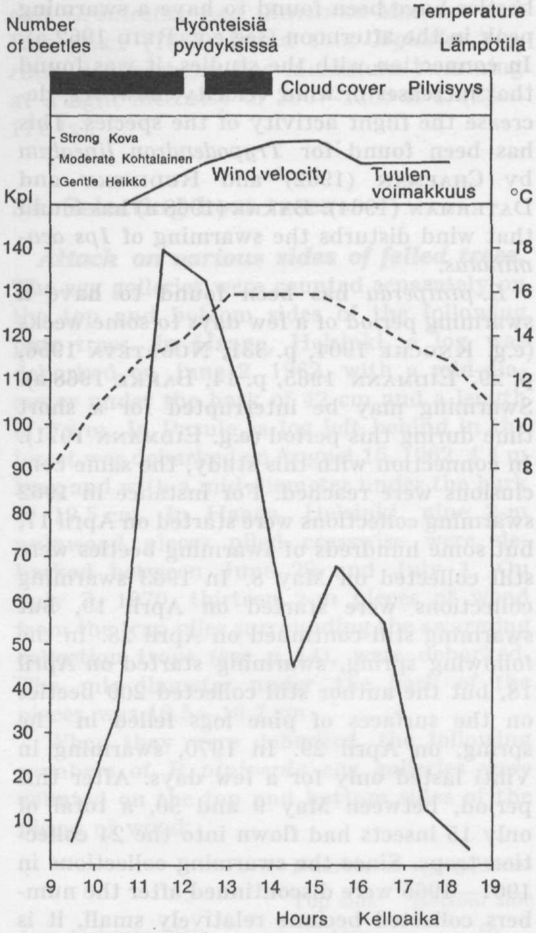


Figure 4. Hourly numbers of *B. piniperda* beetles which flew into collection traps in Vihti on May 5, 1970 (continuous line). Broken line = temperature.

Kuva 4. Vihdissä 5. V. 1970 eri tunteina keräyspyydyksiin lentäneiden pystynävertäjien lukumäärät (yhtenäinen viiva). Lämpötila (katkoviiva) mitattiin varjossa kahden metrin korkeudella maasta.

B. piniperda beetles flew into the traps on May 1, with a temperature of 10° C in the shade. The maximum temperature of the two following days was under 10° C, and only on May 2 had a few insects flown. The May 4 maximum temperature was 13° C and swarming was at its maximum. During the two next days, temperature continued to rise, and May 7 can be regarded as the end of the swarming period. Between May 8 and 22, only five insects were found in the traps, and between May 22 and 30 about ten.

Figures 4 and 5 show the numbers of

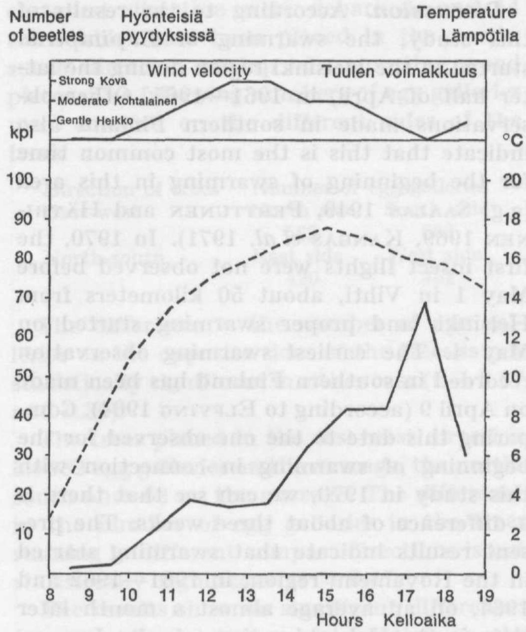


Figure 5. Hourly numbers of *B. piniperda* beetles which flew into collection traps in Vihti on May 6, 1970 (continuous line).

Kuva 5. Vihdissä 6. V. 1970 eri tunteina keräyspyydyksiin lentäneiden pystynävertäjien lukumäärät (yhtenäinen viiva).

insects collected hourly from the traps in Vihti on May 5 and 6, 1970, between 8.00 and 19.00 hrs. The figures indicate that wind velocity has a considerable significance for insect flight activity. On May 5, the most active flight period was from 11.00 to 13.00 hours, with a temperature of 12.5—16.0° C and gentle to moderate wind. With increasing wind velocity, flight activity decreased, even though the temperature was still 16.0° C at 15.00 hrs. After 15.00 hrs, wind velocity decreased, and the flight activity of beetles increased despite a decrease in temperature. On May 6, flight activity increased continuously until 18.00 hours. It was at a maximum at 17.00—18.00 hrs, when there was practically no wind. Thus flight activity decreased on May 5, between 11.00 and 15.00 hrs, as wind velocity continuously increased and the temperature also increased. On May 6, on the contrary, flight activity continuously increased from 12.00 to 18.00 hrs. There was a simultaneous decrease in wind velocity. The temperature rose until 15.00 hrs and then started to decrease.

Discussion. According to the results of this study, the swarming of *B. piniperda* started in the Helsinki region during the latter half of April, in 1961—1965. Other observations made in southern Finland also indicate that this is the most common time for the beginning of swarming in this area (e.g. Saalas 1949, Perttunen and Häyrinen 1969, Kangas *et al.* 1971). In 1970, the first insect flights were not observed before May 1 in Vihti, about 50 kilometers from Helsinki, and proper swarming started on May 4. The earliest swarming observation recorded in southern Finland has been made on April 9 (according to Elfving 1904). Comparing this date to the one observed for the beginning of swarming in connection with this study in 1970, we can see that there is a difference of about three weeks. The present results indicate that swarming started in the Rovaniemi region, in 1961—1962 and 1964, on an average almost a month later than in the Helsinki region (cf. also Lekander 1970).

According to the results of this study, swarming collections were started in the Helsinki region after the maximum day temperature exceeded 11° C. In the Rovaniemi region, swarming was found to begin at a 7.0—8.9° C day maximum temperature at Rovaniemi Airport. It is quite probable that the temperatures were higher at the collection sites on these days. The airport is about 20 kilometers from the study area, and at a much higher and more exposed site. The temperatures found for the beginning of swarming agree with the results of earlier research. Altum (1881) says that swarming starts when the temperature is 8—10° R (10—12.5° C). According to Chararas (1959), the temperature has to be 9° C, and to Hedqvist (1965) 8° C, before swarming starts.

According to the present results, peak swarming occurs after a shade temperature of over 12° C. This has also been found in many previous studies (e.g. Knoche 1904, p. 340, Trägårdh 1911, p. 25, Chararas 1962, p. 228, Bakke 1968 a, p. 489, Eidmann 1971).

In connection with the swarming collections, it was found that *B. piniperda* flight activity was generally at a maximum in the afternoon. This has also been found for instance by Bakke (1968 a). Also other bark beetles have been found to have a swarming peak in the afternoon (see e.g. Reid 1962 a). In connection with the studies, it was found that increases in wind velocity, however, decrease the flight activity of the species. This has been found for *Trypodendron lineatum* by Chapman (1962) and Rudinsky and Daterman (1964). Bakke (1968 a) has found that wind disturbs the swarming of *Ips acuminatus.*

B. piniperda has been found to have a swarming period of a few days to some weeks (e.g. Knoche 1904, p. 331, Nuorteva 1956, p. 29, Eidmann 1965, p. 14, Bakke 1968 a). Swarming may be interrupted for a short time during this period (e.g. Eidmann 1971). In connection with this study, the same conclusions were reached. For instance in 1962 swarming collections were started on April 17, but some hundreds of swarming beetles were still collected on May 8. In 1963 swarming collections were started on April 19, but swarming still continued on April 28. In the following spring, swarming started on April 18, but the author still collected 200 beetles on the surfaces of pine logs felled in the spring, on April 29. In 1970, swarming in Vihti lasted only for a few days. After this period, between May 9 and 30, a total of only 15 insects had flown into the 24 collection traps. Since the swarming collections in 1961—1965 were discontinued after the numbers collected became relatively small, it is probable that there was some swarming even after this.

No attempt was made to study the effect of light intensity in connection with this project. It was, nevertheless, observed during the swarming collections that swarming was greatest on sunny days. The greatest numbers of *B. piniperda* beetles, however, were collected from the shady sides of trap logs. According to Perttunen and Häyrinen (1970) the flight activity of the spring specimens of *B. piniperda* is lower at light intensities of 0.1 and 1 lx than at intentisities of 100 and 1000 lx. They found that the take-off rates were a little lower at a light intensity of 1000 lx than at 100 lx. In relation to the effect of light on the swarming of other bark beetles, Rudinsky and Schneider (1969) have found that light intensity of over 2000 ft-c (186 lx) prevents the swarming of the species *Gnathorichus retursus* Lec.

and *G. sulcatus* Lec. Zethner-Møller and Rudinsky (1967) found that *Hylastes nigrinus* Mannerheim has maximum swarming at a light intensity of 300—1200 ft-c. (28—111 lx).

34. Selecting host trees

Attack on various sides of felled trees. The egg galleries were counted separately on the top and bottom sides of the following pine trees. In Haaga, Helsinki, a log was debarked on June 2, 1962, with a mid-diameter under the bark of 42 cm and a length of 3.4 m. In Pusula, a log left behind in the forest was debarked on August 15, 1962, 4.4 m long and with a mid-diameter under the bark of 19.5 cm. In Haaga, Helsinki, nine 2-m pulpwood pieces piled crosswise were debarked between June 29 and July 1. On July 7, 1970, thirteen 2-m pieces of wood from the trap piles surrounding the swarming collection traps (see p. 14), were debarked. The mid-diameter under the bark of the pieces was 10.5—18.7 cm.

When they were debarked, the following numbers of *B. piniperda* egg galleries were counted on the top and bottom sides of the pieces of wood:

	Number of egg galleries	
	Top side	Bottom side
Log, Helsinki 1962	119	60
Log, Pusula 1962	245	243
2-m pieces, Helsinki 1962	463	408
2-m pieces, Vihti 1970	705	384
Total	1 532	1 095

The difference between the numbers of egg galleries on the top and the bottom sides of the pieces is not statistically significant ($t = 0.67$). Previously, a larger number of egg galleries on the top side has been found by, for instance, H. Sylven (1916, p. 667) and Trägårdh (1921, p. 59). Eidmann (1965, p. 25) has found that in the beginning of swarming, *B. piniperda* more frequently establishes its egg galleries on the top than the bottom sides of logs. But according to him, a few days after swarming started, the bottom sides have as many or more sites attacked than the top sides.

On July 7, 1970, in Vihti, a total of 15 trees felled before swarming and placed in the east-west direction were debarked, and 14 trees which had been placed in the north-south direction on top of supporting wood pieces. The following numbers of egg galleries were counted on the different sides of the trees:

Direction of trees	Number of egg galleries	
East-west	North side	South side
	562	668
North-south	East side	West side
	420	451

The difference in the number of egg galleries on the opposite sides of the trees is not statistically significant in either case ($t = 0.87$ and 0.30).

The trees placed in the east-west direction had 82 egg galleries on the average, the north-south ones 62 on the average. The difference in the number of egg galleries in the trees running in different compass directions is not statistically significant ($t = 0.47$).

The results show no significant differences in egg gallery numbers in relation to the various compass directions. Nuorteva (1950) has previously reached the same conclusion in studies of egg gallery numbers in the basal parts of standing pines broken by the snow. However, Ratzeburg (1839, p. 210) mentions that Pannewitz has found more egg galleries on the east side of wood pieces than in other compass directions.

Attack on debarked and undebarked trap trees. The swarming collections of *B. piniperda* in spring 1961 led the author to think that debarked trap trees attract more bark beetles than undebarked ones. Two small tests were made in the following spring to see whether this is the case. The first test was made in Haaga, Helsinki, where 2-m pieces of trees felled on April 4, 1962, were piled into six trap piles, each with thirteen parallel pieces. All pieces in the three piles were debarked, in the other three none were debarked. *B. piniperda* beetles that flew to the piles were collected on April 21—22 and 24—25, and May 8 in the following way. The collector stayed successive five-minute periods alternately at the debarked and undebarked pile and collected the insects that had flown on the logs. Collections from debarked and undebarked logs each lasted a total of 7 h 25 min. During three hours of this period, there were two collectors, one for the de-

Table 4. The numbers of *B. piniperda* beetles caught with the help of debarked and undebarked trap logs in Vihti in 1970 (for details, see text).

Taulukko 4. Kuorituilla kuorimattomilla ja pyyntipuilla varusteluista pyydyksistä kerättyjen pystynävertäjien lukumäärä Vihdissä keväällä 1970.

Undebarked timber *Kuorimattomat puut*		Debarked timber *Kuoritut puut*	
Trap no. *Pyydyksen numero*	Number of insects *Pystynävertäjiä kpl*	Trap no. *Pyydyksen numero*	Number of insects *Pystynävertäjiä kpl*
7	240	4	252
8	131	5	165
9	93	6	170
16	231	13	138
17	1	14	106
18	34	15	173
22	15	19	412
23	12	20	115
24	27	21	111
Total *Yhteensä*	784	Total *Yhteensä*	1 642

barked and one for the undebarked pile, and collection was continuous. These collections resulted in 148 *B. piniperda* beetles from the debarked piles and 60 from the undebarked ones.

On May 15, 1962, four trap piles were made into a 70-year-old pine stand in the Rural Commune of Rovaniemi, similar to the ones made a month earlier in Helsinki. The timber in two piles was debarked. The *B. piniperda* beetles that flew into the trap piles were collected on May 15 and 16 by one collector, who stayed alternate ten-minute periods at the debarked and the undebarked pile. Collections were made from both debarked and undebarked piles for a period of two hours. 157 beetles were collected from the debarked and 77 from the undebarked trap piles. The design of the experiment in spring 1970 in Vihti has already been described in the part discussing *B. piniperda* swarming (p. 14). The results are summarized in table 4.

According to the table more *B. piniperda* beetles were caught in the traps surrounded by debarked trap logs. The difference is statistically significant ($t = 2.11^*$).

The results for 1962 indicate that more beetles were collected from debarked timber surfaces than undebarked trap logs. However, since the trap piles were not always watched continuously, it is possible that part of the insects which flew on undebarked timber had time to hide into bark crevices while the collector was at the other pile. In the 1970 Vihti experiment this possibility was prevented by the method of study. In this case it was possible to positively show that debarked trap timber attracted more *B. piniperda* beetles than undebarked ones. It is probable that the debarked trees emit more insect-attractant odors to the surroundings than undebarked ones. The importance of odors emitted by trees on the selection of the host for breeding has been shown and discussed in several studies (e.g. TRÄGÅRDH 1921, p. 63, KANGAS 1955, 1959, 1968 a, CHARARAS 1962, p. 227, PERTTUNEN et al. 1970).

Table 5. The numbers of *B. piniperda* beetles collected with help of traps with transparent, white and black acrylic sheets in Vihti in spring 1970 (for details, see text).

Taulukko 5. Läpinäkyvillä, valkoisilla ja mustilla akryylilevyillä varusteluista pyydyksistä kerättyjen pystynävertäjien lukumäärä Vihdissä keväällä 1970.

Type of timber next to trap *Pyydyksen vierellä olleiden pölkkyjen laatu*	Number of beetles in traps		
	Transparent sheet *Läpinäkyvä akryylilevy*	White sheet *Valkoinen akryylilevy*	Black sheet *Musta akryylilevy*
Traps without timber *Ei pölkkyjä*	18	0	4
Traps without timber *Ei pölkkyjä*	1	1	0
Debarked timber *Kuorittu*	252	165	170
Debarked timber *Kuorittu*	138	106	173
Debarked timber *Kuorittu*	412	115	111
Undebarked timber *Kuorimaton*	240	131	93
Undebarked timber *Kuorimaton*	231	1	34
Undebarked timber *Kuorimaton*	15	12	27
Total *Yhteensä*	1 307	531	612

Effect of collection trap color. The 1962 experiments described above, and observations made at swarming collections in several years led to testing whether the light color of the debarked trap trees had an attractant effect on swarming *B. piniperda* beetles. In spring 1970, an experiment was carried out in Vihti to determine the collection results using traps with transparent, white or black acrylic sheets. The experimental design has been described on page 14. The results are shown in table 5.

Table 5 shows that the transparent-acrylic-sheet traps caught over twice the number of beetles than the ones with a white or black sheet. The insects have thus seemed to keep away from the colored trap sheets. They have probably not seen the transparent trap sheet as well as these. The results agree with those of Chapman and Kinghorn (1958), indicating that swarming *Trypodendron lineatum* avoided glass sheets painted with various colors, in collection traps. The present results indicate that the light color of for instance debarked trap trees probably has no attractant effect on *B. piniperda*. The larger collections from the debarked timber are probably only due to the fact that it emits more insect-attractant odors than timber with bark, as was already stated above. The large number of *B. piniperda* beetles collected from drying laundry by Krausse (1922 c, p. 771) is probably not a result of the light color of the laundry, either. It is possible that also in this case the constituents of the detergent used attracted the insects. Whether pine soap, for instance, was used for washing, is not known.

Attack on growing trees. Two observations made by the author of *B. piniperda* attack on trees, which appeared quite healthy on the outside, are described in the following. The first observation was made on August 17, 1964, in Myllypuro, Helsinki, where a well-growing 7.2 m tall pine was felled after numerous *B. piniperda* attack sites were discovered on its bole. The above-bark diameter at breast height of the tree was 9.5 cm. During the preceding winter, a one-meter high pile of two-meter, undebarked pine timber had been piled against the tree. After the tree was felled and debarked, a total of 45 *B. piniperda* attack sites were counted in its base. The egg galleries were 3—52 mm long, with a mean length of 25 mm. 34 of the egg galleries were less than one meter from the ground. The others were 1.0—1.6 m from the ground. Except for two egg galleries, all were located below the top level of the timber piled against the tree. Many egg galleries had numerous egg niches and visible egg fragments. No larval feeding mines started from any of the egg galleries, and no live or dead parent insects were found in the egg galleries.

The other observation made by the author of *B. piniperda* attack on a tree which still looked quite healthy was in Pihlajamäki, Helsinki, June 6, 1965. The tree was an 8.5 m tall pine with an over-bark DBH of 25.0 cm. About one meter of garden soil had been brought to the base of the tree in summer 1963. The time of observation was at 17.00—18.00 hrs at a temperature of about 20° C. In the part of the stem up to two meters from the base, about 150 attack holes of *B. piniperda* were found; a large quantity of resin had flowed or was still flowing out of these. A dead adult insect was found in the resin which had flowed out of one of the holes. At the time of observation, insects were seen to push out resin from several egg galleries. Four insects were seen moving on the surface of the tree stem, and one of these flew away.

B. piniperda was not successful in establishing its egg galleries in the tree in this case. The tree was still growing well in summer 1971.

In the tree studied in Myllypuro, Helsinki, *B. piniperda* had tried to establish its egg galleries at the base only up to the level of the timber piled against the tree. This is probably due to the fact that the volatile substances emitted by the cut wood have led the beetles to mistake the growing tree as also a suitable breeding site. Another reason for the attack may be the attractant effect of the pheromones emitted by thosein dividuals, which had attacked the timber piled against the tree. Schönherr (1972) has recently found that the females of *B. piniperda* excrete a pheromone which attracts males and females of the species (see also Oksanen et al. 1970). It should be mentioned here, that McCambridge (1967) made individuals of the species *Dendroctonus ponderosae* Hopk. attack growing trees, on which he had attached pieces of timber containing insects of the same species which had attacked these pieces previously. He explains that the result is due to the pheromones excreted by the insects in the pieces of timber.

The attack by *B. piniperda* in Pihlajamäki, Helsinki, on the pine with the base covered by a one-meter layer of garden soil is possibly due to insect-attractant odors emitted by the tree, even though its vigor has been only temporarily weakened. This observation has significance also in practical forest management. By increasing tree growth which has slowed down for some reason, by for instance fertilizing, it is possible to increase the resistance of trees against bark beetles (see MERKER 1967).

The *B. piniperda* attack on growing trees was unsuccessful in both cases described above (see also A. SYLVEN 1916, p. 155, TRÄGÅRDH 1921, p. 43, KANGAS 1934 c, p. 24—25, LEKANDER 1955, p. 12). It is apparent that the large resin flow prevented egg development and forced the parent insects out of the trees, (see also LARROCHE 1971). NUORTEVA (1950) has previously found that *B. piniperda* eggs have not developed, due to resin flow, in pines with tops broken by the weight of snow (see also KANGAS 1934 c). Resin flow has been found to prevent the development of eggs of other bark beetle species also. REID (1963, p. 231) found that 32 per cent of *Dendroctonus monticolae* Hopk. eggs were prevented from developing by resin flow (cf. also other bark beetle species, KANGAS 1939, MERKER 1967, see also BERRYMAN and ASHRAF 1970).

It has been found that abundant resin flow forces out the parent insects of other bark beetle species also, from too vigorously growing trees. For instance BERRYMAN (1969) has found that resin flow forced out the beetles of the species *Scolytus ventralis* Le Conte, from resistant *Abies grandis*, after they had proceeded some distance in establishing their egg galleries.

Attack on stumps of various sizes. The following method was used to determine the numbers of *B. piniperda* egg galleries in various-sized stumps. In Ruovesi, Kuorevesi, Evo (Lammi) and Tuusula, a total of 84 stumps of pines felled in the preceding winter were debarked in August 1963. In the process of debarking, the numbers of egg galleries and also of exit holes of the new-generation beetles in the bark were counted. The numbers of new-generation beetles is discussed later. On the stumps, the diameter under the bark of the cutting surface, the stump height from ground level, and the diameter under the bark midway between the cutting surface and the ground were measured. The surface area of the stump bark was estimated as the surface area of a cylinder with the diameter measured at half the height of the stump (see SALONEN 1964). The mean under-bark diameter of the stumps was 27.1 cm at the cutting surface, and the total bark surface area 13.8 m².

Table 6. The mean numbers of *B. piniperda* egg galleries in stumps of different sizes (for details, see text).

Taulukko 6. Pystynäverläjän emokäytävien lukumäärä eri kokoisissa kannoissa.

Class *Kannon läpimittaluokka*	Mean stump under-bark diameter, cm *Keskiläpimitta kuoren alla cm*	Mean stump bark surface area, cm² *Luokan kantojen keskimääräinen kuoripinta-ala cm²*	Mean number of egg galleries *Emokäytäviä keskimäärin* per stump *kpl/kanto*	 per m² *kpl/m²*
1	14.6	0.067	13	147
2	20.3	0.100	21	170
3	26.9	0.134	20	177
4	30.1	0.166	22	140
5	32.8	0.195	27	131
6	37.4	0.261	32	161

The stumps were classified into six diameter classes according to the diameter of the cutting surface. The first diameter class consisted of the 14 smallest stumps, the second one of the 14 second smallest etc. The mean numbers of egg galleries in the stumps of the various diameter classes are summarized in table 6.

The results indicate that the number of egg galleries per stump probably increases with increasing stump size. This has previously been found by ELGSTRAND (1924, p. 60). If the numbers of egg galleries per unit bark area are examined, it is found that these have been about the same for various-sized stumps.

35. Penetrating the bark

In 1962—1964, a total of 902 such *B. piniperda* egg galleries were excavated in the field from various breeding materials, where egg-laying had not yet started. All the insects which were alone in the egg galleries were collected into the same bottle. When there were two insects in the egg gallery, the ones that were ahead were collected in one, and those which were behind, into another bottle.

Sex determination of the insects gave the following results:

	Males	Females
Insects which were alone	30	224
Ahead in gallery	7	641
Behind in gallery	559	19

According to the results 88 per cent of the insects alone in the galleries were females. Where two insects were in the gallery, 99 per cent of the ones ahead and 3 per cent of the ones behind in the gallery were females.

These results support earlier observations that the *B. piniperda* female starts digging the egg gallery (e.g. HOLMGREN 1867, ALTUM 1881, TRÄGÅRDH 1911, 1921, GRÖNBERG 1914, WOLFF 1920, EIDMANN 1965).

Where the male was alone or ahead in the egg gallery, it may have entered an egg gallery which the female had left for some reason. It is also possible that these were cases of feeding and not egg gallery establishment (see HENNINGS 1908, p. 27). When the insect behind was a female, it had probably entered an egg gallery established by another female, which the male had left or which the male had not yet entered.

36. Copulation and pair formation

The author has observed *B. piniperda* copulation and pair formation during the swarming collections in 1961—1965. The observations indicate that copulation has been very common after the female has already half penetrated the bark. A few times copulation was observed to take place already before egg gallery excavation had started. After egg laying had started, copulation was also observed in the copulation chamber at the beginning of the egg gallery. A total of 966 *B. piniperda* beetles were collected on May 15, 1962, in Rovaniemi Commune on the surfaces of debarked trap trees. Of these, seven pairs were found copulating. Since the insects were on debarked trees, however, the relative number of pairs copulating can not be considered typical of copulation before egg gallery excavation.

The author has observed that copulation takes from two minutes to 34 minutes. The copulation time has thus been clearly longer than e.g. the 10—60 seconds observed for *Dendroctonus monticolae* (REID 1958).

According to the author's observations, the male usually comes to the female when the female has started egg gallery excavation, but is still partly visible. It seems, however, that the male may leave the female even after copulation.

Examples of observations made by the author concerning male behavior during bark penetration by the female, will follow:

1. A female had just started to excavate the egg gallery. A male was rapidly moving next to the female, trying to copulate now and then. When a log shading the pair from the sun was moved away, the male left the female. When it had moved to about half a meter from the female, it was collected. After about an hour the female had entered the bark almost entirely, and another male was after it.

2. A female had excavated the egg gallery to the depth of its own length. It was followed under a bark scale by two males.

3. A female had penetrated the bark to half its length. A male was behind it. After a while another male entered, pushed the male following the female to the side from behind and took its place. However, the first male attacked the newcomer and managed to drive it away after a short battle. The loser-male moved into a 3 cm long egg gallery, with a lone female, about half a meter away.

The observations made in connection with this study on *B. piniperda* copulation agree with earlier findings. Copulation prior to bark penetration by the females or during gallery excavation into the bark has been found by e.g. RATZEBURG (1839), BOS (1891), HESS (1898), TRÄGÅRDH (1911), GRÖNBERG (1914), WOLFF (1920) and ESCHERICH (1923). Copulation in the copulation chamber at the beginning of the egg gallery has been mentioned by e.g. BARGMANN (1907), KRAUSSE (1922 a) and ESCHERICH (1923). Copulation of this species can sometimes occur already at the overwintering site before swarming (see KNOCHE 1904, p. 548, JØRGENSEN and BEIER PETERSEN 1951, p. 478).

37. Feeding in the shoots in the spring

In 1965, the first swarming *B. piniperda* specimens were seen in the Helsinki region on April 20. Less than two weeks later the author found several beetles which had bored themselves into pine shoots in a pine stand growing on peat in the Helsinki City area. After a more thorough inspection, a total of 46 insects were found in the shoots. Of these, 25 were males and 21 females. All moved towards the terminal bud. Some individuals were already within the terminal bud; the abdomens of others were still visible at the entrance hole to the shoot. Only in one case the entrance hole to the shoot was on the side of the 1963 shoot growth. In one shoot, there were two insects in the same burrow. Fresh resin flowed out of all shoot entrance holes. The longest egg galleries in logging slash on the ground were about two centimeters long and they contained about ten eggs. There were, however, also plenty of egg galleries where egg laying had not started.

Also in the springs 1969 and 1970, the author collected tens of *B. piniperda* beetles from pine shoots some days after swarming started. In other years, tree shoots were not inspected in the spring.

It is probable that the beetles found in pine shoots in these cases in the spring had flown there immediately after leaving their overwintering sites. These are probably beetles which had not had time to become sexually mature during the preceding fall and winter (see also KNOCHE 1904, p. 549, JØRGENSEN and BEIER PETERSEN 1951, p. 469). Since insects were found in the shoots in all the three years when they were looked for, it is probable that part of the beetles leaving their overwintering sites go into the shoots every year.

4. EFFECT OF TEMPERATURE ON BROOD DEVELOPMENT

41. General

The results of numerous studies concerning the effect of temperature on the rate of insect development have been published (see the review by SCHWERDTFEGER 1963). The development of insects from egg to adult has been found to take place within definite temperature limits. The lowest temperature at which development takes place is called the zero point of development. This has been found to vary among various insect species and even the various developmental stages (see e.g. the review by SCHWERDTFEGER 1963).

In general, we may say that the rate of development of the insect is faster the higher the incident temperature. The rate does not, however, rise linearly with temperature; usually the time of development/temperature relationship more or less follows an S-shaped curve. This is due to the effect of development-retarding factors at high and low temperatures (SCHWERDTFEGER 1963). Studies have been carried out in the laboratory concerning the effect of temperature on for instance the rate of brood development in bark beetles; the findings of such studies can not always be extrapolated to apply to field conditions also. The lack of temperature fluctuations in the laboratory, for instance, may result in a different development rate than fluctuating field temperatures (see SAALAS 1917, p. 26—27, UVAROV 1931, p. 159—160, JUUTINEN 1955, p. 102). BODENHEIMER (1927, p. 105) and FRIEDERICHS (1930, p. 168) have found that the time of insect development is somewhat longer in the field than at the same temperature in the laboratory (see also JUUTINEN 1955, p. 19). Laboratory experiments have been carried out in order to explain the significance of even and fluctuating temperatures for the rate of insect development. In the experiments, part of the insects have been grown at even and another part at fluctuating temperatures, maintaining the same mean temperature in both cases. The results have been variable (see SCHWERDTFEGER 1963, p. 137).

After it was found that the development rate of insects increases with increasing temperatures, mathematical formulas have been fitted to data concerning insect development rates (see SCHWERDTFEGER 1963, p. 141—142). The basis for all formulas proposed has been the RGT rule of van't HOFF presented in 1884, stating that the rate of a chemical reaction can be described by the formula

$$\frac{V_t + 10}{V_t} = Q_{10}$$

where V is the reaction rate, t the temperature and Q_{10} a constant.

The significance of temperature on *B. piniperda* development rates has been studied by some investigators (e.g. KNOCHE 1904, BAKKE 1968 a). In the present project, the effect of temperature on the rate of egg-laying, the rate of lengthening of egg galleries, and the duration of various stages of development have been studied. In a series of experiments in the laboratory, an attempt was made to find out the effect of temperature and also that of moisture on pupal development. During the study, an attempt was also made to determine the zero temperature points for the development of the insect at various developmental stages; this information has not previously been available. With the aid of these zero points for development, equations for calculating the duration of various developmental stages have been constructed.

42. Material and methods

Controlled development in pine logs. The method used in these experiments has already been described (see p. 8). The following experiments were carried out:

1. A total of 12 males and 30 females were put into four boxes on January 30, 1964. The insects were collected from overwintering sites in the bases of trees. A temperature of 23 ± 1° C was maintained in the boxes. Only the new-generation beetles, which came into

the glass tubes at the ends of the boxes were counted on a daily basis, in this experiment.

2. A total of 180 males and the same number of females were put into fifteen boxes on May 21, 1964. The insects had been collected about a week earlier in the Rural Commune of Rovaniemi after they had flown on felled trap trees. Temperatures of 10 ± 0.5° C, 20 ± 1° C and 26 ± 1° C were maintained in the boxes. This experiment was carried out to determine the duration of the egg-stage, the larval stage and the pupal stage, and the time the new-generation beetles remain within the bark, at various temperatures. For these determinations, some egg galleries were opened daily during the period when there was reason to believe that the developmental stage changed. The period from the release of the parent insects on the log to the emergence of new beetles from the bark was also determined. During the experiment, the lengthening of the egg galleries and the rate of increase in egg numbers, and their totals, were also followed in egg galleries excavated at the temperature of 10 ± 0.5° C. Egg galleries were inspected on these days after releasing the insects on the log: 1, 2, 3, 6, 8, 9, 11, 18, 20, 22, 26, 36, 38, 42, 44, 49 and 57.

Table 7. The days (×) of *B. piniperda* egg gallery inspections counted from the beginning of the experiments (at Viikki in 1965).

Taulukko 7. Pystynävertäjän emokäytävien tarkastuspäivät (×) Viikissä 1965 suoritetussa kasvatuksessa laskettuna kokeen alkamisesta lukien.

Temperature in box °C *Lämpötila kasvatuslaatikossa °C*	Days *Vuorokausia kokeen alkamisesta* 1	2	3	4	5	6	7	8	10	11	12	13	14	15
15	×		×	×		×		×		×		×		×
20	×	×	×	×		×		×	×		×		×	
25	×		×	×	×	×	×	×	×		×		×	

	Days *Vuorokausia kokeen alkamisesta* 17	19	21	24	25	27	29	30	31	41	44	45
15	×	×		×					×	×		
20	×		×	×		×	×	×			×	×
25	×	×	×	×	×				×			

3. 5 males and 10 females were put into a box on June 29, 1964. The insects had been collected from stumps brought to a temperature of 1° C at the end of March. The experiment was carried out to determine the length of the entire development period, as in experiment 1, but at 27 ± 1° C.

4. A total of 360 males and the same number of females were put into twelve boxes on January 8, 1965. The insects were collected from the bases of trees in the field. Temperatures of 15 ± 0.5° C, 20 ± 1° C and 25 ± 1° C were maintained in the boxes. The same inspections were made in this experiment as in experiment 2. The progress of egg gallery lengths and egg numbers was also followed, by excavating at each inspection and for each temperature five egg galleries. Egg gallery lengths were measured, and the numbers of eggs and larval mines were counted as long as egg laying continued. The lengths of the egg galleries were measured on the days shown in table 7.

Separate pupal development experiments. The duration of the pupal stage at various temperatures and relative humidities was also studied by the following method. In February, blocks of pine timber were placed into boxes described previously (see p. 8), and on top of the blocks, about twenty pairs *B. piniperda* beetles collected from overwintering sites in pine bases were released. The timber was debarked after most of the larvae had bored themselves into the tree bark for pupation. The larvae collected from the bark were then put into 1.5 × 1.5 cm partitions made of brass netting, inside a two-sided glass selection container of the same type used for instance by Perttunen and Häyrinen (1969). The relative humidity in the containers was regulated with water, NaCl and $MgCl_2$ (see p. 9). The containers were kept at 15 ± 1° C, 22 ± 1° C and 30 ± 1° C. At 15° C the containers were kept in the refrigeration room of the laboratory, at 22° C in the room, and at 30° C in a warming oven. Three containers were kept at each temperature. Each container had 150 larvae at the two lower temperatures, and 125 larvae at the highest temperature. In the experiment, the development of 1275 larvae was followed. The inspections of the containers were made after every 12 hours.

Observations made in the field. The development of *B. piniperda* galleries in the field was followed especially in 1961—1965. In 1965, progeny development was followed in Pihlajamäki, Helsinki, at a timber storage area with piles of 2-meter pulpwood. The pulpwood was debarked at 2—3 day intervals, on various sides, to reveal 10—50 galleries. The stages of development in these were recorded. In the other years, the inspections were less regular.

43. Development of egg gallery length

In this study, the egg gallery lengthening measurements for *B. piniperda* gave the results shown for the different temperatures in figure 6. The curves shown in the figure for the temperatures 15° C, 20° C and 25° C have been drawn on the basis of three-figure moving averages, of the mean length of the five egg galleries excavated during each inspection. At 10° C, only a single egg gallery was measured during inspections, and the three-value moving averages for these single galleries were used for the figure. Figure 6 shows that egg gallery length has not increased, at 25° C, after 14—15 days from releasing the parent insects on the log. At

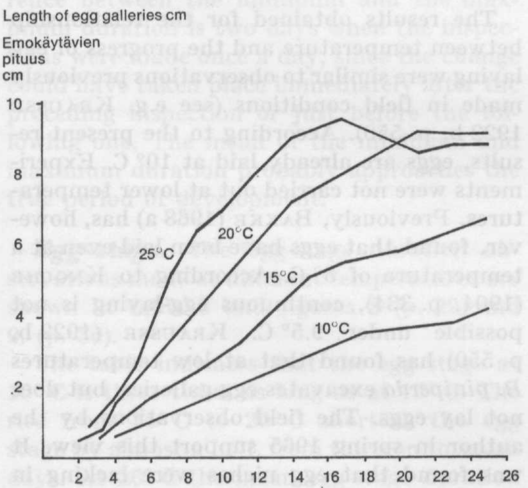


Figure 6. Lengthening of *B. piniperda* egg numbers at various temperatures.

Kuva 6. Pystynävertäjän emokäytäväpituuden kehitys eri kasvatuslämpötiloissa.

20° C, the lengthening of the egg galleries has stopped after 20—21 days from this event. At the two lowest temperatures, the lengthening of the egg galleries has continued through the duration of the experiment, and the figure does not show the end of egg gallery lengthening at these temperatures. On the basis of inspections, it was found that generally the egg gallery length did not increase at 15° C after 40 days from the beginning of the experiment, or at 10° C after 70 days.

The full length of the egg galleries at the various temperatures was about 8—9 cm. Egg gallery density was about the same in all the experiments, about 150 galleries per square meter of bark surface area. Previous findings indicate that *B. piniperda* may start egg gallery excavation already at 5° C (see Bakke 1968 a). This could also be seen in connection with this study: underneath and within the stumps kept at 5° C in the laboratory cold store, bark dust created by parent insect activity was found. These stumps had been brought into cold storage in late winter 1963. Annila (1969) has found that *Ips typographus* can also establish an egg gallery at this temperature.

The result of this study that *B. piniperda* excavates egg galleries faster at higher temperatures is not new (see e.g. Krausse 1922 c, Saalas 1949, p. 355).

44. Oviposition rate

The results of the laboratory development experiments concerning the rate of egg laying at various temperatures are shown in figure 7. The curves for increasing numbers of eggs at the three highest temperatures are based on the mean numbers of eggs plus larval mines in the five galleries which were excavated in each inspection. At 10° C, only one egg gallery was usually excavated, and the numbers of eggs counted in the inspection. The results for the individual inspections are shown by crosses in the figure, and the curve drawn through them has been smoothed by the eye. The period during which egg numbers could be recorded at the highest temperatures was shorter than the one for lower temperatures, due to the quicker development in these conditions of larval mines, which prevented the accurate counting of the egg numbers.

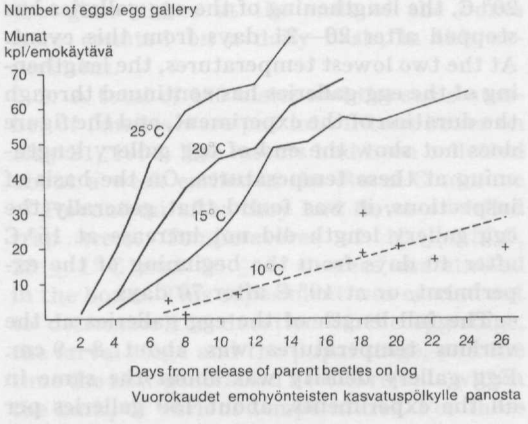


Figure 7. Increase in *B. piniperda* egg numbers at various temperatures.

Kuva 7. Pystynävertäjän munamäärien lisääntyminen eri kasvatuslämpötiloissa.

Figure 7 shows that the first eggs were found at various temperatures after the following numbers of days from the release of parent insects on the logs:

Temperature °C	Days
10	7
15	4
20	3
25	2

At 10° C, the first eggs were found after seven days from the release of parent insects in the boxes, but the egg gallery which was excavated already had four eggs. It is probable that there were eggs in this gallery at least a day or possibly two days earlier. The development curve as smoothed by the eye would indicate that egg laying at 10° C starts an average six days after the release of the parent insects on the log.

The distances from the egg gallery entrance on the log surface to the first egg niche and the numbers of egg galleries measured at various temperatures are summarized in the following table.

	Temperature in boxes 15° C	20° C	25° C
Number of egg galleries measured	45	35	30
Distance from entrance to first egg niche, mm	8.9	7.6	6.5

Egg laying seems to start closer to the entrance, the higher the temperature in the box. The length of the front part of the egg gallery is statistically significantly greater at 15° C than at 25° C (t = 3.93***) and statistically significantly greater at 20° C than 25° C (t = 2.37*). There was however, no statistically significant difference between these lengths at 15° C and 20° C. The following average egg numbers were found for the first 10-day period after egg laying started:

Temperature °C	Total number of eggs	Egg laying rate eggs/day
10	15	1.5
15	45	4.5
20	55	5.5
25	65	6.5

The results indicate that the egg-laying rate increases from 10° C to three times at 15° C. At higher temperatures consecutive 5° C increases result in relatively smaller egg-laying rate increases.

In connection with this study, no attempt was made to determine the differences among the total numbers of eggs laid at the various temperatures. This was mainly due to the fact that after sixty eggs had been laid, larval mines started to make further accurate counts impossible. Possible differences among the various temperatures in numbers of eggs laid per unit egg gallery length were not studied, either.

The results obtained for the relationship between temperature and the progress of egg laying were similar to observations previously made in field conditions (see e.g. Krausse 1922 b, p. 550). According to the present results, eggs are already laid at 10° C. Experiments were not carried out at lower temperatures. Previously, Bakke (1968 a) has, however, found that eggs have been laid even at a temperature of 5° C. According to Knoche (1904, p. 334), continuous egg-laying is not possible under 9.5° C. Krausse (1922 b, p. 550) has found that at low temperatures *B. piniperda* excavates egg galleries, but does not lay eggs. The field observations by the author in spring 1965 support this view. It was found that egg niches were lacking in the last excavated centimeter of most egg galleries after a cold spell of a week. The egg galleries were 3—4 cm long. During the week preceding the inspection, the highest mean day temperature was 6.9° C and the lowest 2.8° C at the Viikki meteorological observation station nearby. The relationship between temperature and egg laying in other bark beetle species is indicated by the results of Reid (1962 a) showing that *Dendroctonus monticolae* stops laying eggs after the temperature goes below 7° C (45° F).

It is difficult to explain why egg-laying starts further away from the gallery entrance at low temperatures than higher ones.

During the present study oviposition of *B. piniperda* was not studied at temperatures higher than 25° C. In earlier work, 30° C has been found to be the highest temperature at which eggs are laid (Bakke 1968 a). According to his work, *B. piniperda* no longer laid eggs at 32° C. Temperatures as high as these were not studied in connection with egg laying in this project.

45. Duration of various developmental stages

General. The minimum, maximum, and mean duration of the various *B. piniperda* developmental stages at various temperatures has been recorded. The minimum duration means the shortest duration of the stage that would have been possible because of the spacing of the inspections, and maximum the longest possible. Thus the difference between the minimum and the maximum duration is two days when the inspections were made once a day, since the change could have taken place immediately after the preceding inspection or just before the following one. The mean of the minimum and maximum duration probably approaches the true period of development.

Egg-stage. The egg-stage duration observations made at different temperatures are shown in table 8 and figures 8 (p. 29) and 9. (p. 30).

The table indicates that the egg stage at 10° C is three times as long as at 15° C. The rise from 15° C to 20° C shortens the egg stage by almost a half, from thirteen to seven days. At 26° C the mean egg-stage duration has been only four days.

In his experiments, rearing *B. piniperda* at various temperatures, Bakke (1968 a) found the first larvae after the following number of days from the beginning of the experiment: 24 at 12° C, 12 at 22° C, and 6 at 27° C.

Table 8. The duration of the egg stage of *B. piniperda* in the laboratory at various temperatures.

Taulukko 8. Pystynävertäjän muna-ajan pituus eri lämpötiloissa suoritetuissa laboratoriokasvatuksissa.

Mean rearing temperature *Kasvatuslämpötila keskimäärin* °C	Egg stage, days *Muna-aika vrk* Minimum *Minimi*	Mean *Keski-määrin*	Maximum *Maksimi*
10.2	37	40	43
15.1	12	13	14
20.6	6	7	8
21.4	6	7	8
25.2	4	5	6
26.0	3	4	5

The present results agree well with these. At 26° C, the author found the first larvae six days after the beginning of the experiment, just as Bakke at 27° C. At 22° C, Bakke found the first larvae after twelve days, and the present author observed the first larvae at slightly lower temperatures, 21.4° C and 20.6° C, after nine and ten days from the start of the experiment. The difference between these and the longer duration found by Bakke (1968 a) at the higher temperature is due to the fact that Bakke's inspection interval was six days. It is quite interesting that Bakke observed larvae after no more than 24 days from the beginning of the experiment at 12° C. Comparing this observation with the result of the present study, where larvae were found 57 days after the beginning of the experiment, or following the inspection at 51 days, at 10° C, we can see that the egg stage was lengthened to over double by a temperature decrease of only 2° C. There were probably no other essential differences affecting the results between the two experiments except temperature.

In spring 1965, *B. piniperda* swarming in the Helsinki region started on April 20. Still on May 16, only eggs were found in the egg galleries. Three days later, however, larvae were also seen. Since it takes some days after the attack before egg laying starts, the egg-stage duration can be estimated as about three weeks. According to results from the laboratory experiments, this would correspond to a mean temperature between 10° C and 15° C. The mean temperature of the period was, however, only 6.5° C according to the records of the nearby Viikki meteorological observation station. The highest daily mean temperature was 10.9° C and the lowest 2.8° C. The discrepancy between the laboratory and field observations can be explained by the laboratory results at different temperatures. The results have clearly shown that the development rate increases faster, for the same temperature rise in degrees, at higher than at lower temperatures. One has to remember too, that in the mean daily temperature in nature are included also those temperature values which do not yet have influence on different insect develepmental stages. The daily mean temperatures measured in the field do not, therefore, give a correct picture of the actual sum effect of temperature on the rate of development. The heat sum question will be discussed in more detail later on.

Since field temperatures vary annually during *B. piniperda* progeny development, it is understandable that field observations concerning the duration of the egg stage are variable. For instance, according to TRÄGÅRDH (1911), the egg stage lasts about fourteen days. However, EIDMANN (1965) found the first larvae five weeks after swarming, which means an egg stage of about a month. According to BAKKE (1968 a), the duration of the egg stage in Norway varies between twelve and forty-five days.

According to SAALAS (1919, 1949), larvae are not yet found in Finnish conditions in

Table 9. Mean April–September temperatures in Ilmala, Helsinki, in 1962–1965.

Taulukko 9. Huhti–syyskuun keskilämpölilat Ilmalassa Helsingissä vuosina 1962–1965.

Month *Kuukausi*	Mean of the period 1931–60 *Normaali*	1962	1963	1964	1965
April *Huhtikuu*	2.6	3.9	2.8	2.6	3.5
May *Toukokuu*	8.9	8.4	12.6	9.3	6.9
June *Kesäkuu*	14.0	11.8	14.6	14.5	14.8
July *Heinäkuu*	17.2	14.8	16.5	16.7	14.5
August *Elokuu*	16.0	13.1	16.7	14.7	14.4
September *Syyskuu*	11.1	10.0	13.0	10.8	12.8

May, even though swarming takes place at the end of April or the beginning of May. This would mean a length of about a month for the egg stage. According to the author's observations, larvae are frequently found in the Helsinki region already in mid-May. This was the case for example in 1965, despite that the spring was cooler than normally (see table 9).

Larval stage. The duration of the larval stage, as indicated by the laboratory experiments at various temperatures, is shown in figures 8 and 9. Attention is drawn in the figures to the considerable increase in the length of the larval stage, and also that of the other development stages, especially after temperature decreases below 15° C. The results obtained for the length of the larval stage are shown in the following summary table.

Temperature °C	Larval stage, days Minimum	Mean	Maximum
10	102	106	110
15	35	36	37
19–20	18	22	26
25–26	13	15	17

The duration has been calculated according to the same principle as for the egg stage previously.

The 60-day larval stage length found for 12° C by BAKKE (1968a) agrees well with the results of this study; it is a little shorter than the about 65 days indicated by figure 8 curve smoothed by the eye. It may be that the smoothed curve should go through a lower point at this temperature. The differences between the larval-stage durations found by BAKKE (1968a) and those determined in this study, at higher temperatures, are explained by the inspection interval differences: the stage change was recorded within a day in this study, and within six days in BAKKE's work, in the next inspection.

In nature, the length of the larval stage depends on weather conditions and varies annually. According to TRÄGÅRDH (1911), the larval stage is 7—8 weeks long. CHARARAS (1962) reports it as 55—85 days in France. According to the author's observations, the larval stage lasted only about four weeks in spring 1965, on the upper surfaces of felled trees in the Helsinki region. According to

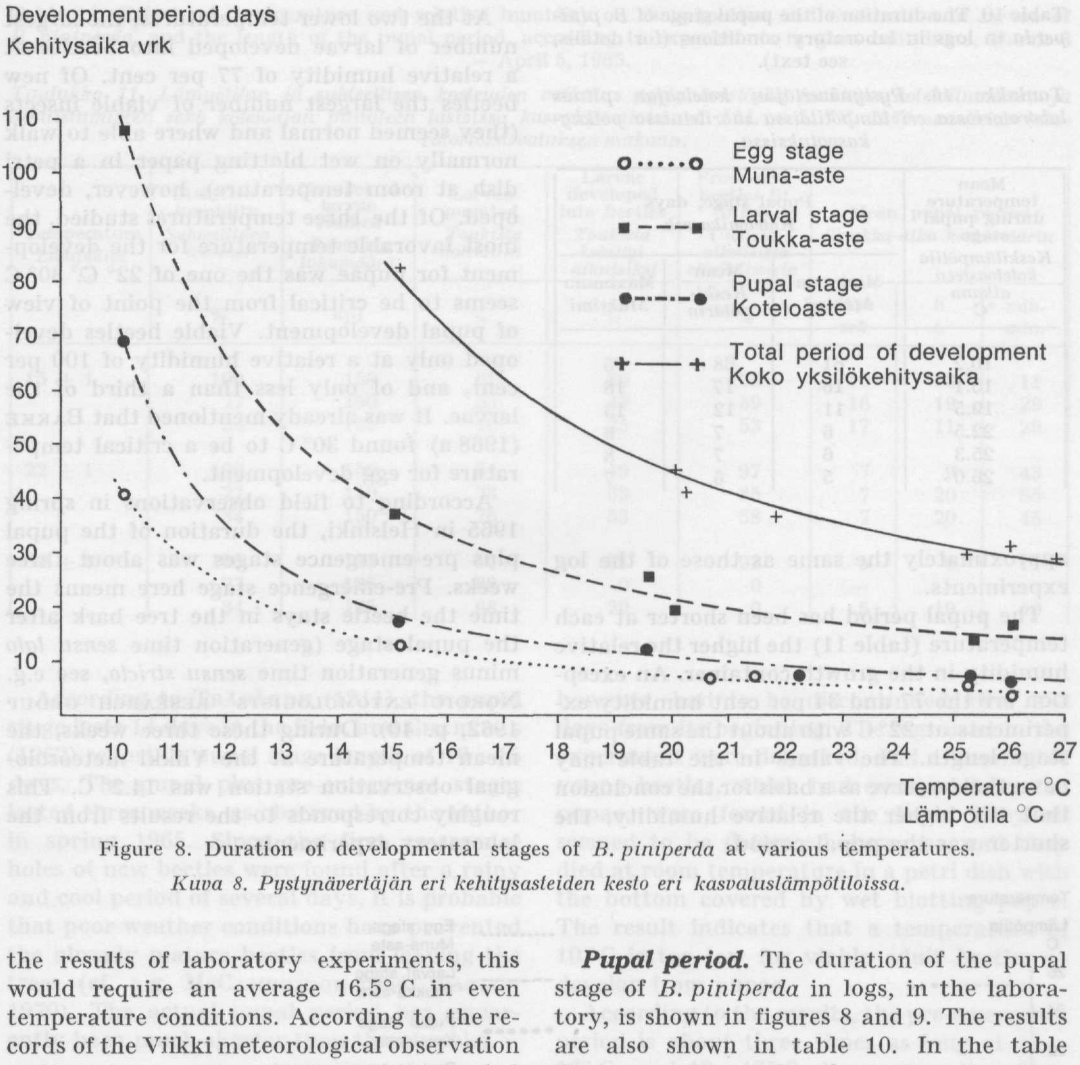


Figure 8. Duration of developmental stages of *B. piniperda* at various temperatures.

Kuva 8. Pystynävertäjän eri kehitysasteiden kesto eri kasvatuslämpötiloissa.

the results of laboratory experiments, this would require an average 16.5° C in even temperature conditions. According to the records of the Viikki meteorological observation station, the mean temperature of this period was, however, only 11.7° C. The highest daily mean temperature was 19.2° C and the lowest 4.4° C. The apparent contradiction between the laboratory and field results is due to the fact, already mentioned, that the high day temperatures in the daily means affect the development rate relatively more than the low ones.

The larval-stage duration observed by the author in the field in 1965, about four weeks, must be considered exceptionally short. The reason must be found in the exceptionally warm weather period during the larval stage before the middle of June, raising the mean temperature of June as a whole above normal (see table 9).

Pupal period. The duration of the pupal stage of *B. piniperda* in logs, in the laboratory, is shown in figures 8 and 9. The results are also shown in table 10. In the table the temperature value shows the mean temperature in various experiments during the pupal stage.

The table shows that the pupal stage lengthens considerably as the temperature decreases from 15.1° C to 10.2° C.

In studies concerning the duration of the pupal stage in glass containers with different relative humidities, the results in table 11 were gotten. At 30° C, development at a relative humidity of 77 % was unsuccessful for one reason or another. Of the larvae released, 68 % pupated but did not develop into a single new beetle. According to the table, the mean duration of the pupal stage varied at 15° C from 16.5 to 17.5 days, and at 22° C from 7.4 to 7.9 days. The results are thus

Table 10. The duration of the pupal stage of *B. piniperda* in logs in laboratory conditions (for details, see text).

Taulukko 10. Pystynävertäjän koteloajan pituus laboratoriossa eri lämpötiloissa suoritetuissa pölkkykasvatuksissa.

Mean temperature during pupal stage *Keskilämpötila koteloasteen aikana* °C	Pupal stage, days *Koteloaika vrk*		
	Minimum *Minimi*	Mean *Keskimäärin*	Maximum *Maksimi*
10.2	61	68	75
15.1	16	17	18
19.5	11	12	13
22.5	6	7	8
25.3	6	7	8
26.0	5	6	7

approximately the same as those of the log experiments.

The pupal period has been shorter at each temperature (table 11) the higher the relative humidity in the growth container. An exception are the 77 and 34 per cent humidity experiments at 22° C with about the same pupal stage length. The values in the table may nevertheless serve as a basis for the conclusion that the higher the relative humidity, the shorter was the pupal period.

At the two lower temperatures, the largest number of larvae developed into beetles at a relative humidity of 77 per cent. Of new beetles the largest number of viable insects (they seemed normal and where able to walk normally on wet blotting paper in a petri dish at room temperature), however, developed. Of the three temperatures studied, the most favorable temperature for the development for pupae was the one of 22° C. 30° C seems to be critical from the point of view of pupal development. Viable beetles developed only at a relative humidity of 100 per cent, and of only less than a third of the larvae. It was already mentioned that Bakke (1968 a) found 30° C to be a critical temperature for egg development.

According to field observations in spring 1965 in Helsinki, the duration of the pupal plus pre-emergence stages was about three weeks. Pre-emergence stage here means the time the beetle stays in the tree bark after the pupal stage (generation time *sensu lato* minus generation time *sensu stricto*, see e.g. Nordic entomologists' research group 1962, p. 40). During these three weeks, the mean temperature at the Viikki meteorological observation station was 14.2° C. This roughly corresponds to the results from the laboratory experiments.

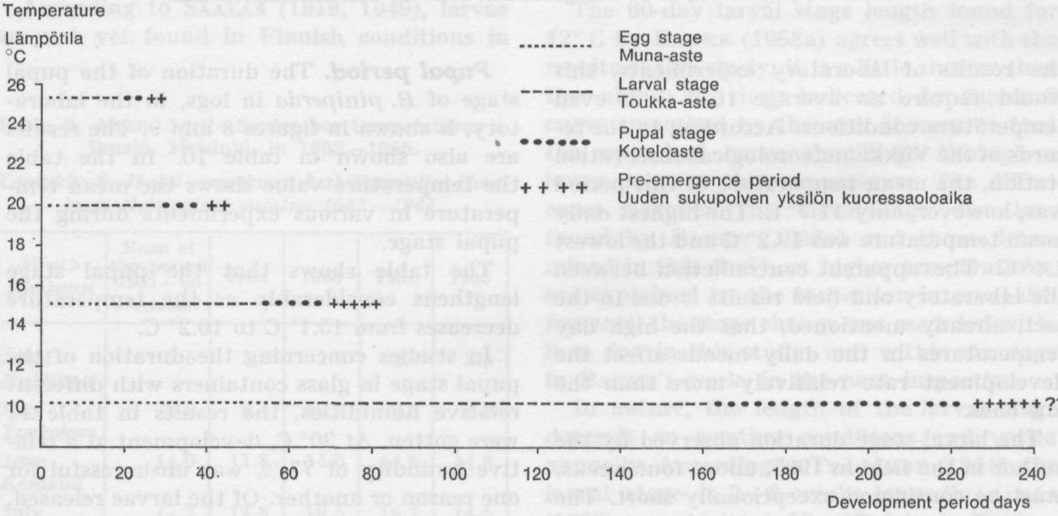


Figure 9. Duration of developmental stages of *B. piniperda* at various temperatures according to experiments in spring 1964.

Kuva 9. Pystynävertäjän eri kehitysasteiden kesto eri lämpötiloissa keväällä 1964 suoritettujen kasvatusten mukaan.

Table 11. Effect of temperature and relative humidity on the pupation and maturation of larvae of *B. piniperda*, and the length of the pupal period, according to experiments in glass containers, March 6 — April 5, 1965.

Taulukko 11. Lämpötilan ja suhteellisen kosteuden vaikutus pystynävertäjän toukkien koteloitumiseen ja aikuistumiseen sekä koteloajan pituuteen lasisissa kasvatusastioissa 6. III. — 5. IV. 1965 suoritetun laboratoriokasvatuksen mukaan.

Temperature *Lämpötila* °C	Relative humidity *Suhteellinen kosteus* %	Number of larvae studied *Toukkien lukumäärä* kpl	Larvae pupated *Toukista koteloitui* %	Larvae developed into beetles *Toukista kehittyi aikuisiksi* %	From new beetles fit to live *Uusista aikuisista elinkelpoisia* %	Mean pupal period *Toukka-aika keskimäärin* days *vrk*	h *t.*	min. *min.*
15 ± 1	100	150	61	39	95	16	13	11
	77	150	55	47	89	16	19	29
	34	150	40	25	53	17	11	29
22 ± 1	100	150	64	49	97	7	9	43
	77	150	78	63	85	7	20	55
	34	150	76	53	58	7	20	45
30 ± 1	100	125	56	31	92	5	0	17
	77	125	68	0	0	—	—	—
	34	125	68	20	0	5	19	46

According to Trägårdh (1911), the pupal stage lasts 14 days in the field, and Chararas (1962) reports a pupal stage length of 10—15 days. The pupal plus pre-emergence stages lasted three weeks, as observed by the author in spring 1965. Since the first emergence holes of new beetles were found after a rainy and cool period of several days, it is probable that poor weather conditions have prevented the already mature beetles from leaving the trees (cf. e.g. McCambridge 1964, Watson 1970). The actual pupal period has apparently been much shorter than three weeks.

Pre-emergence period. The length of the pre-emergence period at various temperatures in the laboratory experiments is shown in the following table.

Temperature °C	Pre-emergence period days
15 – 16	11
18 – 19	4
25 – 26	2

According to the results, the pre-emergence period is lengthened considerably as the temperature decreases from 18—19° C to 15—16° C. An attempt was made to determine the length of the pre-emergence period also at a temperature of 10° C. The experiment, however, had to be discontinued after 232 days from its beginning. The logs used in the experiment were debarked, and a number of young beetles, which had emerged from the pupae, were found in the bark. They all seemed to be deformed, however, and they died at room temperature in a petri dish with the bottom covered by wet blotting paper. The result indicates that a temperature of 10° C is too low for viable adult beetles to develop from pupae.

According to the results, the pre-emergence period is about three times as long at 15—16° C as at 18—19° C. A corresponding slowing down of development in the egg and larval stages was not found before the temperature dropped from 15° C to 10° C. It is apparent that there is a factor which slows down the emergence of the young beetles from the bark at the 15—16° C temperature level. The result is partly explained by the findings of Perttunen and Boman (1965) that flight activity of new-generation beetles which have come out of the bark can not be seen before the temperature rises to over 15° C.

Total period of development. The total period of development in this connection refers to the time from the release of the

Table 12. The total period of development of *B. piniperda* according to laboratory development studies (for details, see text).

Taulukko 12. Pystynävertäjän koko kehitysaika (emohyönteisten kasvatuspölkylle panosta uusien yksilöiden kuoresta esiin tuloon) eri lämpötiloissa laboratoriokasvatusten mukaan.

Temperature *Lämpötila* °C	Time in days *Kehitysaika vrk*		
	Minimum *Minimi*	Mean *Keskiarvo*	Maximum *Maksimi*
10	—	250[1]	—
15	80.0	80.5	81.0
20–22	35.0	40.3	45.0
25–27	28.0	29.4	32.5

[1] Estimated value

[1] *Arvioluku*

parent insects on the surface of the log to the emergence of the new-generation beetles. Thus it differs to some extent from the real development period (from egg laying to emergence), but describes in this connection better the development of *B. piniperda* as compared to the field conditions. The results of the experiments at various temperatures are shown in figure 8 (p. 29) and in table 12. The experiment at 10° C had to be discontinued before the new-generation beetles had emerged from the bark. The total period of development has, however, been estimated at 250 days. The results discussed previously in connection with the pre-emergence period, however, indicated that no such insects will probably develop at the temperature of 10° C, which are able to leave their tree of birth.

Table 12 shows that the total period of development was about 30 days at 25°—27° C and about 40 days at 20°—22° C. According to Chararas (1964) the total period of development lasted 41 days at 22° C and 33 days at 26° C. According to Bakke (1968 a) the length of the total period of development was 33 ± 3 days at 22° C and 21 ± 3 days at 27° C.

According to observations in the field, the development of *B. piniperda* progenies lasted in the Helsinki region, as counted from the beginning of swarming to the appearing of the first new generation exit holes, about two months in 1963 and two and a half months in 1965. The differences are due to the more favorable temperatures, in 1963, from the point of view of insect development (see table 9). According to results from laboratory experiments, the total development period of a little over two months would correspond to a mean temperature of 17° C. In the field, considerably lower mean temperatures were measured during the progeny development period in both years (see table 9). The explanation for the difference is the same as has already been discussed in connection with the larval period temperature relationships. The author's determinations of the total development period of *B. piniperda* in the field agree with those given by Saalas (1919, 1949). In Sweden, the length of the development period has been found to be about the same. In 1963, for example, progeny development from the beginning of swarming lasted 71 days according to Eidmann (1965).

The experimental results from this study indicate that the rate of *B. piniperda* progeny development is temperature-dependent to a considerable degree. This matter was first experimentally studied by Knoche (1904). In his greenhouse experiments at 12—26° C, the total development period was 65 days as contrasted with the 132 days for field development in the same year. Chararas (1962) also stresses the significance of temperature for the rate of development. He reports that field development in favorable conditions lasts 55 days, but in unfavorable conditions it may last as long as 100—130 days.

Relative duration of the various stages of development. On the basis of the curves in figure 8 (p. 29), the per cent shares of the various developmental stages in the total development period can be determined. The following per cent values for these shares are means, calculated from the individual values for the temperatures 12, 15, 18, 21, 24 and 27° C.

Egg stage	15 %
Larval stage	50 %
Pupal stage	23 %

The combined share of the period the parent insect stays in the tree before it starts laying eggs, and the pre-emergence period, is 12 %. About half of this represents each of these periods, as has been shown by the studies concerning the beginning of egg-laying and the length of the pre-emergence period (see p. 26 and p. 31).

Figure 8 also shows that the share of the egg and pupal stages, in the total development period *sensu stricto* is decreased by increasing temperature, while the share of the larval development period is increased.

46. The zero-development points for the various developmental stages

Methods. On the basis of the heat sum rule presented by BLUNCK (1914, 1923), the relationship between the rate of insect development to maturity and temperature can be expressed by the equation $y = \frac{a}{x - b}$ (see SCHWERDTFEGER 1963, p. 141—142). In the equation, y is the period of development in days, a the effective heat sum computed on the basis of daily mean temperatures, b the zero-development point, and x the experimental temperature.

In connection with this study, the zero-development points for the various developmental stages were calculated as follows. The duration of the various developmental stages at various temperatures was determined in laboratory experiments. In the equation shown above, x and y are thus known from the laboratory trials. According to the heat sum rule also stated above, the sum of effective degrees of temperature is a constant. Thus we can write $a = y_1 (x_1 - b) = y_2 (x_2 - b) \ldots\ldots = y_n (x_n - b)$. The subindex numbers refer to the various experiments. The values for y and x which were known from the experiments were inserted into the equation, and the value of b was then computed.

Results and discussion. The following zero-development values were found for the various stages of development:

Stage	Temperature °C
Egg stage	8.4
Larval stage	8.0
Pupal stage	8.8
Total period of development	8.5

The zero point for the pre-emergence period was found to be 13.1° C. This result is, however, based on results from experiments at only three temperatures. The zero-development points for the egg, larval and pupal stages have been determined on the basis of experiments at six different temperatures, and the zero-development point for the whole development period at seven temperatures. On the basis of pupal development studies in glass growing containers, the zero-development point found for the pupal stage was 8.7° C, which deviates by only 0.1° C from the zero-development point computed on the basis of experiments using logs as the breeding material.

According to the results reached in this study, the zero-development points for the various *B. piniperda* development stages differ to some extent. The zero points for all stages are, however, between 8.0 and 9.0° C. For other bark beetles, the zero-development points for the various stages have also been found to be different. WILLMANN (1951), for instance, found the following values for the zero-development points of the various stages in the life history of *Ips typographus*: egg stage 8.9° C, larval stage 7.8° C and pupal stage 7.0° C. According to ANNILA (1969), there are marks of development at the various stages of the life history of *Ips typographus* still at 5° C. VITÉ and RUDINSKY (1957) have found that the embryal development of *Dendroctonus pseudotsugae* stops as the temperature goes below 8° C.

47. The heat sums required by the various stages

Summing up the effective heat sums above the zero-development points for the various developmental stages, on the basis of daily mean temperatures, gives the following results.

Developmental stage	Sum of effective day-degrees (d.d.) of temperature °C
Egg stage	82
Larval stage	255
Pupal stage	107
Pre-emergence period	24
Total period of development	503

Using these heat sums, we can determine the duration of the various developmental stages in days, at a known experimental temperature, from the following equations. The

Table 13. Heat sums (dd > ± 0° C) required at various developmental stages of *B. piniperda* according to KNOCHE (1904), to observations made in the field in Pihlajamäki, Helsinki, in 1965 and to laboratory experiments carried out in 1964—1965.

Taulukko 13. Pystynävertäjän eri kehitysasteiden vaatimat lämpösummat (dd > ± 0°C) KNOCHEN (1904) sekä kirjoittajan Pihlajamäessä Helsingissä vuonna 1965 luonnossa tekemien havaintojen ja vuosina 1964—1965 tehtyjen laboratoriokasvatusten mukaan.

Developmental stage *Kehitysaste*	Field observations *Luonnon havainnot*				Laboratory experiments *Laboratoriokasvatukset*	
	KNOCHE		Observations in 1965 *Havainnot vuonna 1965*			
	Heat sum *Lämpösumma* °C	Mean temperature *Keskilämpö* °C	Heat sum *Lämpösumma* °C	Mean temperature *Keskilämpö* °C	Heat sum *Lämpösumma* °C	Mean temperature *Keskilämpö* °C
Egg stage .... *Muna-aste*	409[1]	9.1	182	6.5	408	10.2
Larval stage .... *Toukka-aste*	513	15.1	326	11.7	541	15.0
Pupal stage .... *Koteloaste*	154	17.0	283	14.2	257	15.1
Pre-emergence period *Nuoruusaste*	142	15.9	—	—	169	15.4
Total development period .... *Koko kehitysaika*	1 218[1]		791[1]		1 375[2]	

[1] Cumulated from swarming
[1] *Laskettu parveilusta alkaen*

[2] Cumulated from release of parent insects in boxes
[2] *Laskettu emohyönteisten kasvatuspölkylle panosta alkaen*

experimental temperature is represented by x and the duration in days by y.

1. Egg stage $y = \dfrac{82}{x - 8.4}$

2. Larval stage $y = \dfrac{255}{x - 8.0}$

3. Pupal stage $y = \dfrac{107}{x - 8.8}$

4. Pre-emergence period $y = \dfrac{25}{x - 13.1}$

5. Total period of development $y = \dfrac{503}{x - 8.5}$

The equations shown above for computing the duration of the various developmental stages are hyperbolic functions. It is probable that the true development function is somewhat different (cf. also SCHWERDTFEGER 1963). According to ANNILA (1969), the heat-sum/pupal-stage-duration function computed from different temperatures for *Ips typographus* is more or less S-shaped.

KNOCHE (1904) has computed the heat sums required at the various developmental stages of *B. piniperda* in the field, on the basis of his observations in 1899, by summing the daily mean temperatures (d.d. > ± 0° C) during these stages. According to his results, a heat sum of 1312.8—1218.6° C was required for the entire period of development from the beginning of swarming to the emergence of new beetles, depending on whether the sum is calculated from the first or the last swarming period. The heat sums he got for the various developmental stages are shown in table 13. The same table also shows heat sums computed by the method used by KNOCHE, from laboratory experiments in Viikki in 1964—1965 and from field observations in 1965. The heat sums from the laboratory experiments are shown for those cases, in which the mean temperature has been closest to the one reported by KNOCHE. The table shows that the heat sums in the field are smaller than the ones determined in the laboratory. The difference between the laboratory results and the 1965 field results is especially clear. The differences are probably due to the fact that in the field, the temperature in the tree bark is higher in sunny periods than the air temperature at the regular meteorological observation site at two meters from the ground (see SCHIMITSCHECK 1931, HAARLØV and BEIER PETERSEN 1952, ANNILA 1969).

Even at the same site, bark beetles may develop at different rates due to microclimatic variations (see e.g. ANNILA 1969). On June 14, 1964, the author observed that almost all *B. piniperda* parents had left the egg galleries on the top surfaces of pulp logs, but the parents on the bottom surface of the logs were still in the process of laying eggs, and even the furthest developed larvae were still quite small. In a trap tree examined on June 11, 1965, the larvae had already bored themselves into the bark on the upper side of the log, while the maximum length of the larval mines on the bottom side was 2.5 cm (see also KANGAS 1934 c, p. 44, NUORTEVA 1950, p. 41). The faster rate of bark beetle development on the top side is due to the fact that the sun warms it up more than it does the bottom side (SCHIMITSCHEK 1931, HAARLØV and BEIER PETERSEN 1952, ANNILA 1969). According to ANNILA (1969), temperatures in *Ips typographus* egg niches at the northern boundary of a clear-cutting area varied, in a spruce felled and lying from west to east, from 21.4 to 53.9° C, depending on the compass direction of the egg niches in the tree. He also found that the various developmental stages of *Ips typographus* required a greater heat sum on the southern sides of felled trees than on the other sides. ANNILA (1969) attributed this fact to the smaller effect of temperatures exceeding 40° C on development than on the accumulation of the heat sum.

5. DEPARTURE OF PARENTS FROM THE EGG GALLERY

51. Material and methods

B. piniperda males leave the egg galleries before the females (e.g. KNOCHE 1904, p. 389, TRÄGÅRDH 1921, p. 22, EIDMANN 1965, p. 15, LARROCHE 1971). In connection with this study, an attempt was made to find out when this happens.

In 1962—1964, 294 egg galleries were excavated in various breeding materials in the field at the time egg laying was ending. The sex of the insects found in the egg galleries was identified. At the inspection, a record was made of whether egg laying was still going on or whether it had already ended. Egg laying was considered to have ended, when the length of the terminal end of the egg gallery, from the last egg niche, exceeded 4 mm. This figure was arrived at by making measurements of this distance in egg galleries, where the female had not layed more than 10—30 eggs.

52. Results and discussion

The count of the male and female numbers in the 294 egg galleries, inspected at the time when egg laying was ending, gave the following results:

Egg laying stage	Egg galleries with male and female	Egg galleries with female only	Egg galleries total
Egg laying going on	84	12	96
Egg laying ended	5	193	198
All egg galleries	89	205	294

Statistical analysis of the results, using the Latin square method, gives $\chi^2 = 226.9^{***}$, indicating a highly statistically significant difference. Males thus leave the egg gallery at the end of egg laying. The male's task is to push the frass cut by the female out the egg gallery (GRÖNBERG 1914, SAALAS 1949). It seems that the ending of this task when the female starts feeding serves as a stimulus for the male to leave. This view is also supported by the laboratory observations made in connection with the present study. For instance in an/experiment carried out at 20° C, the first two males came to the glass tubes at the ends of the growth chamber on June 4, fourteen days after the experiment had been started on May 21, 1964. Figure 6 shows that the egg galleries had reached almost their full length at that time.

Males may leave the egg galleries without feeding there. According to PERTTUNEN and BOMAN (1965) and PERTTUNEN and HÄYRINEN (1969), the flight activeness of females taken from the egg galleries at the end of egg laying is very low, but that of the males is almost the same as in the spring. According to their work, this is due to the stunting of the female flight muscles during egg laying.

Both males and females fly from the egg galleries to the crowns of pines growing in the neighborhood. On June 16, 1964, the author collected a total of 90 *B. piniperda* beetles from pine shoots.Among these, 51 were males and 39 females. All were old beetles which apparantly had left the egg galleries. The beetles from the new generation had not yet flown into shoots at that time.

The attacks of *B. piniperda* adults in the shoots in the different parts of pine crowns were studied at Lammi on August 27, 1963, on the basis of two pines (7 and 8 m tall) felled on that date. A total of 271 entrance holes was recorded in the shoots in the area of the uppermost meter in the crown, 219 holes in the area of the next meter and only 38 holes in the area of the third meter. Also *B. minor* adults are feeding in the pine shoots (see e.g. SAALAS 1949). All the beetles collected from the pine shoots at Lammi, however, were *B. piniperda*. The concentration of the feeding *B. piniperda* adults in the uppermost parts of the crown has been known earlier (see e.g. SAALAS 1919, ELGSTRAND 1924, JUUTINEN 1953, ANDERSSON 1961).

In the field, males and females leave egg galleries during a relatively long period of time. This is due to the different rates of egg gallery construction at different sites and even on different sides of the same tree.

On June 14, 1964, for instance, the author found that several larvae had already pupated on the upper surfaces of the two-meter long trap trees. Egg laying had ended, and in most cases the female had already left the egg gallery. On the lower surface of the trees, there were several egg galleries where no larvae had yet developed from the eggs, and both the male and the female were in the egg gallery.

6. OVERWINTERING

61. General

In the cool climatic zone, bark beetles generally overwinter as adults, but also at other stages in their life history. Overwintering may take place in various sites. Species overwintering on the ground, among litter, include for instance *Trypodendron lineatum* (e.g. Löyttyniemi 1967) and *Blastophagus minor* (e.g. Sierpinski 1959). *Ips acuminatus* mostly overwinters under the bark, at its birth site in tree branches or stems (e.g. Bakke 1968 a). *Ips typographus* is also among the species overwintering like this (Annila 1969). Species overwintering in the basal parts of growing trees include *Trypodendron signatum* F. (Nuorteva 1962 a) and *B. piniperda* (e.g. Schwerdtfeger 1957). Overwintering *B. piniperda* beetles have sometimes been found higher up in the stem, up to a height of about two meters (Wolff 1920, Krausse 1922 b, Escherich 1923, Kangas 1934 c, Schwerdtfeger 1957). In southern Europe, the species has been reported overwintering also in the shoots still on the tree (Masutti 1969). The report may, however, in this case also refer to the species *B. destruens* (see Lekander 1971). According to Larroche (1971) *B. piniperda* overwinters in South-France both on the ground, among the litter, and in the bark crevices of growing trees. Kailides (1964) reports that the species often overwinters in eastern Macedonia at the larval stage. In these cases, the eggs have been laid in October and November (see also Chararas 1962).

It has been found that *B. piniperda* beetles enter their overwintering sites in the bases of trees in northern Europe, at the turn of September and October (e.g. Grönberg 1914, Saalas 1949, p. 356). In Central Europe, the movement to the overwintering sites takes place about a month later (Schwerdtfeger 1957). So far, the effect of air temperature changes or other possible factors on the movement of the species into overwintering sites has not been fully studied.

The snow cover provides the species, which overwinter in the litter layer and in the bases of trees, with good protection against cold (see Pulliainen 1966, Bakke 1968 a). Above the surface of the snow it may be very cold, and at the same time the soil may stay unfrozen (Cloudley-Thompson 1962, Coulianos and Johnels 1963). Winter may be lethal to the bark beetles at various stages of their life history overwintering above the snow surface (e.g. Bakke 1968 a, Berryman 1970).

An attempt has been made in connection with this study to find out the significance of temperature in the movement of *B. piniperda* into its overwintering sites and in its mortality during the winter. In this work, the significance of tree size and location, in terms of suitability for overwintering sites for the species has also been studied.

62. Moving into overwintering sites

Material and methods. The movement of *B. piniperda* into its overwintering sites was observed in the area of the City of Helsinki in 1962—1968. In 1963 and 1964, the author inspected in Pihlajamäki, at 1—2 day intervals after September 10, the bases of 10—20 pines during each inspection. The trees were 15—18 meters tall. In the other years, less regular inspections were carried out in various parts of the City area.

In fall 1968, observations were made about the movement to the overwintering sites in Jakomäki, Helsinki, in ten trees, during September 14 — October 27. The over-bark breast-height diameter of the trees was 9.6—16.7 cm and their height 5.6—8.4 m. Between September 14 and October 4, the inspections were carried out on a daily basis, except for the days September 20 and 21, when there were no inspections. There were also inspections on October 7, 12, 20 and 27. In the inspections, the insects were dug out with a sharp-tipped knife. The entrance hole into the bark could be seen by the frass the insects had cut from the bark. On September 19, the inspection was carried out in the morning, on the other days, between 17.00 and

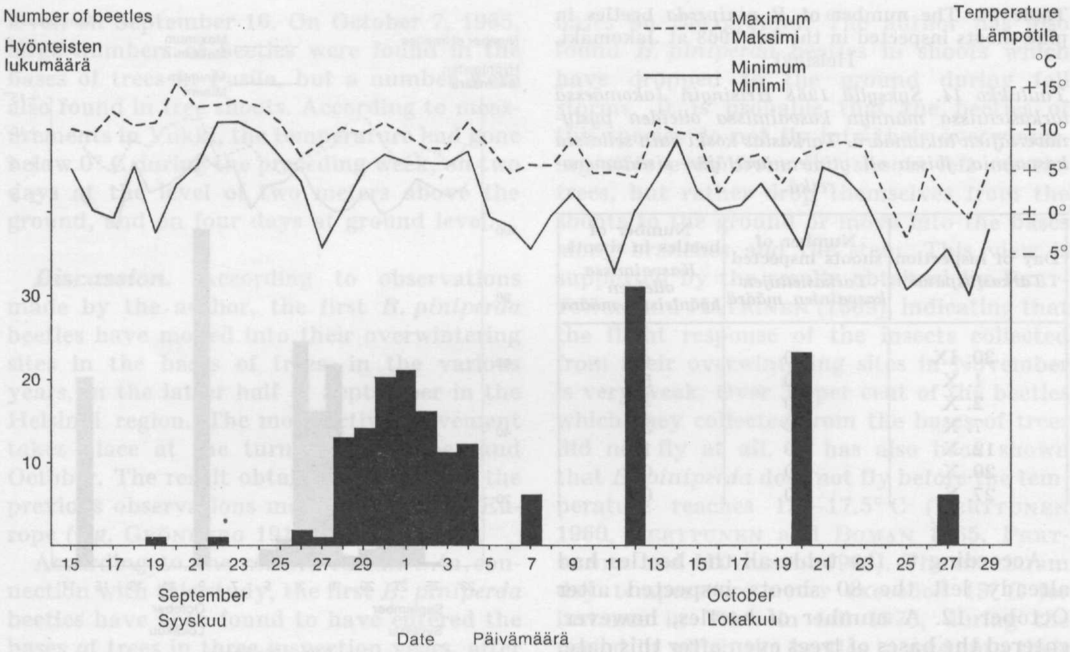


Figure 10. Number of *B. piniperda* beetles which entered sample tree bases in Jakomäki, Helsinki, in the period 15 September — 31 October 1968.

Kuva 10. Koepuiden tyviin menneiden pystynävertäjien lukumäärä Helsingin Jakomäessä 15. IX. — 31. X. 1968 välisenä aikana.

18.00 hours. In the same stand, on September 30 and October 1, 2, 7, 12, 20 and 27, a total of 230 shoots which had a *B. piniperda* entrance hole were inspected. During each inspection, 20—50 shoots were inspected. The shoots were split, and the insects which were found were collected. Weather observations were obtained from the Malmi Airport meteorological observation station, about one kilometer from the study area.

In fall 1970, during the period between September 22 and October 9, the bases of a total of 30 sample trees were inspected daily in Vihti, between 7.00 and 8.00 hours. The last inspection was on October 16, 1970. The over-bark breast- height diameter of the trees was 17.6—39.7 cm and their height 14.5—22.6 m. The method used in the inspections was the same as that used in fall 1968. The inspections were made by the author, except on September 29 and 30, and on October 4—8, when they were made by a technician. The temperature measurements were made in the study area with a Lambrecht thermo-hygrometer at two meters above ground level.

Results. In fall 1968, the first *B. piniperda* beetle that had moved into its overwintering site was found in Jakomäki, Helsinki, on September 19 (figure 10). The temperature had gone below 0° C (—0.6° C) at the Malmi meteorological observation station, which is about one kilometer from the observation area, for the first time during the fall on September 17. On the same day that the first insect was found in the base of a tree, the minimum day temperature was —2.5° C. Most of the insects moved into the bases of trees during a few days after the temperature on September 27 fell to —3.8° C. During the period September 28 — October 4, an average of 17 beetles had still entered the bases of the trees daily, between October 7 and 12, six beetles, between October 12 and 20, three, and between October 20 and 27, one beetle per day. The daily maximum temperatures between September 27 and October 4 were from 6.7 to 10.7° C. In this area, in inspections of shoots with *B. piniperda* entrance holes, the following results presented in table 14 were obtained.

Table 14. The number of *B. piniperda* beetles in pine shoots inspected in the fall 1968 at Jakomäki, Helsinki.

Taulukko 14. Syksyllä 1968 Helsingin Jakomäessä tarkastetuissa männyn kasvaimissa olleiden pystynävertäjien lukumäärä. Tarkastus koski vain sellaisia kasvaimia, joissa oli ytimennävertäjän sisäänmenoreikä.

Day of inspection *Tarkastuspäivä*	Number of shoots inspected *Tarkastettujen kasvainten määrä*	Number of beetles in shoots *Kasvaimissa olleiden hyönteisten määrä*
30. IX	30	4
1. X	20	5
2. X	20	4
7. X	50	3
12. X	30	1
20. X	50	0
27. X	30	0

According to the table all the beetles had already left the 80 shoots inspected after October 12. A number of beetles, however, entered the bases of trees even after this date.

In fall 1970, the first *B. piniperda* was found in Vihti in the base of a tree on September 25 (figure 11). The minimum temperature of the preceding night at two meters from the ground level was 0.2° C according to the thermo-hygrometer reading. The small numbers of insects found in the bases of trees on September 29 and 30, and October 4—8, are probably due to the fact that the inspecting person was not very familiar with the job. This was found in control inspections which he carried out jointly with the author. Therefore it is probable that more insects entered their overwintering sites during these periods, September 29—30 and October 4—8, than were reported in the results. The value for October 1 is probably larger than the actual one, as is the figure for October 9, since they include earlier entrants. The movement of *B. piniperda* into the bases of pines seems to have been very active during the period between September 27 and October 3, when the daily minimum temperature was 0° C or lower on five days. During this period, there were two days with a maximum temperature of 12° C. The largest number of beetles was found to enter the overwintering sites on October 3, 1970, when the minimum temperature was 5° C and the maximum temperature of the day 6° C.

The author's earliest observations of the

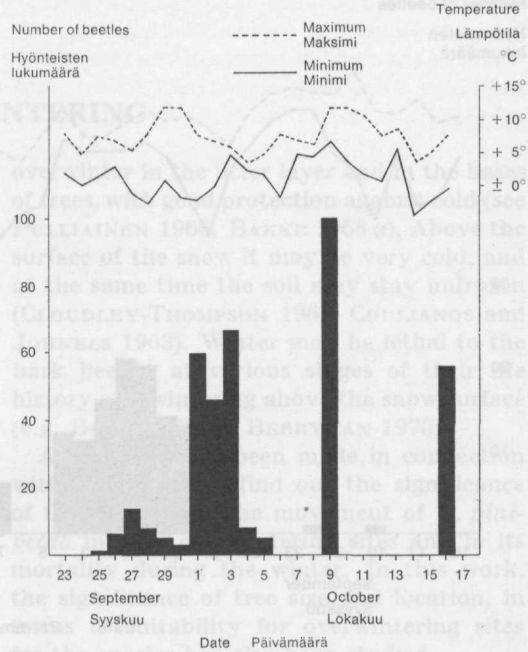


Figure 11. Number of *B. piniperda* beetles which entered the bases of sample trees in Vihti in the period 23 September — 16 October 1970.

Kuva 11. Koepuiden tyviin menneiden pystynävertäjien lukumäärä Vihdissä 23. IX. — 16. X. 1970 välisenä aikana.

movement of *B. piniperda* into the bases of pines were on September 13, 1964, in Pihlajamäki, Helsinki. At the nearby Viikki meteorological observation station, temperature had gone below 0° C (—0.7° C) during the previous day for the first time during that fall. There were, however, still large numbers of *B. piniperda* in the shoots of pines, growing in the area, on September 13. In the inspection on October 27 in the same area, numerous insects were found in their overwintering sites in the bases of pines. During the preceding week, temperature had gone twice below 0° C in Viikki at the level of two meters from the ground.

In 1965, the author found the first beetles of the species in the bases of pines in Pasila, Helsinki, on September 21. Since there were no earlier inspections in the area, it is probable that the insects had entered the tree bases after temperature had gone below 0° C (—0.7° C) for the first time, in measurements made in Viikki at two meters above ground level, on September 16. On October 7, 1965, large numbers of beetles were found in the bases of trees in Pasila, but a number were also found in tree shoots. According to measurements in Viikki, the temperature had gone below 0° C during the preceding week, on two days at the level of two meters above the ground, and on four days at ground level.

Discussion. According to observations made by the author, the first *B. piniperda* beetles have moved into their overwintering sites in the bases of trees, in the various years, in the latter half of September in the Helsinki region. The most active movement takes place at the turn of September and October. The result obtained agrees with the previous observations made in northern Europe (e.g. GRÖNBERG 1914, SAALAS 1949).

According to the results obtained in connection with this study, the first *B. piniperda* beetles have been found to have entered the bases of trees in three inspection years, after the temperature at nearby meteorological observation stations had gone below 0° C. In the fourth year when inspections were made, the first insect was found to have entered the tree base after the minimum temperature at two meters from ground level was 0.2° C. It seems that the decrease in temperature below or at least close to the freezing point is a stimulus releasing the movement into the overwintering sites. KNOCHE (1904, p. 545) was thus apparently quite close to the truth, as he said that the movement into the overwintering sites starts when temperatures in the fall go down to the threshold at which the insects in the spring leave their overwintering sites. In connection with this study, this has previously been stated to happen at least at a temperature of 3—5° C (see also KANGAS 1968). According to the present results, however, a subfreezing temperature stimulus is apparently needed to start the movement into the overwintering sites. Since temperatures were not, however, measured from within the shoots, this remains uncertain to some degree.

There are no detailed studies concerning the manner in which the insects move from the shoots to the bases of trees. According to ALTUM (1881, p. 258), the majority of the insects drop to the ground inside the shoots in the fall and move into the tree bases on the ground. The author has also found *B. piniperda* beetles in shoots which have dropped to the ground during fall storms. It is probable that the beetles of this species do not fly into their overwintering sites even from the shoots left on the trees, but rather drop themselves from the shoots to the ground or move into the bases along branches and the stem. This view is supported by the results obtained by PERTTUNEN and HÄYRINEN (1969), indicating that the flight response of the insects collected from their overwintering sites in November is very weak. Over 30 per cent of the beetles which they collected from the bases of trees did not fly at all. It has also been shown that *B. piniperda* does not fly before the temperature reaches 15—17.5° C (PERTTUNEN 1960, PERTTUNEN and BOMAN 1965, PERTTUNEN and HÄYRINEN 1969). The maximum day temperature never exceeded 15° C for instance in Vihti in fall 1970, during the period in which the beetles moved into their overwintering sites. In fall 1968, the maximum day temperature at the Malmi meteorological observation station exceeded 15° C (15.6° C) on one day during the weeks in which the movement into overwintering sites was observed.

63. Relationship between tree size and location and the number of overwintering beetles

Material and methods. The significance of tree size and location for the numbers of *B. piniperda* beetles overwintering in their bases was studied in Haaga, Helsinki, on the basis of data collected in the winters 1961—1962 and 1962—1963 from a forest bordering pine peatland previously used for collecting fuel peat. During the preceding years, large quantities of earth fill had been brought into the area. Because of this activity, and because of active construction work in the area, many pines have been weakened or stunted and have become suitable breeding material for *B. piniperda*. Additional breeding material has been provided by freshly cut undebarked logs. The *B. piniperda* population in the area has therefore become very large. Due to peat extraction, the peatland surface is typified by a pattern of alternating 4—5 meter wide higher peat ridges in the places where peat has not been extracted, and 5—6 meter wide depressions, with the surface about half a meter below that of the ridges, representing peat extraction places.

In December 1961, a total of 18 pines were felled in the area, all of them with numerous overwintering *B. piniperda* beetles in their bases. The stumps of the felled trees were dug out of the soil and left into the forest, covered with snow. The sizes of the stumps, measured from the cut surface, were the following:

	Diameter under bark cm	Bark thickness mm	Height from the ground cm
Largest value	20.5	30	45
Smallest value	12.0	14	17
Mean value	16.6	19	30

The stumps were brought into the laboratory on April 11—13, 1962, and put into paper bags. On the side of the bags, an oil lamp glass with a diameter of seven centimeters was attached. The outer end of the glass was closed with wire netting. The insects that came into the glass from the stumps were collected daily during a period of a week. After this period, seven of the stumps were debarked and the beetles found during debarking were collected. Eleven stumps were left in the bags and debarked on June 11—12, 1962, after the new-generation beetles which had been born in them had been collected. Before debarking, the exit holes of the new-generation beetles in the bark were counted (see p. 58). In connection with debarking, the parent insects which were found in the stumps and which had also overwintered in them, were collected.

In the beginning of March, 1963, a total of 40 pines were felled in the same area, and their stumps were used for experimental purposes. Seventeen of the pines grew in the peat-extraction depressions, and eighteen on the ridges in between. Five of the pines grew at the boundary of the ridge and the depression, so that part of their roots grew in the ridge soil and part down in the depression. The sizes of the trees, and the snow depth at their bases on February 28, 1963, are summarized in table 15.

On the ridges between the peat extraction depressions, the snow melted at the bases of the trees already in early March (cf. Yli-Vakkuri 1960, p. 3). The stumps were first stored in the forest, under snow, for a couple of weeks. As the snow started to melt, they were moved into the cold storage of the Department of Agricultural and Forest Zoology of the University of Helsinki, to a temperature of 0° C. On June 1—11, 1963, they were brought into a plastic bag at room temperature, after they had first been kept for 24 hours at a temperature of 5° C. The beetles which left their overwintering galleries were collected during a couple of days. The stumps were then debarked, and the live and dead *B. piniperda* beetles found were collected from them.

Table 15. The location and size of the pines felled in March, 1963, and the depth of snow at their bases on February 28, 1963 (for details, see text).
Taulukko 15. Maaliskuussa 1963 kaadettujen mäntyjen sijainti ja koko sekä lumen syvyys niiden tyvillä 28. II. 1963.

	Peat extraction depressions *Turpeenottopainanteet*	Ridges *Välialueet*	Ridge/depression boundaries *Välialueen reunat*
Number of trees *Puiden lukumäärä*	18	17	5
$D_{1.3}$ above bark, cm *$D_{1.3}$ kuoren päältä cm*	8.2 – 16.2	6.2 – 17.0	10.3 – 16.6
Height of trees, m *Puiden pituus m*	3.6 – 8.2	3.5 – 7.6	4.4 – 7.2
Snow depth at bases of trees, cm *Lumen syvyys puiden tyvellä cm*	50 – 60	20 – 40	10 – 20

In addition to the materials described above, those ten sample trees which were studied in Jakomäki, Helsinki in fall 1968, and in which the *B. piniperda* beetles were counted as has been previously described (see p. 38), were also used to determine the effect of tree size on the numbers of overwintering insects in their bases.

Results. A total of 2174 overwintering *B. piniperda* beetles were found in the bases of the eighteen pines felled in December 1961. Among these, 1402 were collected from the collection glasses attached to the paper bags, during a couple of days after the stumps had been put into the bags. 772 beetles were collected from the egg galleries they had constructed into the stumps. An average 121

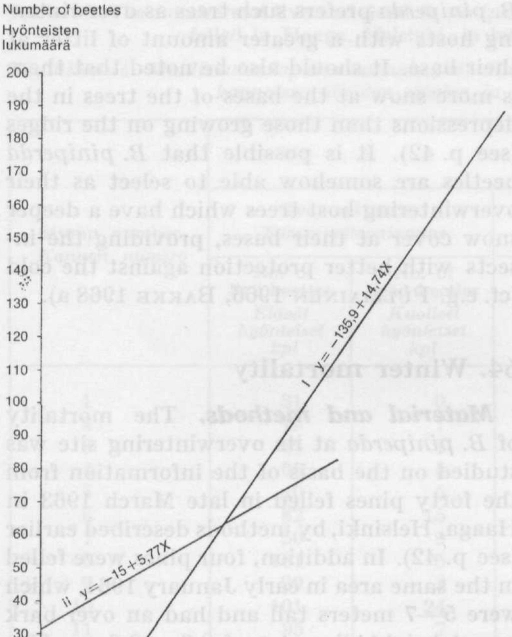


Figure 12. Regression of the number of *B. piniperda* beetles, overwintering in the bases of the trees, on DBH over bark (for explanations, see text).

Kuva 12. Puiden tyvissä talvehtivien pystynävertäjien lukumäärien riippuvuutta puun kuoren päältä mitatusta rinnankorkeusläpimitasta kuvaavat regressiosuorat. Kuvaaja I esittää joulukuussa 1961 Haagassa Helsingissä kaadetuista 18 männystä saatua tulosta ja kuvaaja II samalta alueelta maaliskuussa kaadetuista 40 männystä saatua tulosta. Kuvaaja III on saatu Helsingin Jakomäessä syksyllä 1968 tutkittujen 10 koepuun perusteella.

beetles per tree were found overwintering. The greatest number of beetles found in a single tree was 234. As the diameter of the stump cutting surface increased, the number of overwintering insects in the bases of trees increased according to the relationship indicated by the regression equation $y = 135.9 + 14.74\ x$ (figure 12, curve I), were y is the number of insects overwintering in the base of the tree and x the diameter of the stump cutting surface under the bark, in cm.

In the stumps of the forty pines felled in March 1963, a total of 2018 living and 240 dead (considered to have died during the

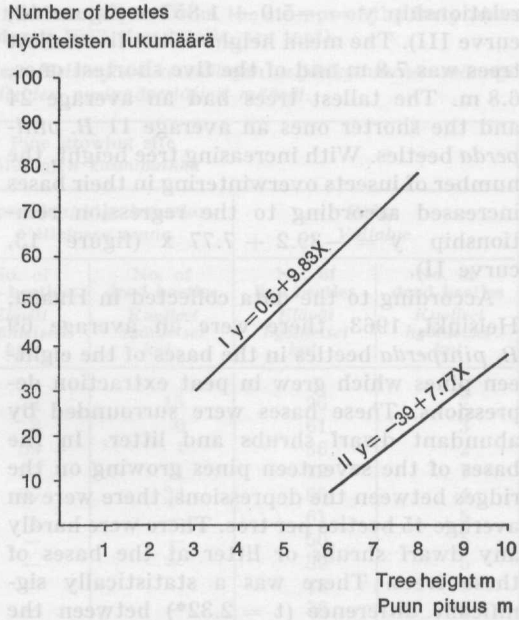


Figure 13. Number of *B. piniperda* beetles overwintering in the bases of trees of various heights (for explanations, see text).

Kuva 13. Puiden tyvissä talvehtineiden pystynävertäjien lukumäärän riippuvuus puun pituudesta. Regressiosuoran I arvo on laskettu maaliskuussa 1963 Helsingin Haagassa kaadettujen 40 koepuun perusteella ja regressiosuoran II Helsingin Jakomäessä syksyllä 1968 tarkastettujen 10 koepuun perusteella.

winter) *B. piniperda* beetles were found. An average 56 beetles were found per tree. With increasing tree diameter at breast height, the number of insects overwintering in the bases increased according to the relationship $y = —15.0 + 5.77\ x$ (figure 12, curve II). With increasing tree height, the number of *B. piniperda* beetles overwintering in the tree bases increased according to the regression relationship $y = 0.5 + 9.83\ x$ (figure 13, curve I), where y is the number of overwintering insects and x the height of the tree in meters.

The mean over-bark diameter at breast height of the pines inspected in Jakomäki, 1968, was 14.3 cm for the five largest and 10.1 cm for the five smallest-diameter trees. An average 21 *B. piniperda* beetles were collected from each of the bases of the larger trees, and 14 from the bases of the smaller-diameter trees. With increasing tree diameter, the number of insects overwintering in their bases increased according to the regression relationship y = —5.0 + 1.857 x (figure 12, curve III). The mean height of the five tallest trees was 7.8 m and of the five shortest ones, 6.8 m. The tallest trees had an average 24 and the shorter ones an average 11 *B. piniperda* beetles. With increasing tree height, the number of insects overwintering in their bases increased according to the regression relationship y = —39.2 + 7.77 x (figure 13, curve II).

According to the data collected in Haaga, Helsinki, 1963, there were an average 69 *B. piniperda* beetles in the bases of the eighteen pines which grew in peat extraction depressions. These bases were surrounded by abundant dwarf shrubs and litter. In the bases of the seventeen pines growing on the ridges between the depressions, there were an average 45 beetles per tree. There were hardly any dwarf shrubs or litter at the bases of these trees. There was a statistically significant difference (t = 2.32*) between the greater number of beetles in the trees growing in the depressions and the smaller number in the bases of those growing on the ridges.

Discussion. According to the results of the present study, a larger number of *B. piniperda* beetles overwinters in the bases of pines, as the breast height diameter and the height of the trees increases. Earlier studies have also stated that the species selects as its host, at least for breeding, preferably the bases of large trees (e.g. Krausse 1922 b, Saalas 1949, p. 358). The number of overwintering beetles in a single tree may sometimes be quite considerable. For instance, the author collected about five hundred beetles from the base of a 16 meter tall tree in fall 1962, although only half of the base was inspected. The other half probably had about an equal number of insects, since their bark frass was visible in approximately equal quantities on all sides of the tree.

According to the present results, there was a statistically significant difference between the greater number of beetles overwintering in the bases of trees growing in peat extraction depressions and the smaller number in the bases of trees growing on the higher ridges between these depressions. Since there was more litter and more dwarf shrubs at the bases of the trees in the depressions than those growing on the ridges, it seems that *B. piniperda* prefers such trees as overwintering hosts with a greater amount of litter at their base. It should also be noted that there is more snow at the bases of the trees in the depressions than those growing on the ridges (see p. 42). It is possible that *B. piniperda* beetles are somehow able to select as their overwintering host trees which have a deeper snow cover at their bases, providing the insects with better protection against the cold (cf. e.g. Pulliainen 1966, Bakke 1968 a).

64. Winter mortality

Material and methods. The mortality of *B. piniperda* at its overwintering site was studied on the basis of the information from the forty pines felled in late March 1963 in Haaga, Helsinki, by methods described earlier (see p. 42). In addition, four pines were felled in the same area in early January 1964, which were 5—7 meters tall and had an over-bark breast height diameter of 8.6—12.6 cm. The stumps of the trees were dug out of the ground and taken to the laboratory, where they were debarked. In connection with the debarking, the live and dead beetles found in the stumps were counted.

In early January 1964, six fresh pine stumps were split into pieces in Pihlajamäki, Helsinki, at a construction site. The pieces were taken into the laboratory and debarked, and the live and dead *B. piniperda* beetles found were counted.

Results. The numbers of live and dead (those assumed to have died during the same winter) *B. piniperda* beetles were collected from the stumps of the forty pines felled in Haaga, Helsinki, in late March 1963, are summarized in table 16. According to the results, there was no significant difference in the mortality in the bases of pines growing at different sites, among the overwintering insects.

A total of 1298 living and 135 dead insects were found in the stumps of the four pines felled in early January 1964, and in these of the six pines felled at the same time in Pihlajamäki, Helsinki. The dead insects thus represented 9.4 per cent of the total, which is the same number as was found to have died in Haaga, Helsinki, in the preceding year, in the bases of both the pines

Table 16. The numbers of live and dead *B. piniperda* beetles collected from the stumps of the forty pines felled in Haaga, Helsinki, in late March 1963 (for details, see text).

Taulukko 16. Maaliskuun lopussa vuonna 1963 Haagassa Helsingissä kaadettujen neljänkymmenen männyn kannoissa olleiden elävien ja kuolleiden pystynävertäjien määrät.

Stump number *Kannon numero*	Pine growing site *Mäntyjen kasvupaikka*					
	Peat extraction *Turpeenottopainanne*		Depression/ridge boundary *Välialueen reuna*		Ridge *Välialue*	
	No. of live beetles *Elävät hyönteiset kpl*	No. of dead beetles *Kuolleet hyönteiset kpl*	No. of live beetles *Elävät hyönteiset kpl*	No. of dead beetles *Kuolleet hyönteiset kpl*	No. of live beetles *Elävät hyönteiset kpl*	No. of dead beetles *Kuolleet hyönteiset kpl*
1	31	0	72	15	26	7
2	16	1	8	0	61	3
3	45	1	59	1	36	2
4	65	5	25	1	12	7
5	40	5	67	34	65	4
6	82	15	—	—	61	5
7	50	9	—	—	50	5
8	161	5	—	—	39	5
9	29	3	—	—	48	6
10	101	24	—	—	38	3
11	95	7	—	—	14	1
12	18	7	—	—	22	0
13	76	3	—	—	23	2
14	31	8	—	—	40	1
15	56	7	—	—	65	3
16	54	5	—	—	34	17
17	53	1	—	—	62	2
18	88	10	—	—	—	—
Total number of beetles *Hyönteisiä yhteensä*	1 091	116	231	51	696	73
per cent *prosenttia*	90.4	9.6	81.9	18.1	90.5	9.5

growing in the peat extraction depressions and on the ridges between these.

Discussion. It was found in this study that about ten per cent of the *B. piniperda* beetles overwintering in the bases of growing trees died during the winter. In earlier studies, higher mortality rates have been reported. Butovitsch (1925, p. 42) presumes that mortality at the overwintering sites is about forty per cent. According to Nuorteva (1950, p. 126), twenty per cent of the beetles which had laid eggs in the preceding year die of old age at the overwintering sites. According to Trägårdh and Butovitsch (1935, p. 121), fifty per cent of the bark beetles die during fall and winter time under attacks from predators and diseases. At least part of the smallness of the mortality figure reached in this study, as compared with those mentioned above, is due to the fact that the role of predators has not been determined. The studies were only concerned with insects which were found intact in the overwintering galleries. Predators may have eaten *B. piniperda* beetles even before they have had time to bore into the tree bark. It should also be remembered that the insects were taken from their overwintering sites before the spring. It is probable that predators feed on bark beetles especially during the period in the spring following emergence from the overwintering niche, but before the latter have started swarming. According to the author's field observations, the larvae of *Raphidia* species and the adults of *Thanasimus* species are found at the bases of trees during this period, and sometimes their level of activity is quite high. *Raphidia* larvae seem to use old *B. piniperda* overwintering niches as their overwintering sites. In connection with this study, *Thanasimus* adults have also been found to overwinter at the bases of the same trees as *B. piniperda*.

During the study, the reason for the death of the insects which were found dead at the overwintering sites was not studied. It is probable that fungal diseases are the major cause of their death (cf. e.g. NUORTEVA and SALONEN 1968, p. 51). It is noteworthy that mortality has been equally high in the bases of pines growing in the peat extraction depressions and those growing on the ridges. This was the case despite that the temperature went under —20° C (on March 19, 1963, to —28.1° C) on eleven days, according to measurements made in Viikki, during the period after snow had already melted from the bases of the pines growing on the ridges. At this time, the bases of the pines growing in the depressions were still completely covered with snow. The result obtained also supports the view that the bases of trees provide rather good protection for overwintering insects even in the case where they are not covered with snow (see also JOHNSON 1967). The fact that the low temperatures did not increase mortality in overwintering *B. piniperda* may also be due to the adaptation of the overwintering insects to survive very low temperatures (cf. JOHNSON 1967, ANNILA 1969). According to ANNILA and PERTTUNEN (1964), *B. piniperda* beetles which had been fed fresh sapwood, lived only a few minutes at a temperature of —20° C. However, the digestive tract of overwintering beetles may, be empty, enabling them to withstand lower temperatures. This is supported for instance by experiments carried out on *Ips typographus* (see KUHN 1949, ANNILA 1969).

7. FACTORS AFFECTING BROOD SIZE

71. General

In connection with this study, only a limited number of the listed factors known to regulate brood size (see e.g. KANGAS 1954) have been examined, namely egg gallery density (intraspecific competition), quality of breeding material, sex ratio and to some extent also meteorological factors.

72. Egg gallery density

General. With increasing egg gallery density, the progeny of bark beetles is decreased, expressed as numbers per gallery (see the review by THALENHORST 1958). This is due to the shortening of the egg gallery, and to a decreasing number of eggs laid with increasing gallery density (THALENHORST 1958). The most important cause of decreased progeny size is, however, the scarcity of food due to the excessive density (TRÄGÅRDH 1921, KANGAS 1953, 1954, THALENHORST 1958, JAMNICKY 1962, COLE and AMMAN 1969). With a higher egg gallery density, diseases, predators, and parasites are also in a better position to destroy the progeny (e.g. HANSON 1940, p. 516, NUORTEVA 1964, p. 1—2). BUROV (1968) states that each species has its optimum density, and a greater or smaller egg gallery density will have a negative effect on the size of the populations. Several studies (e.g. NUORTEVA 1954, 1964, EIDMANN and NUORTEVA 1968) have been carried out on *B. piniperda* to determine the effects of density on the length of egg galleries and on the numbers of progeny.

Material and methods. The effect of egg gallery density on brood size was studied in Viikki, Helsinki, in the outdoor experiments in 1962—1964, by methods described previously (see p. 8). The parent insects used in these experiments were collected after swarming from trap trees, by digging them carefully out with a sharp knife. Only parents which had not started egg-laying were used in the experiments. Altogether, 1195 males and the same number of females were used in the experiments through the years. The dimensions of the logs and numbers of insects used in the experiments in the various years are shown in table 17.

The logs used in the experiments were debarked in the fall, and the lengths of the egg galleries were measured to the clossest

Table 17. Sizes of pine logs used in outdoor development experiments, and the numbers of parent beetles released on each block, in the various years.

Taulukko 17. Ulkokasvatuksissa eri vuosina käytettyjen kasvatuspölkkyjen mitat ja niiden päälle pantujen pystyväveräjäparien lukumäärät.

	Date when experiment was started *Kasvatuksen aloituspäivä*	Number of pine log *Mäntypölkyn numero* 1	2	3	4	5	6	7	8
Mid-diameter of pine	1. V. 1962	15.0	14.2	15.0	14.4	11.7	11.6	11.0	11.8
log under the bark, cm	23. IV. 1963	12.2	12.8	12.6	12.6	12.1	14.6	12.9	13.0
Pölkyn kuoreton keskiläpimitta cm	3. V. and 24. V. 1964	8.9	11.2	9.0	12.3	11.9	—	—	—
Bark thickness,	1. V. 1962	6—12	6—12	6—12	6—12	2—4	2—4	2—4	2—4
mm	23. IV. 1963	4	11	7	13	9	16	11	23
Kuoren paksuus mm	3. V. and 24. V. 1964	6	5	8	8	7	—	—	—
Number of pairs	1. V. 1962	10	30	50	75	10	30	50	70
of parent beetles	23. IV. 1963	10	10	20	30	50	50	70	70
Pystynäverräjäparien lukumäärä	3. V. and 24. V. 1964	250	100	150	50	10	—	—	—

millimeter. In 1963, the exit holes of the new-generation beetles in the bark and the larval mines leaving the egg galleries were also counted.

The effect of egg gallery density on the numbers of new-generation beetles was also studied in natural conditions, from pine stumps, in 1963.

Effect of density on egg gallery length. The results of the experiments, carried out in Viikki in 1962—1964 to determine the effect of *B. piniperda* egg gallery density on the length of the egg galleries, are shown in figure 14. The curves have been drawn, smoothed by the eye, on the basis of the results from the various years. According to the figure, the average length of the egg gallery decreases as density increases. The cumulative length of the egg galleries, on the contrary, increases up to an egg gallery density of over 800 galleries per square meter. At higher densities, the cumulated length of the egg galleries appears to be rather constant i.e. about six meters per square meter.

Comparing these results with those obtained by EIDMANN and NUORTEVA (1968), we find that the mean egg gallery lengths in the various density categories are practically the same as what they got. The cumulated egg gallery length per square meter has, however, been found to be greater in the present study than in their material, in large egg gallery density classes.

According to the present results, the total egg gallery length per unit area increases with increasing density, quickly at first, but then at an ever slower rate. The same has also been found for other bark beetles (see e.g. JAMNICKY 1962). The shortening of the individual egg gallery with increasing density has also been found in previous studies (NUORTEVA 1964, EIDMANN and NUORTEVA 1968).

Effect of density on brood size. The results of the experiments, carried out in Viikki in 1963 to find the relative numbers of adults emerging from the larval brood, are shown in figure 15. According to the figure, the percentage of larvae developing into adults decreases with increasing egg gallery density (see also THALENHORST 1958, p. 25). At an egg gallery density of 63 galleries/sq.m, 78.3 per cent of the larvae have developed into adults. At a higher density of 319—327 egg galleries/sq.m, *only* 8.9 per cent of the larvae have become adults. These figures do not indicate only larval mortality at various egg gallery densities; they also include mortality at the pupal stage. It is probable, however, that mortality at the pupal stage has

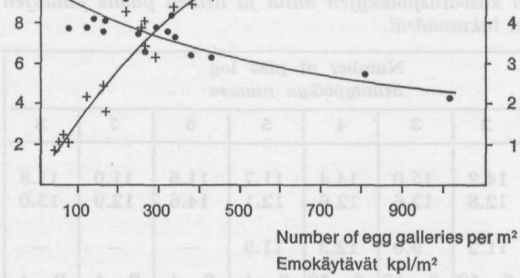


Figure 14. Relationship between *B. piniperda* egg gallery length and gallery density in the rearings in 1962—1964.

Kuva 14. Pystynävertäjän emokäytäväpituuden riippuvuus tiheydestä vuosina 1962—1964 suoritettujen kasvatusten mukaan.

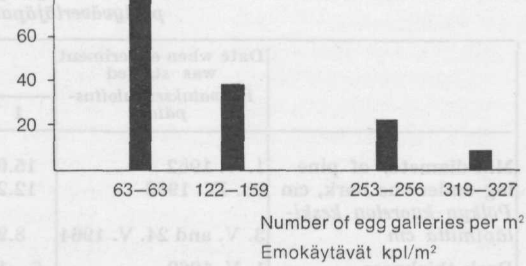


Figure 15. Maturing percentages of larvae at various egg gallery densities in experimental conditions in Viikki, 1963 (for explanations, see text).

Kuva 15. Toukkien aikuistumisprosentit eri emokäytävätiheyksissä Viikissä 1963 suoritetun kasvatuksen mukaan.

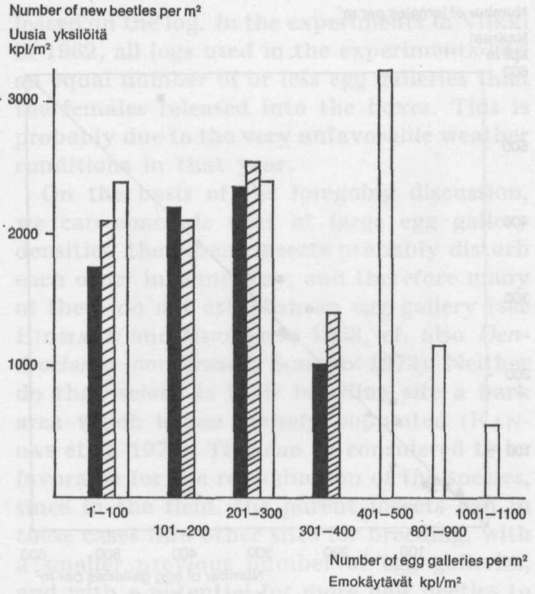


Figure 16. Relationship between egg gallery density and number of emerging beetles, on square meter basis, in experiments in Viikki, 1962–1964. Black columns = 1962, hatched columns = 1963 and white columns = 1964.

Kuva 16. Emokäytävätiheyden vaikutus neliömetriä kohti laskettuihin uusien yksilöiden lukumääriin Viikissä vuosina 1962–1964 suoritettujen kasvatusten mukaan. Mustat pylväät = 1962, vinoviivoitus = 1963 ja valkoiset pylväät = 1964.

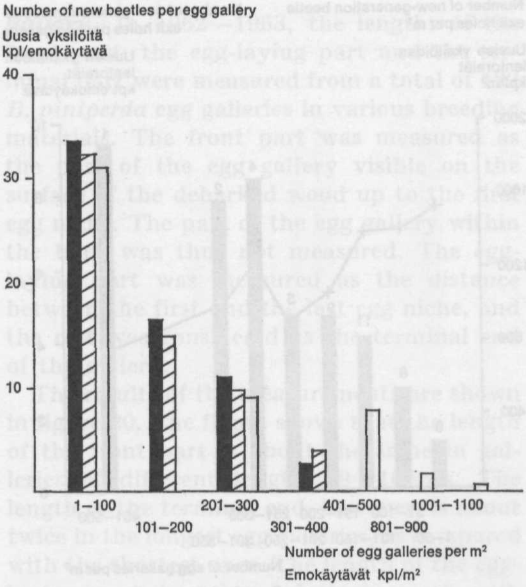


Figure 17. Relationship between egg gallery density and number of new beetles per gallery in experiments in Viikki, 1962–1964. (for explanation, see figure 16).

Kuva 17. Tiheyden vaikutus emokäytävää kohti laskettuihin uusien yksilöiden lukumääriin Viikissä vuosina 1962–1964 suoritettujen kasvatusten mukaan. Katso selitystä kuvassa 16.

been small and of about the same magnitude at various egg gallery densities (cf. *Leperisinus fraxini* Panz., JAMNICKY 1962).

The results of studies of the effect of egg gallery density on the numbers of new beetles, in the experiments in Viikki, are shown in figure 16. The figure indicates that the greatest number of beetles per square meter (about 2300/sq.m) developed in 1962 and 1963 at an egg gallery density of 201—300 per square meter. In 1964, the largest number of beetles developed at an egg gallery density of 401—500 galleries/sq.m. The latter result is based on a single log, from which 3163 new beetles per square meter developed, at an egg gallery density of 427 galleries/sq.m. This result, which deviates from the general pattern, may be due to the fact that the parent insects in the log had been collected from Lapland, and the experiment was started a month later than the other experiments in that year. The result may thus be due also to the origin of the parent insects, or more favorable weather conditions during brood development. The present results agree quite well with previous ones, indicating that new *B. piniperda* beetles are developed in largest numbers per square meter at an egg gallery density of 200—300 egg galleries/sq.m (see NUORTEVA 1964, EIDMANN and NUORTEVA 1968). According to figure 17, the number of new beetles per egg gallery decreases rapidly as egg gallery density starts to increase. At an egg gallery density of 100 galleries/sq.m, over thirty new beetles develop from a gallery, but at a density of 201—300 galleries /sq.m, only about ten beetles on the average develop from a single gallery. In the 1964 experiments, only 1.4 beetles were developed per gallery at a density of 807 egg galleries /sq.m. The results obtained agree very well with those presented previously by EIDMANN and NUORTEVA (1968). It has also been found in several other studies that the number of new adults emerging per egg gallery decreases for bark beetles as the egg gallery density

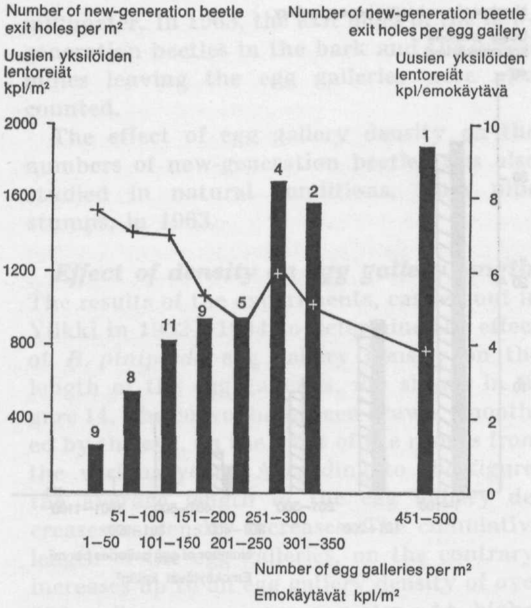


Figure 18. Number of exit holes of new beetles in pine stumps debarked in clearcutting areas in the Evo (Lammi) and Korkeakoski (Ruovesi) Forest Districts, in August 1963, per square meter bark surface area (black columns) and egg gallery (crosses) at various gallery densities. The figures above the columns indicate the number of stumps debarked in each egg gallery density class.

Kuva 18. Uusien yksilöiden lentoreikien lukumäärät Evon ja Korkeakosken hoitoalueissa elokuussa 1963 avohakkuualoilla tarkastetuissa männynkannoissa kannon kuoripinta-alan neliömetriä (pylväät) ja emokäytävää (ristit) kohti laskettuna eri emokäytävätiheyksissä. Pylväiden päässä olevat luvut ilmoittavat kussakin emokäytävätiheydessä tarkastettujen kantojen määrän.

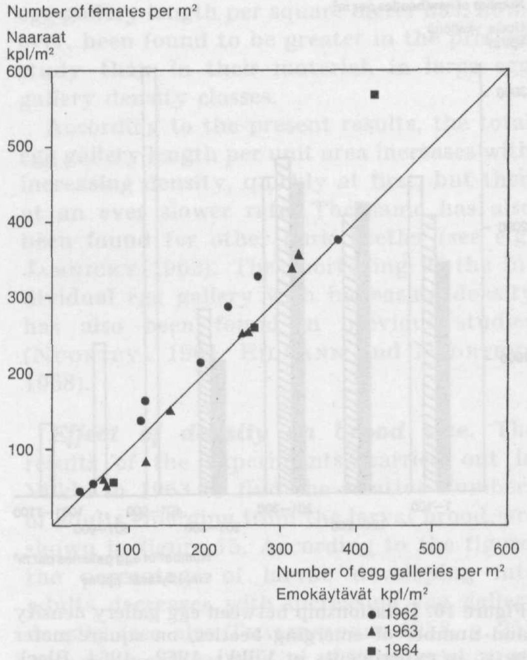


Figure 19. Numbers of females released in boxes and which established egg galleries in experiments in Viikki, 1962–1964.

Kuva 19. Kasvatuspölkyille pantujen naaraiden ja niiden perustamien emokäytävien lukumäärät Viikissä 1962–1964 suoritetuissa kasvatuksissa.

increases (e.g. Trägårdh 1934, Hanson 1937, Nuorteva 1954, 1964, Jamnicky 1962, Stark and Borden 1965, Berryman 1968).

Figure 18 shows the numbers of exit holes representing the new-generation beetles, in pine stumps, in the field studies in 1963. It is interesting to compare these results obtained in field conditions with the laboratory experiment results obtained for various egg gallery densities. In comparisons between the numbers of new-generation beetles per square meter, we find that at an egg gallery density of under 100 galleries/sq.m, about 2000 new beetles emerged per square meter, but there were only 400 exit holes in the stumps at this density. The difference is thus fivefold. At increasing egg gallery densities, the ratio decreases. At a density of 200—300 galleries /sq.m, only about twice the number of beetles emerging from pine stumps in the field had developed in laboratory conditions.

It is well known that *B. piniperda* females may establish several egg galleries (e.g. Knoche 1907). Figure 19 shows the results obtained during this study from experiments using logs and variable numbers of parent insects, concerning the numbers of egg galleries. According to the results, there were more egg galleries in the logs than the number of parents put into the log container, at an egg gallery density of under 250 galleries /sq.m. According to Eidmann and Nuorteva (1968), there are more egg galleries than females when there are less than 200 egg galleries/sq.m. The results are thus of the same order of magnitude. As density increases above these values, all females do not establish an egg gallery. In this study, only 57 per cent of the females established an egg gallery, when 1790 females/sq.m were released on the log. In the experiments in Viikki in 1962, all logs used in the experiments had an equal number of or less egg galleries than the females released into the boxes. This is probably due to the very unfavorable weather conditions in that year.

On the basis of the foregoing discussion, we can conclude that at large egg gallery densities, the parent insects probably disturb each other in some way, and therefore many of them do not establish an egg gallery (see EIDMANN and NUORTEVA 1968, cf. also *Dendroctonus ponderosae*, SCHMID 1972). Neither do they select as their breeding site a bark area which is too densely populated (KANGAS et al. 1971). This can be considered to be favorable for the reproduction of the species, since in the field, the parent insects can in these cases find other sites for breeding, with a smaller previous number of egg galleries, and with a potential for more new beetles to emerge from each egg gallery.

The length of the front part, the egg-laying part and the terminal end of the gallery. In 1962—1963, the lengths of the front part, the egg-laying part and the terminal part were measured from a total of 122 *B. piniperda* egg galleries in various breeding materials. The front part was measured as the part of the egg gallery visible on the surface of the debarked wood up to the first egg niche. The part of the egg gallery within the bark was thus not measured. The egg-laying part was measured as the distance between the first and the last egg niche, and the rest was considered as the terminal end of the gallery.

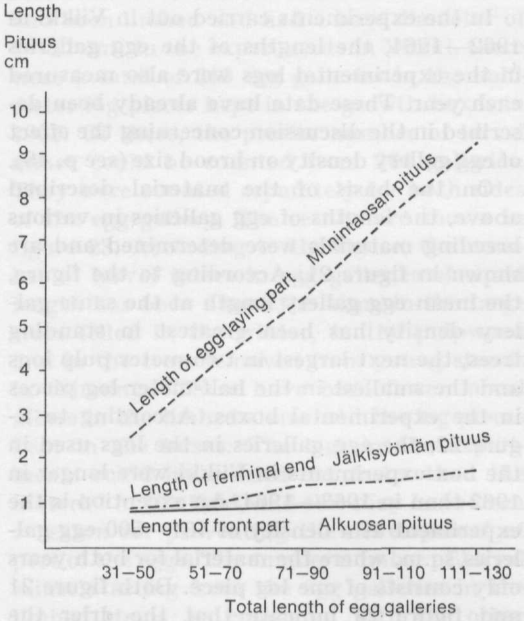


Figure 20. Lengths of front part, egg-laying part and terminal end of egg galleries of varying lengths in various breeding materials in 1962 – 1963.

Kuva 20. Emokäytävän alkuosan, munintaosan ja jälkisyömän pituudet erilaisista lisäänlymismateriaaleista vuosina 1962 – 1963 mitaluissa emokäytävissä.

The results of the measurements are shown in figure 20. The figure shows that the length of the front part is about the same in galleries of different lengths, 9—10 mm. The length of the terminal end, however, is about twice in the longest egg galleries, as compared with the shortest ones. The length of the egg-laying part increases relatively most with increasing egg gallery length.

73. Quality of breeding material

General. In addition to the quantity of available food, its quality is also very important in determining brood development in the insect species living in tree bark (e.g. KANGAS 1954, 1959, JUUTINEN 1955, NUORTEVA 1956, THALENHORST 1958, AMMAN 1971, SCHMID 1972). One of the most usual changes in the quality of the breeding material is its drying out at a too early stage (TRÄGÅRDH 1921, KANGAS 1934 c, 1954, 1959, HANSON 1937). Thin bark, and a small diameter, increase the rate of drying, and brood numbers of *B. piniperda* in field conditions become smaller in thin-barked than thick-barked areas. In addition to faster drying, this is also caused by a greater parasite and predator activity in the thinner-bark area (HANSON 1937). Sometimes bark beetles attack trees, which are so vigorous that the broods are destroyed (KANGAS 1934 c, 1954, 1959). It has already been stated earlier in connection with this study that *B. piniperda* eggs have not developed in vigorously growing trees. It has also been found that the cell tissue which is so vigorous as to pose a threat to brood development offers, however, the best conditions for reproduction (THALENHORST 1949, KANGAS 1959).

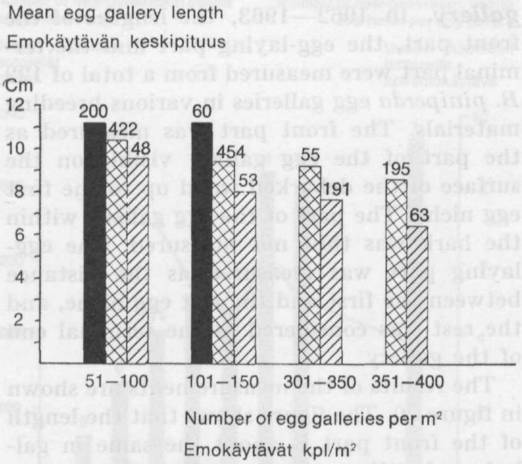


Figure 21. Mean egg gallery lengths in various breeding materials in 1962–1964. Black columns = standing trees, cross-hatched columns = 2-meter pulp logs, hatched columns = 0.5-meter-long log blocks used in experiments. The figures above the columns indicate the number of egg galleries measured.

Kuva 21. Emokäytävien keskipituudet erilaisissa lisääntymismateriaaleissa vuosina 1962–1964. Mustat pylväät = pystypuut, ristiviivoitus = 2-metriset paperipuut ja vinoviivoitus = 0.5 metrin pituiset kasvatuspölkyt. Pylväiden päissä olevat luvut ilmoittavat mitattujen emokäytävien lukumäärän.

Effect of breeding-material quality on egg gallery length. Only a small amount of information is available in the literature concerning the effect of the breeding-material quality on the *B. piniperda* egg-gallery length (cf. however, TRÄGÅRDH 1921, p. 59, NUORTEVA 1950, p. 51). In connection with this study, the following data were used to study this problem.

In 1962—1964, egg gallery lengths were measured on a total of eight pines which had dried standing, separately for the parts of the stem at 0.0 to 1.0 and 1.0 to 2.0 meters from the ground level. The measurements were always carried out after the egg galleries had reached their full length and the parent insects had left them. The total debarked surface was 7.0 sq.m. A total of 615 egg galleries were measured in the trees.

In Haaga, Helsinki, in 1962, the length of 876 egg galleries was measured on two-meter pulp logs, which had been cut during the preceding winter and then piled crosswise. The total bark area in the logs was 17.9 sq.m.

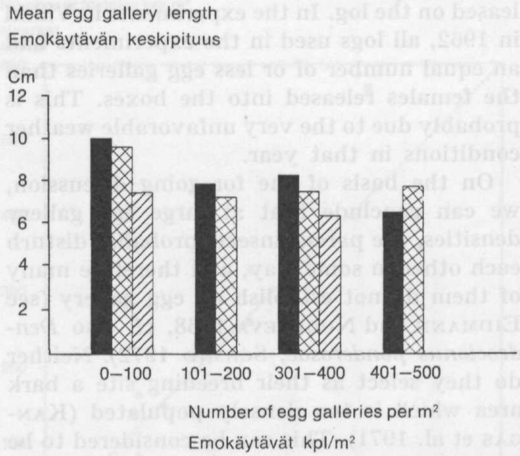


Figure 22. Mean egg gallery lengths in outdoor experiments in Viikki, in 1962–1964, in various egg-gallery density classes. Black columns = 1962, cross-hatched columns = 1963 and hatched columns = 1964.

Kuva 22. Emokäytävien keskipituudet Viikin ulkokasvatuksissa eri tiheysluokissa vuosina 1962–1964. Mustat pylväät = 1962, ristiviivoitus = 1963 ja vinoviivoitus 1964.

In the experiments carried out in Viikki in 1962—1964, the lengths of the egg galleries in the experimental logs were also measured each year. These data have already been described in the discussion concerning the effect of egg gallery density on brood size (see p. 48).

On the basis of the material described above, the lengths of egg galleries in various breeding materials were determined and are shown in figure 21. According to the figure, the mean egg gallery length at the same gallery density has been greatest in standing trees, the next largest in two-meter pulp logs and the smallest in the half-meter log pieces in the experimental boxes. According to figure 22, the egg galleries in the logs used in the box experiments in Viikki were longer in 1962 than in 1963—1964. An exception is the experiment at a density of 401—500 egg galleries/sq.m, where the material for both years only consists of one log piece. Both figure 21 and figure 22 indicate that the drier the breeding material, the shorter is the length of the egg gallery. At the debarking of the experimental logs in Viikki in fall 1962, they were found to be very moistbarked. The May —June precipitation was 107.2 mm in 1962, 53.6 mm in 1963 and 50.4 mm in 1964, according to measurements in Ilmala, Helsinki. The normal May—June precipitation in Ilmala is 92 mm. These results agree well with those obtained, for instance, by Johnson (1963). According to his work, the egg galleries of *Dendroctonus pseudotsugae* were longer, the higher the moisture content of the trees (see also Reid 1962 b, Beanlands 1967). Eidmann (1965) has found that the egg galleries of *B. piniperda* are longer in late-felled trees.

Number of larval mines departing from egg galleries in various breeding materials. In connection with the measurement of egg gallery lengths, the numbers of larval mines starting from the egg galleries in the field were measured in the following number of egg galleries in various breeding materials: large trees felled in the winter, 52 galleries, two-meter pulp logs, 42 galleries, trees felled in the thinning of dense tree stands, 55 galleries and small-diameter stems, 123 egg galleries. The trees felled in the thinning of thickets had not been limbed. Their base diameter was 4—7 cm. The small-diameter stems had been limbed and had a base diameter of 7—12 cm. In the experiments in Viikki, there were a total of 315 egg galleries in the half-meter log pieces kept in the growth boxes in 1963. Of these, the precise number of larval mines could be counted from 264 galleries. They were counted separately for both sides of the egg gallery. The results are shown in figure 23. According to the figure, the number of larval mines in egg galleries of equal length has been about the same in the large trees felled in the winter, in the pulpwood and in the trees removed from young stands in thinnings. There have been fewer larval mines in the limbed stems and the log pieces kept in the boxes. The logs in the experiments could have dried out faster than the material in the field, and this may have been a reason for preventing the development of part of the eggs. The smaller number of larval mines starting from the egg galleries in the limbed stems, as compared with the other materials in the field, is difficult to explain totally on the basis of faster drying, since at the time of barking they did not appear drier than for instance the trees felled in the thinning of the thickets. It is possible that in this case, various types of predators eating

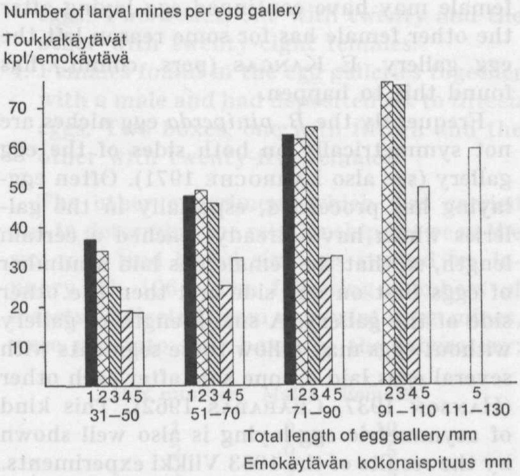


Figure 23. Number of larval mines in egg galleries of various lengths and in various breeding materials. 1 = pines felled in the winter, 2 = 2-meter pulp logs, 3 = trees felled in connection with thinning of thickets, 4 = delimbed stems and 5 = 0.5-meter log blocks.

Kuva 23. Toukkakäytävien lukumäärä eri pituisissa emokäytävissä erilaisissa lisääntymismateriaaleissa. 1 = talvella kaadetut männyt, 2 = 2-metriset paperipuut, 3 = tiheikön harvennusten yhteydessä kaadetut puut, 4 = karsitut rangat ja 5 = 0.5 metrin pituiset kasvatuspölkyt.

eggs laid by *B. piniperda* into the stems have had a marked effect. The stems were in piles, which may have caused them to attract predators more than any other material studied in the field. The numbers of eggs laid by *B. piniperda* in the egg galleries studied have been larger than the numbers of larval mines found at them, since part of the eggs will always fail to develop or be destroyed due to one reason or another (e.g. Butovitsch 1925, p. 41). Figure 23 indicates that the number of larval mines increases with increasing egg gallery length. This is a direct result of the fact already reported that the length of the egg-laying part increases, as the length of the egg gallery increases (see p. 51, see also Trägårdh 1921, p. 59). The greatest number of larval mines the author has counted in a single egg gallery in the field was 189 and in the box experiments 95. The lengths of the corresponding egg galleries were 240 and 126 mm. Hanson (1937) has also counted 189 larval mines starting from a single egg gallery. Females might thus lay almost 200 eggs. It is, however possible that in these cases a female may have continued egg laying after the other female has for some reason left the egg gallery. E. Kangas (pers. comm.) has found this to happen.

Frequently the *B. piniperda* egg niches are not symmetrically on both sides of the egg gallery (see also Larroche 1971). Often egg-laying has proceeded, especially in the galleries which have already reached a certain length, so that the female has laid a number of eggs first on one side and then the other side of the gallery. A small length of gallery without eggs may follow these segments with several eggs laid on one side after each other (Hanson 1937, Chararas 1962). This kind of asymmetric egg-laying is also well shown by the results of the 1963 Viikki experiments. According to these, an average 16.4 larval mines had started from one side of the egg gallery and 27.2 from the other.

Effect of breeding material quality on brood size. In summer 1963, an attempt was made to study the effect of breeding material quality on brood size separately in the trees felled in connection with thicket thinnings, in limbed stems which were thicker than the thinnings and in piles, in a large-diameter tree blown over by the wind, and in the stumps of large trees. For the study, ten half-meter pieces were sawed from the bases of the 4—7 cm diameter trees felled during the previous winter in thicket thinning-operations. The trees were sawed on June 26, 1963. Ten pieces of the same length were sawed from the limbed stems, and two pieces from the tree felled by the wind, on the same day. The log pieces were put into growth boxes kept outdoors in Viikki, and the new-generation beetles that developed were collected. In the fall, the pieces of timber were debarked, after the exit holes of the new generation had been counted. The lengths of the egg galleries in the pieces of wood were also counted.

The results are shown in figure 24. The figure also indicates the numbers of exit holes counted in pine stumps in clearcut areas in the same year. According to the results, the largest number of new beetles developed from the trees felled in the thinnings of the dense stands and the tree felled by the wind, and the smallest number from the limbed trees and the stumps.

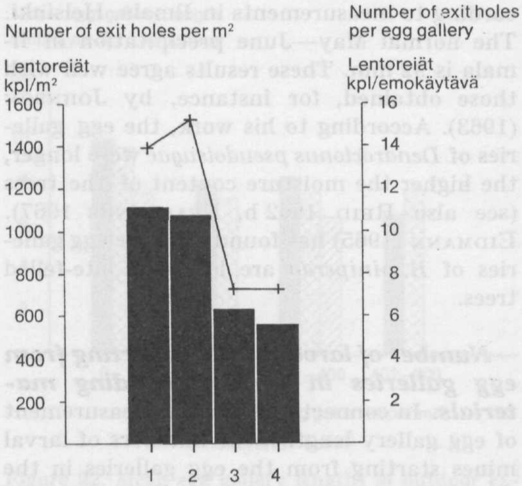
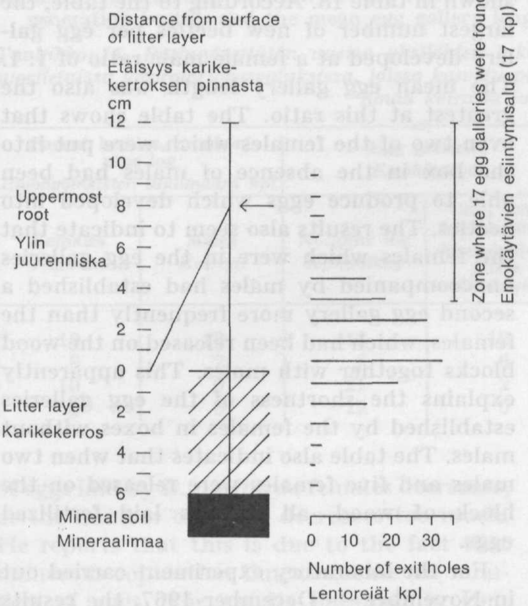


Figure 24. Number of exit holes of new beetles per m² (black columns) and egg gallery (crosses) in various breeding materials in 1963, at an egg gallery density of 51—100 galleries / m². 1 = trees felled in thicket thinnings, 2 = trees felled and uprooted by wind, 3 = limbed, about 10-cm-diameter stems and 4 = pine stumps in clearcut areas.

Kuva 24. Uusien yksilöiden lentoreikien lukumäärä neliömetriä (mustat pylväät) ja emokäytävää (ristit) kohti erilaisissa lisääntymismateriaaleissa vuonna 1963 silloin kun emokäytäviä oli 51—100 kpl / m². 1 = tiheikön harvennusten yhteydessä kaadetut puut, 2 = tuulen juurineen kaatamat puut, 3 = noin 10 cm läpimittaiset karsitut rangat ja 4 = avohakkuualojen männynkannot.

The result may be due to the changing of the quality of the limbed stems and stumps into a less favorable environment for brood development, as compared with other breeding materials. However, the reason may also be that the role of predators, competing species and parasites as causes of brood mortality has been greater in the limbed stems and the stumps. Previously it has been found that for instance *Acanthocinus aedilis* L. larvae markedly decrease *B. piniperda* broods in pine logs (Nuorteva 1962 b). In summer 1963, the drying out of stumps in clearcut areas also had great importance in decreasing the broods. A typical example of this is the case shown in figure 25. The figure is based on data from a pine stump inspected in Evo on August 23, 1963. The figure shows that the largest number of new-generation exit holes were found close to the surface of the litter layer. This was found to be mainly due



Figures 25. Number of exit holes of new beetles at various distances from the surface of the litter layer, in a pine stump debarked in a clearcut area in summer 1963.

Kuva 25. Uusien yksilöiden lentoreikien lukumäärä eri etäisyyksillä karikekerroksen rajasta eräässä tyypilliseksi katsotussa tapauksessa avohakkuualalla kesällä 1963 kuoritussa männyn kannossa.

to the larval mortality connected with the drying of the top part of the stump.

74. Sex ratio

Material and methods. In spring 1963, females taken from egg galleries in the field were put into a total of nine development boxes kept outdoors in Viikki. From eight to twenty-five females were put into each box. The females were divided into four groups as follows:

1. Females found alone in egg galleries which had not yet deposited eggs. Two boxes, one with fourteen and the other with eight females.
2. Females found in the egg galleries together with a male and had not yet started depositing eggs. Three boxes, two with twenty and one with twenty-five females.
3. Females found in the egg galleries together with a male and had deposited one to five eggs. Two boxes, one with twenty and the other with twenty-eight females.
4. Females found in the egg galleries together with a male and had deposited six to fifteen eggs. Two boxes, one with fifteen and the other with twenty-five females.

The other experiment which was carried out to determine the relationship between the sex ratio and brood size was started on January 30, 1964. The following numbers of insects, collected from overwintering mines, were put into four boxes in the laboratory:

Box number	Males	Females
1	0	10
2	0	5
3	2	5
4	10	10

Studies which were more extensive than the preliminary experiments described above, on the relationship between the sex ratio and brood size, were carried out at the Department of Agricultural and Forest Zoology of the University of Helsinki, in a laboratory experiment started on November 7, 1967, and in Vaasa, in a field experiment started on June 20, 1968. The parent insects used in the laboratory experiment had been collected from their overwintering sites in the bases of trees. The parent insects for the experiment in Vaasa had been collected in the spring, from egg galleries after the swarming period but before they had started to lay eggs. Before the start of the experiment, they had been kept for ca. three weeks at a temperature of 4° C. Both development experiments consisted of a total of twenty-four boxes, with blocks of wood inside, and ten females were released on each block. In addition to the females, the following numbers of males were released on the blocks of wood:

Number of box	Number of males
1 – 4	0
5 – 8	3
9 – 12	5
13 – 16	10
17 – 20	20
21 – 24	30

The experimental procedure has been described previously (see p. 8).

Results and discussion. The results of the experiment carried out in spring 1963 are

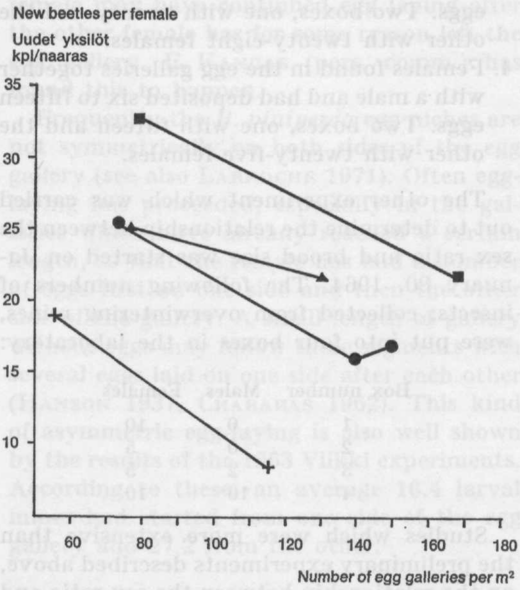


Figure 26. Number of progeny of females after they have been moved from egg galleries to new breeding site away from males. + — + = females were alone in egg gallery before being moved and had not laid eggs. • — • = females were in egg gallery with male before being moved, but had not yet started laying eggs. ▲ — ▲ = females were in egg gallery with male before being moved and had laid 1 – 5 eggs. ■ — ■ = females were in egg gallery with male before being moved and had laid 6 – 15 eggs.

Kuva 26. Naaraiden saama jälkeläismäärä silloin kun ne on siirretty emokäytävistä uuteen lisääntymispaikkaan ilman koirasta. + — + = naaraat olivat olleet ennen siirtoa emokäytävissä yksinään eivätkä olleet vielä munineet. • — • = naaraat olivat olleet ennen siirtoa emokäytävässä koiraan kanssa, mutta eivät olleet aloittaneet munintaa. ▲ — ▲ = naaraat olivat olleet ennen siirtoa emokäytävässä koiraan kanssa ja munineet 1 – 5 munaa. ■ — ■ = naaraat olivat olleet ennen siirtoa emokäytävässä koiraan kanssa ja munineet 6 – 15 munaa.

shown in figure 26. The figure shows that the largest number of new beetles per egg gallery developed in the blocks of wood containing females which had laid 6—15 eggs in the field before they established the second egg gallery. The smallest progenies were found for the females which had not started laying eggs in the field and were not accompanied by a male when found. It should, however be noted that they did produce progeny.

For the experiment carried out in January 1964, in which parent insects collected from overwintering sites were used, the results are shown in table 18. According to the table, the largest number of new beetles per egg gallery developed at a female/male ratio of 1: 1. The mean egg gallery length was also the greatest at this ratio. The table shows that even two of the females which were put into the box in the absence of males had been able to produce eggs which developed into beetles. The results also seem to indicate that the females which were in the egg galleries unaccompanied by males had established a second egg gallery more frequently than the females, which had been released on the wood blocks together with males. This apparently explains the shortness of the egg galleries established by the females in boxes without males. The table also indicates that when two males and five females were released on the block of wood, all females laid fertilized eggs.

For the laboratory experiment carried out in November — December 1967, the results shown in table 19 were obtained for the relationship between the sex ratio and the number of new beetles. In this experiment, also, some females were able to produce progeny despite the fact that they had been taken for the experiment directly from their overwintering sites, and there were no males in the boxes. In this experiment, the largest average numbers of progeny also developed, when an equal number of females and males were released on the blocks of wood. Almost an equal number of new beetles developed however, from each egg gallery already when the male/female ratio was 3: 10 and 5: 10. We can also see in the figure that in cases where the number of males is larger than the number of females, the number of new beetles developed per female is slightly smaller than if there are equal numbers of males and females. The same phenomenon is shown even more clearly in table 20. According to this figure, the females have produced about equal numbers of progeny at male/female ratios of 5: 10 and 10: 10. The fact that also solitary females in this experiment got almost equal numbers of progeny as the ones released in the boxes together with males, can be explained because they had been collected in the field from egg galleries in which they had been together with a male. Thus they had already copulated in the same spring.

Wolff (1920) has found that the number

Table 18. Relationship between the sex ratio of the parent *B. piniperda* beetles and the number of new generation beetles and the mean egg gallery length, in experiments carried out in winter 1964.

Taulukko 18. Pystynävertäjän uusien yksilöiden lukumäärä sekä emokäytävien keskipituus talvella 1964 suoritetuissa laboratoriokasvatuksissa, joissa kasvatuspölkyille pantiin talvehtimispaikoista kerättyjä naaraita ilman koirasta ja niiden kanssa.

Parent beetles, number/pine log *Emohyönteisten lukumäärä kpl*		Egg galleries *Emokäytävät*			New- generation beetles *Uuden sukupolven yksilöt*	
Females *Naaraat*	Males *Koiraat*	No./pine log *Kpl/pölkky*	Ones with larval mines *Emokäytäviä, joissa toukkakäytäviä*	Mean length of all egg galleries, cm *Emokäytävien keskipituus, cm*	No./pine log *Kpl/pölkky*	No./female *Kpl/ naaras*
10	10	13	12	9.0	817	81.7
5	2	6	6	7.1	321	64.2
10	0	21	2	3.9	85	8.5
5	0	12	0	2.6	0	0

of eggs laid by *B. piniperda* females decreases, as the number of males decreases too much. He reports that this is due to the fact that numerous copulation times increase the numbers of eggs. The results obtained in connection with this study support this view. It has also, however been found in the present study that the number of males can be much smaller than that of the females, without a considerable drop in the numbers of progeny on a per female basis. However, it has also been stated that, one copulation time is enough for *B. piniperda* in order to produce a complete egg gallery and a full brood (HENNINGS 1908, KNOCHE 1907, SAALAS 1949, EIDMANN 1965). On the basis of the results now obtained, we can draw the conclusion that to a certain degree there can be less males than females in the swarming population (cf. also SALONEN *et al.* 1968) without depressing the numbers of progeny produced by the population. This is probably due to the fact that *B. piniperda* is not an absolutely monogamous species, as the presently described and previous (see p. 21) observations show. According to the present results, the numbers of progeny per female decreases if the number of males exceeds enough that of the females.

Table 19. Relationship between number of new *B. piniperda* beetles per female and the ratio of males to females in the experimental boxes in laboratory conditions in 1967. The parent beetles were collected from hibernation sites.

Taulukko 19. Seksuaali-indeksin vaikutus pystynävertäjän uusien yksilöiden lukumäärään vuonna 1967 suoritettujen laboratoriokasvatusten mukaan. Emohyönteiset kerättiin talvehtimispaikoista.

Number of males per 10 females *Koiraiden lukumäärä kymmentä naarasta kohti*	Total number of new-generation beetles in four boxes *Uusia yksilöitä yhteensä neljässä kasvatuslaatikossa kpl*	Number of new-generation beetles per female *Uusia yksilöitä kpl/naaras*
0	14	3.5
3	1596	39.9
5	1474	36.9
10	1679	41.5
20	1377	34.4
30	1397	34.9

Table 20. Relationship between number of new *B. piniperda* beetles per female and the ratio of males to females, in experiments in Vaasa, 1968. The parent beetles were collected from egg galleries after swarming and before egg laying started.

Taulukko 20. Seksuaali-indeksin vaikutus pystynävertäjän uusien yksilöiden lukumäärään Vaasassa vuonna 1968 suoritetuissa kasvatuksissa. Emohyönteiset kerätty parveilun jälkeen emokäytävistä ennen muninnan alkamista.

Number of males per 10 females *Koiraiden lukumäärä kymmentä naarasta kohti*	Total number of new-generation beetles in four boxes *Uusia yksilöitä yhteensä neljässä kasvatuslaatikossa kpl*	Number of new-generation beetles per female *Uusia yksilöitä kpl/naaras*
0	661	16.5
3	392	9.8
5	733	18.3
10	701	17.5
20	481	12.0
30	386	9.7

Two of the fifteen females taken directly from their overwintering sites in the winter of 1964 laid eggs which developed into beetles, despite the fact that the females had been released into the box in the absence of males. Among the forty females put into development boxes without males in 1967, directly from the overwintering sites, two also established an egg gallery and produced a viable brood. These females had thus been able to lay viable eggs, despite the fact that copulation must have taken place already before movement into the overwintering site, or in the overwintering mine in the fall. The beetles could also have been old females with eggs they had not laid in the preceding summer, or which still had some male sperm in store from the preceding year, like pointed out in certain species of bark beetles by Francke-Grosmann (1950) and Reid (1958) (cf. also McCambridge 1969).

Parthenogenetic reproduction likely occurs in the bark beetle *Xyleborus germanus* Blam. (Kaneko and Takagi 1965). According to the studies of Hopping (1961, 1962, 1964), Smith (1962), Lanier and Oliver (1966) and Bakke (1968 b) gynogenesis, i.e. parthenogenesis where sperm is necessary to activate the development of the egg, but does not actually fertilize it, occurs in the genus *Ips*.

75. Accuracy of size estimates of new generation

It has been stated in several connections that counting the numbers of new-generation bark beetles in the field on the basis of exit holes usually results in an underestimate (Wolff 1920, Escherich 1923, Hanson 1937, Miller and Keen 1960). The reason for this is that several beetles can emerge through the same hole. Another major reason is that it is difficult to see the exit holes which are in bark crevices. In cases where the exit holes of parasites are interpreted to be bark-beetle entrance holes, a larger than actual population size may be estimated on the basis of counting the flight holes (Hanson 1937).

No figures have been available for *B. piniperda*, for the difference between the number of new-generation beetles and the value counted on the basis of the flight holes. This difference is apparently also greatly dependent on the person who carries out the inventory. The author attempted to study the question on the basis of the following materials:

1. Stumps of trees felled in December 1961, eleven in total.
2. Blocks of timber brought from the field into the development boxes before the new generation had matured, twenty-two in total.
3. Blocks of timber kept in development boxes in Viikki in 1963, used in experiments to determine the relationship between egg gallery density and brood size, nineteen in total.

For the breeding materials described above, all matured new-generation beetles were collected, and the numbers of exit holes visible in the bark were counted as carefully as possible. The results are summarized in table 21.

According to the results, the number of new-generation beetles counted on the basis of the exit holes was an average 12.9 per cent lower than the actual one. The error increases as the bark thickness increases, according to the regression relationship $y = 7.48 + 0.7963\,x$ (figure 27, line I), where y is the error percentage and x bark thickness in millimeters. The value of the regression

Table 21. Comparison of the number of exit holes counted (see text) and the actual number of new-generation beetles of *B. piniperda*.

Taulukko 21. Lentoreikien perusteella laskettu ja todella aikuistuneiden pystynävertäjän uuden sukupolven yksilöiden lukumäärä erilaisessa lisääntymismateriaalissa.

Breeding material *Lisääntymismateriaali*	Exit holes counted *Lentoreiät kpl*	Actual number of new-generation beetles *Uusien yksilöiden todellinen lukumäärä kpl*
Stumps .... *Kannot*	3 299	3 523
Blocks of timber brought from the field .... *Luonnosta tuodut pölkyt*	1 322	1 499
Pine logs used in experiments in Viikki .... *Viikin kasvatuksissa käytetyt pölkyt*	6 531	7 787
Total .... *Yhteensä kpl*	11 152	12 809

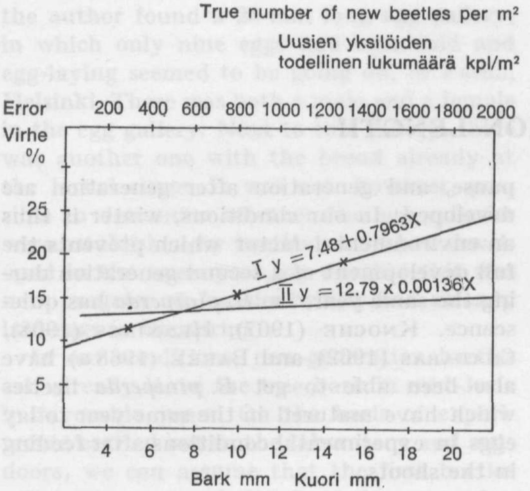


Figure 27. Relationship between bark thickness (line I), and number of new beetles (line II), and the per cent error of estimate derived by counting number of exit holes, as compared with the number of beetles which actually developed.

Kuva 27. Kuoren paksuuden (kuvaaja I) ja uusien yksilöiden lukumäärän (kuvaaja II) vaikutus lentoreikien perusteella saadun lukumäärän virheprosentin suuruuteen todella aikuistuneiden yksilöiden lukumäärästä laskettuna.

equation y thus indicates how many per cent the value reached on the basis of the exit holes was smaller than the actual number of new-generation beetles.

The number of new-generation beetles has only a slight effect on the magnitude of the error percentage. The error percentage increases with the increasing size of the new generation according to the regression relationship $y = 12.8 + 0.00136\,x$ (figure 27, line II), where x refers to an additional new-generation beetle per square meter.

In relation to the results obtained, it should be remembered that they can not be generalized as such, since they only refer to a limited set of data and are based on the observations of one person only. We may probably conclude on their basis, however that estimates of new-generation beetle numbers based on counting the flight holes will be smaller than the actual ones and that the result obtained depends especially on bark thickness.

8. GENERATION LENGTH

81. Material and methods

In spring 1964, offspring (F_1 generation) born in development experiments (experimental series 3, p. 24) of *B. piniperda* beetles collected during swarming were put into a five-liter glass jar containing fresh pine shoots, and kept in the laboratory. After the insects had been in the shoots for 3—4 weeks, their color had changed from straw yellow to the dark color of the adult beetle. They were then moved into a box containing a fresh block of pine timber. After about a month, a large number of new beetles emerged from the block (F_2 generation), and these were again put into a glass jar containing fresh pine shoots. From the shoots, they were in turn moved to a block of pine timber after 3—4 weeks. The rearing of the insects was continued in this way, alternately in shoots and blocks of pine timber. The entire experiment was carried out at room temperature, 22—24° C.

The possibility of a second generation during one year in the field was studied in Viikki in summer 1965. From a pulpwood log, cut in the preceding winter and kept in a pile, a half meter piece was sawed on July 7, 1965, and put into a development box kept outdoors. On July 14, 25 beetles which had matured in the box were put into a three-liter glass jar, which contained fresh pine branches. The mouth of the jar was covered with cheesecloth. On August 5, twelve new-generation beetles were taken from the shoots and put into a development box with a fresh pinewood block. The block was debarked on October 7, and two egg galleries with larval mines were found. Some larvae had bored themselves into the bark, but no pupae were found.

82. Results and discussion

In laboratory conditions, five consecutive generations developed during the period from spring 1964 to spring 1965. The result indicates that *B. piniperda* does not have a diapause, and generation after generation are developed. In our conditions, winter is thus an environmental factor which prevents the full development of a second generation during the same year, i.e. *B. piniperda* has quiescence. KNOCHE (1907), HENNINGS (1908), CHARARAS (1962) and BAKKE (1968 a) have also been able to get *B. piniperda* beetles which have matured in the same year to lay eggs in experimental conditions after feeding in the shoots.

In summer 1965, the progeny of beetles matured in that year and put into development boxes outdoors on August 5, developed to the stage where larvae had bored themselves into the bark for pupation. It should be noted that the timber block was shielded from sunshine, which probably has slowed down the development of the broods (cf. e.g. *Ips typographus* ANNILA 1969, p. 172). In more favorable conditions, the experiment could have been started about three weeks earlier, also. Therefore it seems apparent that in conditions without the mentioned retarding factors, at least part of the progeny would have had time to mature during the fall.

Late in the last century, researchers were quite interested in whether *B. piniperda* regularly had one or two generations in a year (see e.g. EICHHOFF 1881, ALTUM 1881, 1887, BOS 1891, JUDEICH and NITSCHE 1895, HESS 1898). KNOCHE (1904) finally showed that in normal conditions, there is not enough time for more than one generation to develop in one year. However, he considered it quite possible that a second progeny is started during one year. Starting a second generation has also been found by e.g. KANGAS (1954) and EIDMANN (1965). Now it is generally believed that a second generation is possible only in southern Europe in exceptionally favorable conditions (CHARARAS 1962, 1964, BAKKE 1968 a, LARROCHE 1971). LEKANDER (1971) has, however, raised doubts concerning the species involved.

The development of a second generation in Finland has not been recorded with certainty (see KANGAS 1953). On September 21, 1963, the author found a 28 mm long egg gallery, in which only nine eggs had been laid and egg-laying seemed to be going on, in Pasila, Helsinki. There was both a male and a female in the egg gallery. Next to this gallery, there was another one with the brood already at the larval stage. It was not, however, possible to determine whether the egg galleries were established by beetles which had developed in the same year, or whether this was new progeny of females which had already laid eggs in the spring.

In our conditions, new-generation beetles can already leave the tree bark in mid-June in favorable years. On the basis of experiments carried out in the laboratory and outdoors, we can assume that the first beetles which have entered the shoots become sexually mature, in favorable conditions, after about three weeks of feeding in the shoots (see also HENNINGS 1908, p. 476). Consequently this could take place in warm summers around mid-July. If these beetles started an egg gallery in mid-July, their progeny would apparently have time to mature in favorable conditions in the same year. The progeny would have over two months of time for development, before the movement into the overwintering sites starts. Calculated on the basis of the monthly mean temperatures, the effective heat sum (zero-development point 8.5° C, see p. 33) for instance in 1963, from mid-July to the end of September was 524° C in Viikki, Helsinki. This is clearly more than the effective heat sum required for the full process of development in laboratory experiments, which is about 500° C. We should also bear in mind that in the field, development has required a smaller heat sum, calculated on the basis of daily mean temperatures, than the one found in laboratory experiments.

On the basis of these facts it seems that in 1963, temperature would have enabled the progeny of beetles developed in the same summer to mature by fall.

9. GENERAL DISCUSSION

In connection with the present study, it has been found that *B. piniperda* beetles are to be found both in pine shoots and in various breeding materials, from the beginning of the swarming period until late fall. In some cases, egg gallery establishment was found to have started in pine stumps already before swarming started. EIDMANN (1965) has also found that the species established egg galleries in felled trees from spring until the first days of August, although the number of egg galleries established after the actual swarming period was small. In connection with this study, on the basis of observations in the field and results from experiments, the following theoretical picture can be drawn concerning egg gallery establishment in the field. Broods are started by:

1. In March—April, beetles which have overwintered in the stumps of trees felled in the winter.
2. In the latter half of April, beetles participating in normal spring swarming.
3. In the latter half of May, beetles which had entered pine shoots during the swarming period, which were not sexually mature immediately after overwintering.
4. In the latter half of June and in July, beetles which had started a brood in the spring and then gone into shoots.
5. In late July and in August,
   a) beetles developed from broods established after spring swarming and then sexually matured in shoots.
   b) beetles which had entered shoots during the swarming period and then started a brood, after feeding again in shoots.

It is natural that the picture given above is hardly ever accurate, since weather conditions vary considerably among different years. If *B. piniperda* egg laying is so late in any considerable degree that the broods do not have time to mature before the winter, this has to be considered as a significant population dynamic factor, since the species is able to overwinter in our conditions only in the adult stage (KANGAS 1954, EHNSTRÖM 1963, EIDMANN 1965). However, in certain conditions the survival of the population is ensured by the fact that different stages of development occur simultaneously through the summer. Similar conclusions can be drawn from the observations of KANGAS (1954) that the species selects its breeding site bypassing to some extent the optimum sites for both extreme cases, as a security measure.

In connection with the present study, it was found that the optimum breeding material depends on environmental conditions. In some conditions, for instance, the broods on the sunny top side of a fallen tree may be destroyed because of excessive heat and drying of the breeding material (e.g. SCHIMITSCHEK 1931, p. 471, THALENHORST 1958, p. 37). In other conditions, the broods on the top sides develop, but the ones on the bottom side are destroyed for instance because of excessive moisture (SCHIMITSCHEK 1931, p. 475). We can also assume that in 1962, *B. piniperda* broods developed in Lapland only in such breeding materials which were warmed by the sun (cf. KANGAS 1963). The selection of breeding material which is suboptimal, thus undoubtedly has a depressing effect on the population in most conditions (see KANGAS 1950 b, 1953, 1954, 1959), but sometimes it may save the population from complete destruction. THALENHORST (1949) and KANGAS (1952, 1954) have reported that the most favorable breeding material from the point of the development of the individual insects is the cell tissue of the most vigorous trees, i.e. the breeding material which at the same time poses the greatest threat to the survival of the broods.

From the point of view of planning *B. piniperda* control, the results indicate that when the trap tree method is used, it seems to be reasonable to fell them to some extent even after the regular spring swarming period. It is not, however, necessary to debark trap trees felled after mid-July later in the season, if only *B. piniperda* is fought against, since the broods in these do not have time to mature during the summer and will be destroyed during the winter (see also EIDMANN 1965).

10. SUMMARY

In 1961—1970, problems connected with the life cycle and reproduction biology of *B. piniperda* were studied both in laboratory and outdoor development experiments and in natural conditions in the field. Primary attention during the study has been given to the significance of temperature at the various stages of the life cycle. In addition, factors affecting the establishment of the egg gallery, its construction and the quantity of progeny have been studied, and the possibility of a second generation in a year in Finland has been discussed.

The following results have been obtained in the study:

1. When a tree with overwintering beetles of this species in its base is felled during the winter, the overwintered insects can establish an egg gallery into the stump without leaving for swarming flight. The egg gallery can be established in this case already about a month before swarming starts.

2. Swarming starts after temperature in the shade exceeds 10° C. It is at its maximum at a temperature over 12° C and in conditions of no wind. The largest numbers of insects generally fly in the afternoon.

3. The swarming period lasts, depending on weather conditions, from a few days to a few weeks.

4. Swarming starts in southern Finland generally in the latter half of April, and in Lapland from two to four weeks later than in southern Finland.

5. Debarked trap trees attract more insects than trap trees with bark.

6. More insects were caught in collection traps equipped with transparent acrylic sheets than the ones with acrylic sheets painted black or white.

7. No significant difference was found in numbers of egg galleries on various sides of felled trees.

8. In stumps, the number of egg galleries per unit area of bark on the stump was about the same irrespective of stump size.

9. Part of the insects leaving their overwintering sites go into pine shoots for feeding and feed especially on buds.

10. Copulation takes place before egg gallery construction has started, while the female is digging itself into the bark but is still partly visible, and in the copulation chamber in the egg gallery. Copulation lasts from ca. two minutes to half an hour.

11. Pairs are usually formed after the female has started to excavate the egg gallery, but while it is still visible.

12. As the temperature rises, the rate of egg gallery construction and the rate of egg laying increase. The increase in the rates is especially clear between the temperatures 10° C and 15° C. In cool periods, parent insects sometimes only excavate and lengthen the egg gallery, but do not lay eggs.

13. The front part of the egg gallery (distance from the end of the egg gallery visible on the bark surface to the first egg niche) is longer at a low than at a high temperature.

14. With increasing egg gallery length, the length of the front part hardly increases at all, the length of the egg-laying part increases considerably, and the length of the terminal feeding part increases clearly.

15. Egg galleries are longer and there are a larger number of larval mines in fresh breeding material as compared with drier material.

16. The mean length of egg galleries decreases with increasing density. Their total length per unit area, however, increases only to a certain limit.

17. The following values for the zero-development points at the various stages of development were found: egg stage 8.4° C, larval stage 8.0° C, pupal stage 8.8° C.

18. The so-called effective heat sums required at the various developmental stages, computed on the basis of the daily mean temperatures above the zero-development points, were 82° C for the egg stage, 255° C for the larval stage, 107° C for the pupal stage, 24° C for the pre-emergence period (time spent by new beetles in the tree bark after the pupal stage) and 503° C for the entire development.

19. The pupal period increased in laboratory experiments, as relative humidity decreased. The most favorable relative humidity for pupal development was 77 %.

20. The males leave the egg gallery at about the time egg laying ends.

21. In Finnish conditions, *B. piniperda* does not have a diapause.

22. Movement into overwintering sites starts after the minimum daily temperature goes below 0° C.

23. About 10 per cent of the insects found in the overwintering sites in spring were estimated to have died during the winter.

24. With increasing density, the number of new beetles which developed from each egg gallery decreased. Counted on a surface area basis, however, it increased at first, but started to decrease rather quickly after density rose above a certain limit.

25. Some of the females taken from their overwintering sites, and put into experimental boxes in the absence of males, were able to lay eggs which developed into beetles.

26. The number of males may be only about half of the number of females, without a marked effect of the size of the new generation. If there are two or three times more males than females, the size of the broods of the females is decreased.

27. Counted on the basis of flight holes, the number of new-generation beetles was a little over ten per cent smaller than the actual one. The size of the error increased with increasing bark thickness.

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SELOSTE

Puutavaran korjuutekniikassa tapahtuneet muutokset ovat johtaneet ympärivuotisiin hakkuisiin, maakuljetusten lisääntymiseen ja kuorinnan siirtymiseen jalostuspaikalle. Tästä on ollut seurauksena, että puutavaraa pilaavien ja siinä lisääntyvien tuhohyönteisten torjuntaan on jouduttu kiinnittämään yhä suurempaa huomiota. Torjuntatoimenpiteiden suunnittelun ja toteutuksen kannalta on tärkeätä tuntea kulloinkin kysymyksessä olevan tuhonaiheuttajan elintavat mahdollisimman tarkoin.

Pystynävertäjä (*Blastophagus piniperda* L.) kuuluu pahimpiin metsätuholaisiimme. Lisääntymispaikkanaan se käyttää paksukuorista tuoretta mäntyä. Sopivia lisääntymispaikkoja ovat kannot, kuorellinen puutavara, heikentyneet pystypuut, tuulen kaatamat ja katkaisemat puut sekä lumen painosta katkenneiden puiden tyviosat.

Pystynävertäjä aiheuttaa pääasiassa kahdenlaista vahinkoa. Kuorellista puutavaraa se pilaa sekä kuljettamalla siihen sinistäjäsieniä että irroittamalla toukkakäytävillään puuta suojaavan kuoren, jolloin ilmasaastunnan kautta leviävät sienet pääsevät tulemaan puuhun. Mäntymetsissä laji aiheuttaa yhdessä vaakanävertäjän (*B. minor* Hart.) kanssa ns. ytimennävertäjätuhoja syömällä puiden kasvaimet ontoiksi. Nämä tuhot aiheuttavat usein hyvin huomattavia kasvutappioita. Tämän tutkimuksen tarkoituksena on selvittää erityisesti lämpötilan merkitystä pystynävertäjän elämänkierron eri vaiheissa. Sen lisäksi on selvitelty myös eräitä lisääntymiskohteen valintaan ja jälkeisöjen suuruuteen vaikuttavia tekijöitä.

Tutkimuksen aineisto kerättiin vuosina 1961—1970. Tutkimusalueet on esitetty kuvassa 1. Tutkimuksia on suoritettu sekä luonnossa että laboratorio-olosuhteissa.

Pystynävertäjän parveilua ja syömäkuvioiden kehitystä seurattiin luonnossa puutavaravarastoilla ja hakkuualoilla vuosina 1961—1965, jolloin kerättiin koe-eläimiä Helsingin yliopiston Maatalous- ja metsäeläintieteen laitoksella suoritettuun ytimennävertäjien lisääntymiskohteeseensa orientoitumistutkimukseen. Keväällä 1970 seurattiin parveilun kulkua Vihdissä erityisten keräilypyydysten avulla. Hyönteisten kasvatukset on suoritettu puolen metrin pituisissa mäntypölkyissä kasvatuslaatikossa, jonka kannessa oli messinkiverkko. Viikissä vuosina 1962—1964 suoritetuissa ulkokasvatuksissa käytettyjen pölkkyjen läpimitta ja kuoren paksuus sekä kasvatukseen pantujen emohyönteisten lukumäärä on ilmoitettu taulukossa 17. Muissa kasvatuksissa käytettiin suunnilleen samankokoisia pölkkyjä.

Pystynävertäjän talvehtimispaikkoihinsa siirtymistä seurattiin syksyllä 1968 ja 1970 kaivamalla veitsen kärjellä päivittäin koepuiden tyvistä niihin menneet yksilöt. Lajin kuolleisuutta talven aikana selvitettiin kaivamalla maaliskuussa kaadettujen mäntyjen kannot maasta ja laskemalla laboratoriossa niistä tavatut elävät ja kuolleet hyönteiset. Tutkimuksessa saatiin seuraavia tuloksia.

1. Ensimmäiset pystynävertäjät poistuivat laboratoriossa talvehtimiskäytävistään ainakin lämpötilassa 3—5° C. Ne eivät kuitenkaan menneet valossa oleviin lasiputkiin. Lämpötilassa 6—8° C kaikki talvehtimispaikoista lähteneet yksilöt olivat sen sijaan menneet valon puolelle (taulukko 1).

2. Jos puu, jonka tyvessä on talvehtivia lajin yksilöitä, kaadetaan talven aikana, voivat sen tyvessä talvehtineet hyönteiset perustaa syntyneeseen kantoon emokäytävän lähtemättä parveilulennolle. Emokäytävän perustaminen voi tapahtua tällöin jo noin kuukautta ennen parveilun alkamista.

3. Parveilu alkaa lämpötilan noustua varjossa yli 10° C. Se on voimakkainta lämpötilan ollessa yli 12° C (taulukot 2 ja 3, kuvat 2 ja 3). Tuuli haittaa parveilua (kuvat 4 ja 5). Runsaimmin on parveilevia hyönteisiä yleensä liikkeellä iltapäivällä.

4. Parveilu alkaa Etelä-Suomessa yleensä huhtikuun toisella puoliskolla, Lapissa yleensä kahdesta neljään viikkoa myöhemmin. Parveiluaika kestää sääsuhteista riippuen muutamista päivistä muutamiin viikkoihin.

5. Tuoreet kuoritut pyyntipuut houkuttelevat parveilevia hyönteisiä voimakkaammin kuin kuorimattomat (taulukko 4). Tämä johtuu ilmeisesti siitä, että niistä erittyy enemmän pystynävertäjiä houkuttelevia hajuaineita kuin kuorimattomista puista.

6. Läpinäkyvillä acryl-muovilevyillä varustetuista keräilypyydyksistä saatiin hyönteisiä enemmän kuin mustiksi tai valkoisiksi maalatuilla muovilevyillä varustetuista pyydyksistä (taulukko 5).

7. Emokäytävien lukumäärät kaadettujen puiden eri puolilla eivät eroa tilastollisesti merkitsevästi toisistaan.

8. Suurissa kannoissa on emokäytäviä enemmän kuin pienissä kannoissa. Kannon kuoripinta-alaa

kohti laskettuna emokäytävien lukumäärä on kuitenkin suunnilleen yhtä suuri kannon koosta riippumatta (taulukko 6).

9. Osa keväällä talvehtimispaikoista lähteneistä hyönteisistä ei ilmeisesti ole vielä sukukypsiä ja ne lentävät mäntyjen kasvaimiin syömään ravintosyöntiä. Tämä ravintosyönti kohdistuu erityisesti kasvainten kärkiin ja silmuihin.

10. Liian elinvoimaisiin puihin iskeytyneiden emojen munimat munat eivät kehity, ja pihkavuoto pakottaa emohyönteiset pois puusta.

11. Kopulointia tapahtuu ennen emokäytävän kaivamista, naaraan kaivautuessa kuoren sisään, mutta sen ollessa vielä osittain näkyvissä ja emokäytävässä olevassa parittelukammiossa. Kopuloinnin kesto vaihtelee parista minuutista puoleen tuntiin. Parinmuodostus tapahtuu tavallisesti naaraan aloitettua emokäytävän kaivamisen, mutta sen ollessa vielä näkyvissä kaarnanliuskan alla.

12. Lämpötilan noustessa lisääntyy emokäytävän kaivamis- ja munintanopeus (kuvat 6 ja 7). Erityisen selvä on aktiivisuuden lisääntyminen lämpötilan noustessa 10° C:sta 15° C:een. Viileinä kausina emohyönteiset kaivavat joskus vain emokäytävää, eivätkä muni.

13. Emokäytävän alkuosa (pituus puun pinnassa näkyvästä emokäytävän alusta ensimmäiseen munakoloon) on alhaisessa lämpötilassa pitempi kuin korkeassa lämpötilassa.

14. Emokäytäväpituuden kasvaessa alkuosan pituus lisääntyy tuskin ollenkaan, munintaosan pituus erittäin voimakkaasti ja jälkisyömän pituus vähän, mutta kuitenkin selvästi (kuva 20).

15. Samoissa emokäytävätiheyksissä olivat emokäytävät pystypuissa pitempiä kuin kahden metrin pituisissa paperipuissa ja kasvatuksissa käytetyissä pölkyissä (kuva 21). Talvella kaadetuissa tukkipuissa ja paperipuissa oli samanpituisissa emokäytävissä enemmän toukkakäytäviä kuin ohuemmissa puissa tai pienemmissä pölkyissä (kuva 23). On ilmeistä, että verraten tuore lisääntymismateriaali on edullisinta pystynävertäjän lisääntymisen kannalta.

16. Emokäytävien keskipituus lyhenee tiheyden kasvaessa. Niiden pinta-alayksikköä kohti laskettu summapituus sen sijaan kasvaa tiettyyn rajaan asti (kuva 14).

17. Eri kehitysasteiden kehityksen 0-pisteiksi (lämpötila, jonka alapuolella yksilökehitys pysähtyy) saatiin seuraavat arvot: muna-aste 8.4° C, toukka-aste 8.0° C, koteloaste 8.8° C. Eri kehitysasteiden vaatimat ns. vaikuttavat lämpösummat laskettuna edellä esitettyjen eri kehitysasteiden kehityksen 0-pisteiden yläpuolella olleiden vuorokausien keskilämpöjen summan mukaan olivat seuraavat: muna-aste 82° C, toukka-aste 255° C ja koteloaste 107° C. Saatuja tuloksia on kuitenkin vaikea soveltaa luonnon oloihin esimerkiksi siksi, että aurinkoisilla paikoilla on lämpötila puun kuoressa huomattavasti korkeampi kuin kahden metrin korkeudella maanpinnasta, missä lämpötilamittaukset tavallisesti tehdään. Laboratoriokasvatuksissa todettiin eri kehitysasteiden keston riippuvan suuresti kasvatuslämpötilasta (taulukot 8, 10, 11, 12 ja 13 sekä kuvat 8 ja 9).

18. Koiraat poistuvat emokäytävistä mäntyjen kasvaimiin muninnan päättymisen aikoihin. Naaraat siirtyvät kasvaimiin vasta syötyään emokäytävässä munintansa lopettamisen jälkeen ravintosyöntiä.

19. Lisääntymispaikkojen mikroklimaattisista eroista johtuen uuden sukupolven yksilöitä lentää mäntyjen latvakasvaimiin pitkin kesää. Pääosa niistä menee Etelä-Suomessa kasvaimiin kuitenkin heinäkuussa.

20. Toisen sukupolven yksilöt voivat ilmeisesti Suomen oloissakin perustaa joskus jälkeisön, joka ei kuitenkaan ehdi aikuistua ja tuhoutuu talven aikana.

21. Tiheyden lisääntyessä emokäytävää kohti laskettujen uusien yksilöiden lukumäärä väheni (kuvat 17 ja 18). Pinta-alayksikköä kohti laskettuna se kuitenkin aluksi nousi, mutta alkoi laskea verraten nopeasti tiheyden noustua tietyn rajan yläpuolelle (kuvat 16 ja 18).

22. Jotkut talvehtimispaikoista otetut naaraat, jotka pantiin kasvatukseen ilman koiraita, kykenivät munimaan kehityskykyisiä munia (taulukot 18 ja 19).

23. Koiraiden lukumäärä voi olla vain lähes puolet naaraiden lukumäärästä sen silti sanottavasti vaikuttamatta uuden sukupolven suuruuteen. Jos koiraita on enemmän kuin naaraita, vähenee naaraiden saama jälkeläismäärä (taulukot 19 ja 20).

24. Lentoreikien perusteella laskettuna saatiin uusien yksilöiden lukumäärä runsaat 10 % todellista pienemmäksi (kuva 27).

25. Talvehtimispaikkoihin kasvavien puiden tyviin siirtyminen alkaa vuorokauden minimilämpötilan laskettua alle 0° C. Yleensä tapahtuu talvehtimispaikkoihin siirtyminen Etelä-Suomessa syyslokakuun vaihteessa (kuvat 10 ja 11). Pystynävertäjät valitsevat talvehtimispaikoikseen suurikokoisempien puiden tyviä (kuvat 12 ja 13). Noin 10 % keväällä talvehtimispaikoista löytyneistä yksilöistä oli ilmeisesti kuollut talven aikana (taulukko 16).

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