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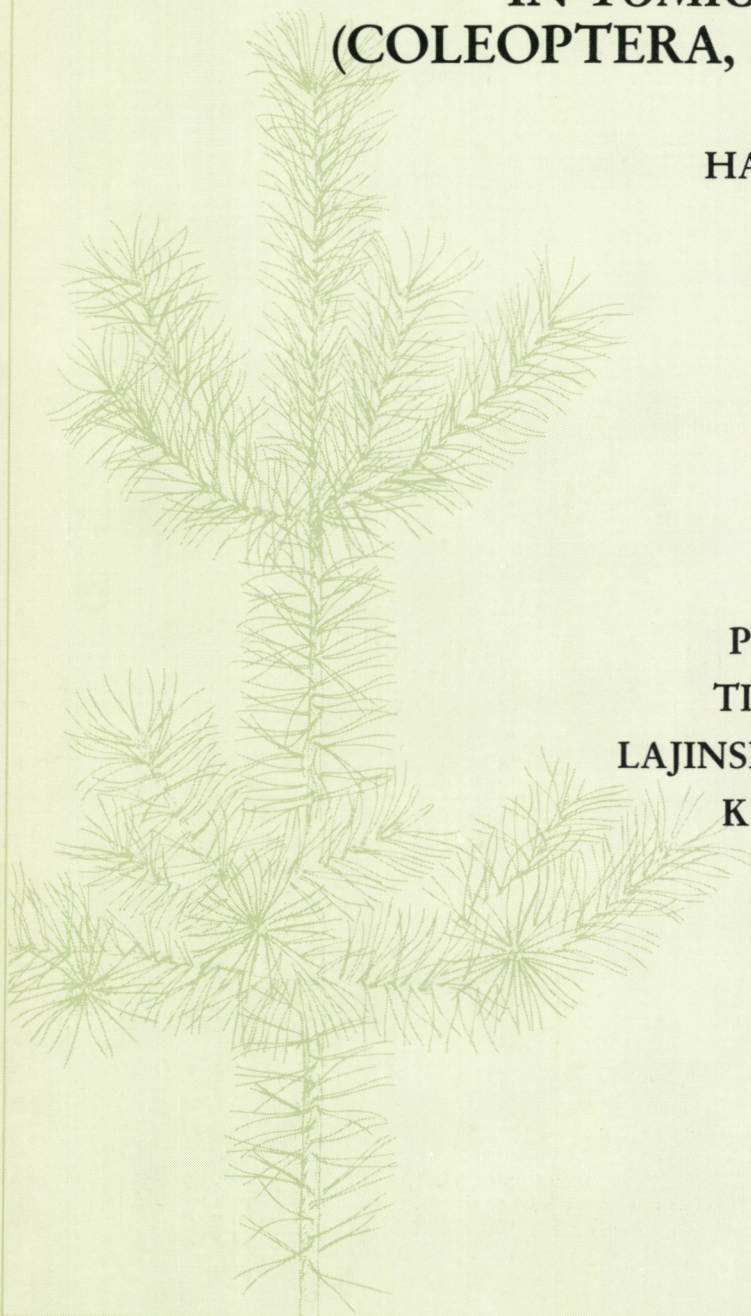
**MODELING THE SPATIAL PATTERN  
AND INTRASPECIFIC COMPETITION  
IN *TOMICUS PINIPERDA*  
(COLEOPTERA, SCOLYTIDAE)**

HANNU SAARENMAA

SELOSTE

**PYSTYNÄVERTÄJÄN  
TILAJÄRJESTYSTÄ JA  
LAJINSISÄISTÄ KILPAILUA  
KUVAAVIA MALLEJA**

HELSINKI 1983





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*Cover (front & back):* Scots pine (*Pinus sylvestris* L.) is the most important tree species in Finland. Pine dominated forest covers about 60 per cent of forest land and its total volume is nearly 700 mill. cu.m. The front cover shows a young Scots pine and the back cover a 30-metre-high, 140-year-old tree.



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The spatial pattern of *Tomicus piniperda* was studied during its developmental period, the emphasis being on the effects of density and spatial pattern on the reproduction and intraspecific competition. The main goal was to develop models for life-table studies in order to explain the mortality and subsequent disappearance of larvae due to intraspecific competition.

The material comprised 83 laboratory bolts and 44 field bolts, which were all exposed to the attack of *T. piniperda*. The bolts were protected against concurring species, predators, and parasites. There were on the average 26 egg galleries and 235 exit holes in each bolt. All the egg galleries and about half of the exit holes were mapped by measuring their coordinates on the surfaces of the bolts. Another data source was a large data base sampled from the field. It was used to derive those parameters not available from the special material.

A selection of different aggregation indices was evaluated, and Pielou's point-to-object index  $\alpha$  was chosen. The aggregation of egg galleries was dependent on density. At densities below 100 egg galleries/m<sup>2</sup> the spatial pattern was clumped, above 200 egg galleries/m<sup>2</sup> regular, and in the intermediate densities random. Bark thickness or its variance did not affect the spatial pattern, but the cortical temperature did. Exit holes were very aggregated over the whole range of densities. However, their pattern was more regular at higher densities.

Different regression and dynamic models describing the emergence of beetles were then evaluated. Two regression models with mere attack density as the independent variable explained 43 % of the variance of the ratio of increase. When  $\alpha$  was introduced into the model, the increment in multiple correlation square was not significant. Another regression model, in which the mean minimum distances to the four closest egg galleries were the independent variables, explained 44 %. A simulation model based on the mortality of larvae as a result of their movement process was the best, explaining 58 % of the variance. So the dynamic model was superior to the regression models. There was, however, lots of unexplained mortality, which was probably not due to intraspecific competition.

The effect of the spatial pattern on the ratio of increase was 0—15 %, being strongest at low densities. The simulation model indicated that the survival could be enhanced with a more regular attack pattern at medium densities. The importance of spatial pattern as a negative feedback mechanism was discussed.

Työssä tutkittiin pystynävertäjän tilajärjestystä sen lisääntymiskautena sekä iskeytymistiheyden ja tilajärjestyksen vaikutusta lajinsisäiseen kilpailuun ja lisääntymistulokseen. Pääarkoituus oli kehittää meillä oleviin *life-table* -tutkimuksiin malleja, joilla toukkien kuolemista ja katoamista lajinsisäisen kilpailun tuloksena voidaan ennustaa ja selittää.

Aineisto käsitti 83 laboratorioissa ja 44 luonnossa pystynävertäjällä iskeytetyttä pölkkyä, jotka oli suojattu kilpailevilta lajeilta, pedoilta ja loisilta. Keskimäärin pölkky sisälsi 26 emokäytävää ja 235 kuoriutumisreikää, joiden paikat oli kartoitettu koordinaatein. Aineiston tukena käytettiin luonnosta säännöllisin näytein kerättyä tietokantaa.

Erilaisia ryhmittymisindeksejä vertailtiin ja käytettäväksi valittiin Pieloun  $\alpha$ . Emokäytävien tilajärjestys riippui tiheydestä. Alle 100 emokäytävää/m<sup>2</sup> tilajärjestys oli ryhmittäinen, yli 200 emokäytävää/m<sup>2</sup> tasainen ja välialueella satunnainen. Kaaran paksuudella tai sen varianssilla ei ollut vaikutusta tilajärjestykseen, mutta kaaran lämpötilan vaihteluilla oli. Kuoriutumisreivät olivat erittäin ryhmittyneitä, mutta niidenkin tilajärjestys muuttui tasaisemmaksi tiheyden lisääntyessä.

Erilaisia jälkeläistuotosta kuvaavia regressio- ja dynaamisia malleja vertailtiin. Kaksi regressiomallia, joissa selittävänä muuttujana oli vain iskeytymistiheys, selittivät 43 % lisääntymiskertoimen varianssista. Kun  $\alpha$  otettiin malliin mukaan, selitysaste ei parantunut. Toinen malli, jossa selittävänä muuttujina olivat keskimääräiset minimietäisyydet 4 lähimpään emokäytävään selitti sekin vain 44 %. Sen sijaan toisessa yhteydessä kehitetty simulointimalli, joka perustuu toukkien kuolemiseen niiden liikkumisprosessin seurauksena, selitti 58 % lisääntymiskertoimen varianssista ja oli paras tutkituista malleista. Selittämättä jäi kuitenkin suuri osa kuolleisuudesta, luultavasti sen takia, ettei se ollut lajinsisäisen kilpailun aiheuttamaa.

Tilajärjestyksen vaikutus lisääntymiskertoimeen oli 0—15 %, ollen suurin alhaisissa tiheyksissä. Simuloinnit osoittivat, että toukkien kuolleisuus voisi olla pienempi, jos tilajärjestys olisi tasaisempi keskitiheyksissä. Tasaisen tilajärjestyksen merkitystä populaatiotason määräävänä negatiivisena takaisinkytkentämekanismina tarkasteltiin.

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## PREFACE

This study has been conducted by the Department of Forest Protection, the Finnish Forest Research Institute, at the Rovaniemi Research Station. It is the first of a series of papers in which the population dynamics of *Tomicus piniperda* L. is being modeled.

Here the modeling approach is based on the concept that modern forest management — of which pest population management is a part — requires a concrete basis for concrete investments. Today we not only need to know what can happen, to forecast the risk on a *qualitative* level, but we also need to *quantify the risk*. This is not so easily done due to the complexity of the life systems of bark beetles. A distant goal of these research activities is to propose models which could be used to forecast the risk probability and simulate the control measures. Such models will perhaps be available for practical use in forestry computer networks in the future.

During the course of the study the author has received help from many persons. Professor Paavo Juutinen has continuously shown interest in the research work and has given valuable advice. The assistance of Mr. Mart de Jong (Wageningen, the Nether-

lands) in the work during his two visits to Rovaniemi is fully acknowledged. The many discussions with him have also been of importance for this study. The discussions with Dr. Bo Långström (Garpenberg, Sweden), Mr. Hannu Räisänen, M.Sc., and Mr. Mauri Timonen, B.Sc., have also been valuable. In the laboratory Mr. Pentti Vitikka has been responsible for most of the measurements. The tree material used in the study has been provided by Mr. Erkki Lepänen and Mr. Toivo Saunavaara of the Experimental Forest District in Kivalo. Mrs. Helmi Saunavaara has been of great help in carrying out the field work. Ms. Anne Immonen has drawn the figures, and Mr. John Derome, M.Sc., revised the language of the manuscript. This paper was read by professor Matti Nuorteva, Dr. Erkki Annila, Dr. Pertti Hari, and associate professor Seppo Niemelä. Their criticism is acknowledged. The continuous inspiration provided by my dear wife Liisa has been invaluable. I express my sincerest thanks to all these persons.

Rovaniemi 20. 5. 1983

*Hannu Saarenmaa*



# 1. INTRODUCTION

The pine shoot beetle, *Tomicus piniperda* (L.), is a major pest of Scots pine, *Pinus sylvestris* L., in the Nordic Countries. A large number of studies have been carried out on the biology and control of the species, the most recent ones being those of Långström (1980, 1983). Living trees are mainly damaged as a result of adult beetles attacking the shoots. The killing of weakened trees has only been observed at very high population levels (e.g. Kangas 1934). Normally the beetle reproduces in felled timber, stumps, logging waste, windfalls, and overtopped trees.

Bark beetles possess very strong dispersal, orientation, aggregation and reproducing abilities. Therefore they are able to utilize almost every piece of suitable food. In endemic conditions, the reproduction of bark beetles is controlled most effectively by the restricted amount of available breeding material (Nuorteva 1954). Other factors — host resistance, intraspecific and interspecific competition, predators, parasites, diseases, weather (see e.g. Nuorteva 1956, Coulson 1979) — interfere after the breeding material has been located. All these factors together form a very complex system (see Coulson 1974, 1979). Understanding the function of the life system and predicting its output is a very problematic task. A minor shift in one subsystem may cause great variation in the behavior of the entire system. The reproduction results of *T. piniperda* have indeed varied extremely much under field conditions (see e.g. Kangas 1953, 1963, Långström 1979), depending on the prevailing key-factor in the particular situation. Beaver (1967) emphasizes that as the conditions change, so do the regulatory mechanisms of *Scolytus scolytus* F.

Under artificial experimental conditions, in which for instance competing species, parasites and predators are excluded, the predictability of beetle reproduction is also poor. In the experiment reported by Eidmann and Nuorteva (1968), the reproduction of *Tomicus piniperda* varied considerably in

spite of the fact that the beetles were reared in cages.

In the case of *T. piniperda*, intraspecific competition is perhaps the most important mortality factor in endemic low level conditions, because it is so closely linked to the amount of breeding material available. When constructing life-tables and survivorship curves for bark beetles, the effect of intraspecific competition is difficult to evaluate. The reason for this is that the dead larvae are absent from the bark samples, due to deterioration or cannibalism. This "disappearance" may account for as much as 80 % of the larval population (c.f. Beaver 1966, DeMars and al. 1970, Berryman 1973). The effect of intraspecific competition on mortality thus has to be modeled if an estimate of it is desired (Berryman and Pienaar 1973). The question then arises, which are the factors that ought to be present in such a model, and moreover, how should the model be designed?

If we assume that intraspecific competition is deterministically described when the attack density is known, the variation should not be as great as that found by Eidmann and Nuorteva (1968). It is evident that the residual mortality and intraspecific competition are also affected by other factors, such as phloem thickness, the quality of parent beetles and the spatial pattern of the egg galleries\*). Ultimately, intraspecific competition is determined by the spatial pattern of larvae changing in time, which is largely a consequence of the spatial configuration of the egg galleries.

The spatial pattern has been studied in some bark beetles. Nilssen (1978) found a regular pattern of *T. piniperda* attacks in two high wind-cut stumps. A regular pattern has also been found for *Scolytus ventralis*

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\*) Spatial pattern is often termed as "spatial distribution". To avoid confusion with the colloquial and statistical meanings of the word "distribution", the spatial arrangement of objects should be called "spatial pattern" (Pielou 1977).

LeConte (Berryman 1968), *Dendroctonus ponderosae* Hopkins (Shepherd 1965, Safra-nyik and Vithayasai 1971), and *D. pseudo-tsugae* Hopkins (Hedden and Gara 1976). It can be assumed that the survival probabilities of the larvae are the greater, the greater is the regularity, because the probability of a larva entering a dead end is smaller in a regular pattern than in a purely random one. As far as I am aware, the only study that has been done on this subject is that of Berryman and Pienaar (1973) on *S. ventralis*. They constructed a simulation model in which the mortality of the larvae was proportional to the overlapping of the area occupied by the vertical larval mines. One of the assumptions in their model was that the spatial pattern of egg galleries was random. However, the possible dependence of spatial pattern on density or other variables would result in a more complicated situation. It therefore becomes necessary to describe the actual spatial pattern, e.g. by means of an aggregation index. The index can then be used as an independent variable in regression analysis. On the other hand, it can be reasoned that it is the variation, intensity, of the spatial pattern which is important for the survival of larvae. Using an aggregation index, or any mean value, does not necessarily reveal the local variation. A realistic model of intraspecific competition ought to utilize the information concerning the actual locations of egg galleries. Moreover, the behavior of the larvae may affect survival. Starting from these assumptions a mechanistic simulation model was developed (Jong and Saarenmaa 1984) parallel with this study. In the model, the movement process of individual larvae is considered, and mortality results in their inability to

move further from a dead end where they are completely surrounded by consumed phloem.

There are several rapidly acting negative feedback processes operating during the reproductive phases of bark beetles, by means of which the severity of competition is controlled. Increasing attack density results in a shortening of the egg galleries in many bark beetles. The number of eggs laid per gallery decreases, and aggregation of the beetles will finally stop completely (for summary see Berryman 1974, Nilssen 1978). The tendency to follow a regular spatial pattern can also be included in the regulatory activities, although no evidence to indicate its dependence on attack density has yet been proposed. Reduction of fecundity and a change in the sex ratio in the following generation are processes acting with longer time lags. The density-dependent effects of parasites and predators are also more serious in the following generations. The negative feedback processes are particularly important, because they have a strong effect on the behaviour of the whole system (Berryman 1981).

This study has three goals: (i) To elucidate the spatial pattern of *T. piniperda* during its reproducing period and to study the factors which affect it. (ii) To develop models for intraspecific competition in *T. piniperda*, and to account the effect of spatial pattern in them. The main use for these models would be in constructing life-tables and survivorship curves. A further goal (iii) is to gain more insight into the competitive processes. This will be done by simulating the effects of age structure and the fast acting negative feedback mechanisms — spatial pattern and aggregation shut off — on the reproduction.



## 2. MATERIAL AND METHODS

### 21. The rearing material

The material consists of two groups of bolts: Those attacked in the laboratory, and those attacked in the field. In the laboratory, the attack density was controlled. A natural spatial pattern was obtained in the case of the field bolts, but the attack density was not under control. The experiments were carried out in 1980 and 1981.

In the laboratory, 83 bolts were placed in plywood cages together with 2 to 74 parent beetles which had been collected during swarming in the vicinity of Rovaniemi, northern Finland. The beetles were sexed in cages into which less than 20 beetles were introduced to ensure an even sex ratio. In the bolts where 1 or 2 couples were introduced, the beetles were forced to bore into the bolts from small plastic cups. The bolts were freshly cut 40 cm long pine sections with a typical bark area of 0.16 m<sup>2</sup>. The ends of the bolts were sealed with paraffin wax. 51 of the cages were put into breeding chambers where the temperature was kept constant and the relative humidity of the air was 95%. The different bolts were kept at temperatures ranging from 15 to 28 C, because the same material was used in a different study in which the effect of constant temperature on the developmental rate of *T. piniperda* was being studied. However, the temperature range used here is within the linear part of the developmental response (unpublished results), and it was assumed that temperature did not affect mortality within this range as the rainfall was absent. The remaining 32 cages were kept at room temperature in the laboratory, where they were moistened daily.

The rearing beetles emerged into glass pots fixed on the walls of the cages, and the bolts were kept in the cages until all the young beetles had reared.

For the field attacks 15 experimental logs, 2 m long, were cut in Rovaniemi in April 1981. One end of each log had thick butt bark and the other reached the thin-barked area. The logs were placed in groups of three, lying in an east-west direction.

In order to determine the effect of warming sunshine on the selection of attack places, the logs were shaded in five different ways as follows: i) no shade; ii) one-fold green mosquito netting; iii) two-fold netting; iv) four-fold netting; and v) dark cotton cloth. The cloth shaded the sun completely. The shades were erected away from the logs so that they did not obstruct the attacking beetles. During swarming at 16.20 on 18.5.1981, when the air temperature was 17.7°C, the following temperatures (°C) were recorded in the logs under the bark:

	upper side	underside
unshaded	30.7	19.5
one-fold netting	26.5	17.0
two-fold netting	22.5	20.0
four-fold netting	20.5	20.1
cloth	16.0	17.0

Swarming started on May 13 when there was still snow on the ground and the maximum air temperature reached 14.1°C. A period of three cool days followed. The main swarming occurred on May 17 and 18, when the maximum air temperatures were 20.2 and 18.3°C respectively. On the 19th of May the logs were enclosed in very fine-meshed white terylene netting so as to prevent other insect species from penetrating the logs. However, this was done too late as Cerambycid *Acanthocinus aedelis* L. had had enough time to attack some of the logs. Their larvae are efficient predators and competitors of *T. piniperda* (Nuorteva 1962), and all the parts of logs where they were found were therefore excluded from the material. The shades and terylene-netting were kept in place until September, when the logs were transferred to the laboratory. Summer 1981 was cooler than normal, and therefore about 30% of the emerging beetles had not emerged by September. They were allowed to exit in the laboratory before peeling the bark off the logs. The 2 m long logs were cut into 40 cm pieces so as to make handling easier and to make them similar to the laboratory bolts for calculating purposes. 31 of the 75 field bolts had to be rejected as a result of *Acanthocinus* attacks to be analyzed later in another context.

The live weight of the emerging young beetles was measured from another data set. In 1982 variable temperatures were used in the breeding chambers. The emerging beetles from 45 cages were weighed and the daily means calculated. The temperature and humidity presumably have an effect on the live weights. As there were 5 different temperature programs in the 5 breeding chambers, the results are considered separately.

### 22. Measurements and transformations

All the experimental bolts, those used in the field as well as those in the laboratory, were numerically mapped by measuring coordinates. After mapping the round bolt surface was considered to be a plane. All the distance measurements and calculations were performed by computer. This procedure permitted flexible trials using various types of calculating methods, not only the ones planned when the experiment was designed.

The measuring procedure is described in detail in the laboratory manual (Saarenmaa and Räsänen 1982). Before peeling, the bolt circumferences at both ends, the bolt length, bark thickness and its variance were measured. The size and number of the crevices in the bark are described by means of the variance of the bark thickness. After peeling, the bolt circumferences were again measured at both ends. The positions of the egg galleries in all the bolts were measured as the coordinates of the starting (entrance) points and the ending points. In addition, more data was gathered from about half of the material (68 bolts). In this case the coordinates of the exit holes were also measured before peeling. In order to facilitate measurement of the distance from the exit holes to the egg galleries, the meandering of the egg galleries was also taken into account by measuring in some cases up to three additional points in the middle of the egg galleries, whenever necessary. Thus the exact shape of a particular gallery was known. Usually, of course, the egg galleries of *T. piniperda* are quite straight.

The starting line for the measurements was a zero line drawn on the upper side of the bolt. A 100 \* 100 mm grid was drawn on the bolt surface over the bark starting from this line and from one end of the bolt. The exit hole coordinates were measured with the aid of the grid. As the scale under the bark is smaller than that over the bark, the coordinates of the exit holes had to be transformed to correspond to the values under the bark. The corner points of the grid were first marked under the bark by means of nails driven through the bark. The bark was then removed, and the coordinates of the nail holes under the bark measured. The grid under the bark had usually typical dimensions 100 \* 85 mm per square. The exit hole coordinates were then transformed using the correction factor obtained for each grid square. The y-coordinate does not need any transformation. The equation for the x-coordinate takes into account any possible skewness in the square resulting from the slight tapering of the bolt. The equations are (for symbols, see Fig 1):

$$y' = y \quad (22-1)$$

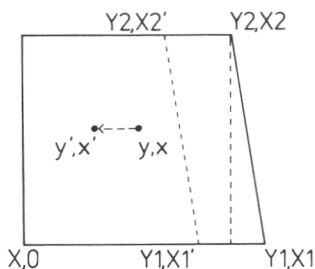


Fig 1. A grid square 100 × 100 mm on the surface of the bark (y, x) and the change in coordinates after transformation under the bark (y', x').

Kuva 1. Yksi 100 × 100 mm verkoston ruutu pölkyn pinnalla (y, x) ja muutos koordinaateissa (y', x') kaarnan alle tehdyn muunnoksen jälkeen.

$$x' = \frac{X1'x}{X1} + \frac{(y - Y1)(X2 - X1)}{Y2 - Y1} \quad (22-2)$$

As the surface was artificially split in the middle along the zero line, no measurements could be made over that without additional transformations. Therefore, additional coordinates were projected for all exit hole and gallery coordinates over the zero line. In other words, the bolt surface was doubled by coupling the opposite bolt ends together along the zero line (Fig 2). The slope due to tapering of the bolt was taken into account using trigonometric correction factors (for symbols, see Fig 2):

$$y'' = \frac{y'}{\cos\beta} + x'\sin\beta - y'\sin\beta \tan\beta \quad (22-3)$$

$$x'' = \frac{x'}{\cos\beta} + (YYY - y') \tan\beta + XTN \quad (22-4)$$

In the equations,  $\beta = \arctan(XTS - XTN/YYY)$  (Fig. 2). The problem with this transformation is that the zero line of the doubled plane is longer than the actual zero line. This is, however, only ostensible, since actually we are dealing with curvilinear planes, which for mathematical convenience are considered as trapezoids (see Pulley and al. 1976).

Salonen (1973) has found that, on the average, 12.9 % of *T. piniperda* emerge out of the same holes or through bark furrows where the exit holes are not detectable. This percentage was directly proportional to bark thickness, but not correlated with the number of offspring, which suggests that the beetles do not emerge through the same holes. The number of beetles collected in the rearing bottles of the cages was only 98.1 % of the number of exit holes in the laboratory material of this study. This indicates that some of the rearing cages were not sealed properly. This is indeed the case, because escaped beetles were observed in the laboratory. This can also be seen from Fig 3. If the first peak in Fig 3 at about 75 % is omitted, then the mean is 109.0 %. This fits well to the model of Salonen (1973). The actual

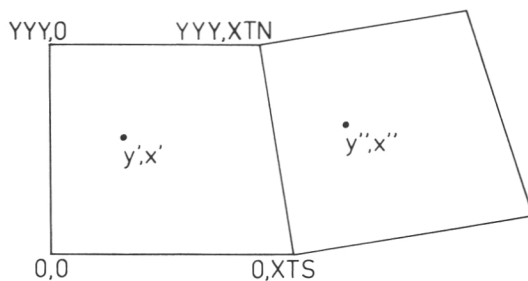


Fig 2. The actual plane under the bark (y', x') and the coupled plane (y'', x'').

Kuva 2. Varsinainen pölkyn pinta kaarnan alla (y', x') ja sama toiseen kertaan liitettyinä nollaviivaa pitkin (y'', x'').

number of emerged beetles was not available for the field material, not for the laboratory material in 1980. The production of new beetles is therefore based only on the number of exit holes in this paper. This may thus result in a slight underestimation of the beetle production numbers. Moreover, those beetles which use the same exit hole as their earlier reared siblings could not be taken into account in the analysis of the spatial pattern.

The ratio of increase (RI) has been calculated from the equation

$$RI = \text{number of exit holes/number of parents}$$

A large data base on the development and survival of bark beetles, especially *T. piniperda*, in Lapland was formed during 1980–83 at the Rovaniemi Research Station of the Finnish Forest Research Institute. In its present state it comprises about one thousand sample bolts ranging from 25 to 50 cm in length sampled from pine logs, pulpwood stacks, windfalls, and thinning areas. The data base also comprises hourly measured temperatures under the bark at all the sampling points. The procedures involved in the collection and retrieval of the data have been described in detail by Saarenmaa and Räsänen (1982). The values of a number of parameters, especially those dealing with oviposition, used later on in the study have been derived from this data base.

### 23. Calculating the spatial pattern

The scale of the spatial pattern in a continuum ranges from extreme aggregation, in which all the individuals have aggregated in a single clump, to perfect hexagonal regularity, in which each individual has six neighbors at equal distance. The

random pattern falls between these extremes. In a purely random pattern the location of one object does not affect the probability where another object is located. In addition to this main variation, the spatial pattern has two other aspects: intensity and grain (see Pielou 1977). If we are interested in describing competition between neighboring larvae, we must have a good estimator for the intensity of the spatial pattern.

The methods used for studying spatial pattern can be divided into two categories: (i) sample plot methods, and (ii) distance methods (Pielou 1977). In order to find the best methods for this study both types of methods were tested. Examining the fit of an observed distribution to a particular theoretical distribution has also been used in studying spatial patterns, but this approach is not considered fruitful (Pielou 1977). Both sample plot methods and distance methods have their own advantages. When the objects are dispersed into discrete sampling units, such as larvae in tree branches, only the former method can be applied. If the objects occur in a continuum, usually on a plane or in the phloem of a log as in this case, both approaches are possible.

The aggregation in the sample plots is described by the variance/mean ratio. Ratios from 0 to 1 indicate regularity, 1 randomness, and  $1 <$  clumpiness. The disadvantage of the sample plot method is that an artificial plot must be restricted, and the size of the plot drastically affects the conclusions. If it is possible to use sample plots of several different sizes, then the disadvantage becomes an advantage, because it is possible to detect the clump size. The variance /mean ratio is greatest in the plots which are of the same size as the clumps (e.g. Bonnicksen and Stone 1980).

Cox (1971) has developed an index of clumpiness, based on a zero-plot diagramme, which is not sensitive to the clump size. It is calculated from the equation

$$I_c = 0.907 a b \quad (23-1)$$

where  $a$  = the proportion of empty plots using a plot size in which one object is observed on the average; and  $b$  = the mean number of objects on the plot size, in which 5% of the plots are empty.  $I_c$  is interpreted as the  $v/m$ -ratio: Values from 0 to 1 indicate regularity, 1 randomness, and  $1 <$  clumpiness. This method has been used in forest regeneration studies because the number of empty plots has a concrete meaning in such cases (e.g. Pohtila 1980). However, calculation of  $I_c$  is rather complicated and inaccurate, at least if interpolation is involved.

The two most popular distance methods were examined: (i) nearest neighbor  $R$ , and (ii) closest individual.

$R$  is obtained by dividing  $r$ , the mean distance between two individuals, by the expected distance in a random pattern

$$R = \frac{r}{0.5 \sqrt{\rho}} \quad (23-2)$$

in which  $\rho$  = the density of individuals /unit area (Clark and Evans 1954).  $R$  is interpreted as follows:

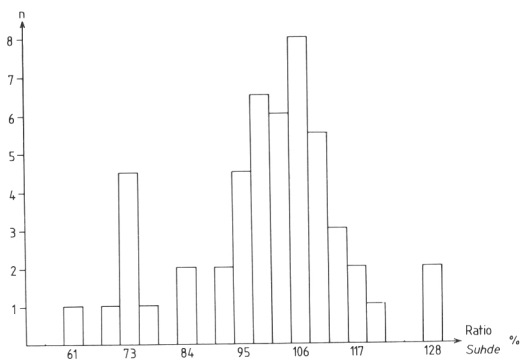


Fig 3. The distribution of the ratio between the number of young beetles collected from the rearing cages and the number of exit holes expressed in %.

Kuva 3. Kasvatuslaatikosta kerättyjen kuoriaisten ja kuoriutumisreikien prosentuaalisen suhteen jakauma.



Values from 0 to 1 indicate clumpness, 1 randomness, and  $1 <$  regularity. The theoretical maximum value is 2.1491 for a hexagonally regular pattern. The statistical significance of any deviation of R from 1 can be tested using the normal distribution. The normal variate (c) is obtained from the equation

$$c = \frac{r - 0.5 \sqrt{\rho}}{0.26136 \sqrt{n\rho}} \quad (23-3)$$

in which n is the number of measurements.

The other distance method used is based on the mean distance measured from a random point to the closest individual. It is obtained from the equation

$$\alpha = \pi \rho \omega \quad (23-4)$$

in which  $\pi = 3.14159$ ,  $\rho =$  the density of individuals /unit area, and  $\omega =$  the mean of the squares of the distances. The values of  $\alpha$  are interpreted as follows: From 0 to  $(n-1)/n$  indicates a regular pattern,  $(n-1)/n$  indicates a random pattern, and  $(n-1)/n <$  indicates an aggregated pattern. The statistical significance of the deviation from  $(n-1)/n$  can be tested, since  $2n\alpha$  is distributed like  $\chi^2$  with  $2n$  degrees of freedom (Pielou 1959). In this study,  $\alpha$  was transformed to relative  $\alpha$  by dividing it with  $(n-1)/n$  thus making it possible to use observations with different numbers of objects in regression analyses.  $\alpha$  thus has the value 1 in a random pattern. As this may alter the distribution of  $\alpha$ , the conclusions concerning individual bolts in Sections 323 and 351 are made on the basis of untransformed values.

R and  $\alpha$  have somewhat different properties. R measures only the small scale distances between neighbors in clumps, and it is perhaps the best estimator of the intensity of the spatial pattern. The starting points for measurements of  $\alpha$  also fall between the possible clumps, and thus  $\alpha$  also measures the grain of the spatial pattern (for complete discussion, see Pielou 1959, 1977).  $\alpha$  has been considered to be perhaps the best of the estimators available (Payandeh 1970). The three estimators of spatial pattern were calculated for the exit holes, entrance holes, gallery end points, and gallery midpoints. When calculating  $\alpha$  and  $I_c$ , 100 random points were sampled and the distances were measured from them. In calculating R, the number of distances measured was that of objects — 1. Numerical mapping of the sample bolts made it possible to use any type of calculating method. No sampling problems were encountered when calculating the nearest neighbor R, since all the objects were used once as the starting point for the measurements (except those too close to the bolt ends — see Section 242). The distances to all the other objects were calculated in order to find the minimum distance to the nearest neighbor /closest individual. The computing costs of this method are exponentially related to the number of objects in the sample. The brute force solution used could perhaps be replaced by a more intelligent algorithm.

The density attributes of the bolts were considered as given for the particular data subset. Separate estimates of the means and variances were not

calculated for the bolts, as suggested by Mountford (1961).

The mean minimum distances to the four nearest egg galleries in all the bolts were calculated. This method considers the objects not as points as the previous ones, but as lines. Of course no test value for randomness can be proposed for these distances, because the lengths of the lines are varying from case to case. The distances were used as independent variables in the analyses. These minimum distances may describe the actual interference between the egg galleries better than the aggregation indices calculated on the basis of certain egg gallery points. Thus it comes close to the approach of Berryman and Pienaar (1973).

## 24. The accuracy and restrictions of the calculating methods

Since the conclusions later on in the text will be made from relatively small differences, and it was planned that the aggregation indices would be used as independent variables in multiple regression analysis, it is important to obtain bias-free estimates. A set of simulations with artificial materials was therefore carried out in order to test the sensitivity of the calculating methods. The tests done here are not exhaustive, because only the random pattern could be considered.

### 241. The accuracy of the transformation under the bark

The procedure used in transforming the coordinates of the exit holes under the bark was rather complicated. The accuracy of the transformation was evaluated in one bolt by nailing all the exit holes and then measuring the coordinates of the nail holes. The nail hole corresponding to each transformed exit hole was identified and the mean distance then calculated. The mean dislocation was 2.99 mm. The transforming accuracy can thus be considered to be good enough.

### 242. The edge effect

When the point from which the distance to the nearest neighbor or the closest individual is measured is closer to the edge of the sampling area than to a real object, a systematic error arises. This error causes the aggregation index to have a value biased towards regularity. This may drastically affect the conclusions (Mawson 1968). Margins in which no point is accepted as the starting point of a measurement, have therefore to be drawn along the edges of the sampling area. However, there were no references in the literature about how wide this margin should be. The margins used in earlier studies (e.g. Mawson 1968, Cox 1971) were too wide to be used as such. Wensel (1975a, b) has presented a procedure by means of which the adjacent ends of sample plots get to contact with each

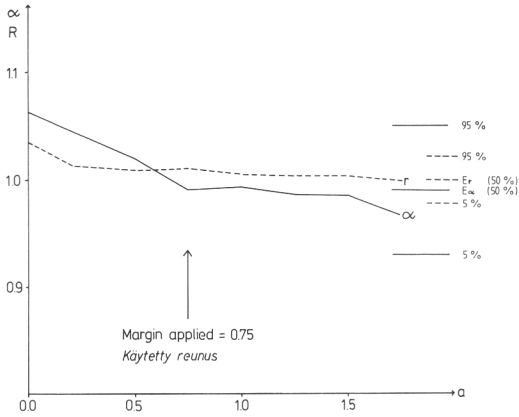


Fig 4. The edge effect. The dependence of the mean values of  $R$  and  $\alpha$  on the margin cut out of the bolt ends. The margin  $m=a d$ , in which  $d=1/2 \sqrt{\rho}$ .

Kuva 4. Reunavaikutus.  $R$ :n ja  $\alpha$ :n keskiarvojen riippuvuus pölkyn päästä pois leikatusta reunuksesta, jolta mittauksia ei aloitettu. Reunus  $m=a d$ , missä  $d=1/2 \sqrt{\rho}$ .

other, and thus no margin needs to be delineated at all. In this study, the adjacent boundaries of the sampling area were projected so as to come into contact with each other, as in a real bolt. However, the bolt ends are not projected in this way.

Let  $\rho$  be the density of individuals /unit area. The mean distance ( $D$ ) between individuals is

$$D = \frac{1}{2 \sqrt{\rho}} \quad (242-1)$$

if they are randomly distributed. An artificial material consisting of 30 bolts each having 100 randomly dispersed objects on their surface, was generated. The margin was allowed to loop from  $0.00D$  to  $2.00D$ , with steps of  $0.25D$ , using 30 replications pro  $D$ . The means of  $R$  and  $\alpha$  are shown in Fig 4. In the case of random objects there should not, of course, be any difference between  $R$  and  $\alpha$ .  $R$  seems to need a narrower margin than  $\alpha$ , but because  $R$  has narrower confidence limits than  $\alpha$ , they both cross the limit at the same point,  $0.2D$ . The error continues to diminish up to  $0.75D$ , which was the margin applied in the further calculations. The margin needed may of course vary depending on the degree of aggregation, but such information, if available, could not be used in the calculations.  $I_c$  and the variance/mean ratio are free from this kind of error, if those sample plots are rejected which partly come over the edge.

### 243. The smallest number of objects

The number of egg galleries in the bolts ranged in the laboratory material from 1 to 58, and in the

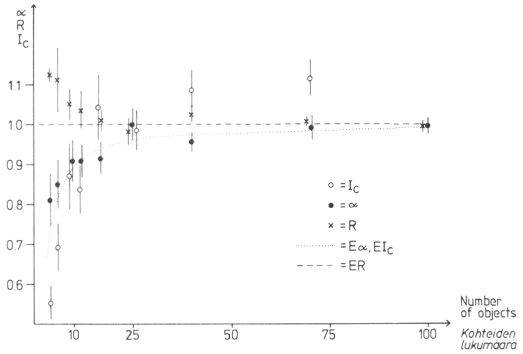


Fig 5. The expected values of  $R$ ,  $\alpha$  and  $I_c$  as a function of the number of objects. The standard errors are shown with lines.

Kuva 5.  $R$ :n,  $\alpha$ :n ja  $I_c$ :n keskiarvot objektien määrän funktiona. Keskiarvot on esitetty pystyvivoiin.

field material from 9 to 71. The mean number of galleries per bolt was 23. This means that in many bolts there were not enough galleries for calculating the aggregation indices for the galleries. The number of exit holes ranged from 19 to 803, the average being 240. These numbers are so great that they cause troubles in mapping, and require very much computer time in searching the nearest neighbors. Thus the bolt size used had to be adjusted to a compromise which would facilitate measuring both the galleries and the exit holes. The low numbers may cause some bias in the results, e.g. due to the edge effect, finite area, and low degrees of freedom. In order to retain as much material as possible in the analysis, the effects of low numbers of objects on the values of  $R$ ,  $\alpha$  and  $I_c$  were studied. A series of artificial bolts with a random spatial pattern was generated. The number of objects were 4, 6, 9, 12, 17, 25, 40, 70 and 100. Each of the 9 classes contained 30 bolts.

Fig 5 shows the observed mean values of  $R$ ,  $\alpha$  and  $I_c$  with their standard errors and the lines of the expected values. The standard error of all the estimators decreases as the number of objects increases (Fig 5).  $\alpha$  follows the expected  $(n-1)/n$  curve all the time within the range of standard error.  $n$  in the expected value of  $\alpha$  is not the actual number of measurements, but the degrees of freedom, which is the smaller of the two values (number of objects, number of measurements). This seems to be the case in  $I_c$ , too.  $R$  is significantly biased towards regularity when less than 12 objects are present. This may be due to the edge effect, because the margin  $0.75D$  had to be made narrower at the two lowest densities. The dependence of the distances, as shown by Cliff and Ord (1975), can also cause bias, since all the objects have been start-

Table 1. Correlation matrix of the different aggregation estimators in different materials.  $n_i$  = number of bolts,  $n/n_i$  = mean number of objects /bolt.  
 Taulukko 1. Eri ryhmittymisindeksien korrelaatiomatriisi eri aineistoissa.  
 $n_i$  = pölkkyjen lukumäärä,  $n/n_i$  = objektien keskilukumäärä pölkkyssä.

	Entrance holes <i>Iskeytymisreiät</i>			Exit holes <i>Kuoriutumisreiät</i>		
	$n_i = 110$ R	$n/n_i = 26$ $\alpha$	$I_c$	$n_i = 59$ R	$n/n_i = 235$ $\alpha$	
Entrance holes <i>Iskeytymisreiät</i>	$\alpha$	-.213*				
Exit holes <i>Kuoriutumisreiät</i>	$I_c$	-.207*	.501***			
	R	-.101 <sup>ns</sup>				
	$\alpha$		.175 <sup>ns</sup>	-.818***		
	$I_c$		-.024 <sup>ns</sup>	-.863***	.921***	

ing points for the measurements.  $I_c$  is strongly biased in opposite directions in the two parts of the range. It was not possible to determine whether the bias is due to some failure in the calculating method or whether the expected value of  $I_c$  is not exactly 1 in a random population. For this reason  $I_c$  is not used in the further calculations. R also had to be rejected, since its predictions were not reliable when there were less than 12 objects present, and it was important to obtain estimates of aggregation over the whole range of densities. Thus only  $\alpha$  could be accepted in the analysis. This agrees well with the conclusion of Payandeh (1970) that alfa is the most reliable of the aggregation indices available. A limit of 6 objects was set on the use of  $\alpha$ .

#### 244. Correlations of the aggregation indices

All the three aggregation indices are correlated with each other as Table 1 shows. The value of the correlation coefficient is highly dependent on the number of objects (galleries or holes). The aggregation indices are correlated to a much lower degree in the case of galleries than in the case of exit holes because of the lower number of objects. The nearest neighbor R, in particular, differs a lot from  $\alpha$  and  $I_c$ . This is probably due to random variation, which is more pronounced in calculating R than in calculating alfa or  $I_c$ . In the first named case only as many distances are measured as there are objects, whereas in the latter two cases the number of distances measured was constantly 100.

### 3. RESULTS

#### 31. Review of the material

Table 2 shows the mean, range, standard deviation, and number of observations of the bark properties, attack density, new beetle production, and egg gallery length. The normality of the distributions of the variables was tested, and in cases where normality was not achieved, the transformations — square root, ln, and log10, were applied in this order. However, none of the transformations were accepted for further use, because no clear suggestion of their usefulness was obtained. In no case was the same transformation usable in both of the groups. The distributions are largely, especially in the laboratory group, artefacts arising from the experimental design and failures, and do not necessarily apply to other materials. When the results from precise statistical tests are interpreted, possible violations of the underlying assumptions can be checked in Table 2.

The laboratory and field bolts are compared with analysis of variance (Table 2). Bark thickness is the same in the laboratory and field bolts. This is due to the aim of standardizing the material. The variance of bark thickness does not differ in the two groups. This is an important point, since the bark beetles have thus had equal possibilities to start their galleries in crevices in both of the groups.

The attack density is on the average much lower in the laboratory bolts than in the field ones. Attack on the field bolts was very heavy due to the high *T. piniperda* population at the study site. Thus the field observations from the lowest densities up to 57 galleries /m<sup>2</sup> are missing. This must be borne in mind when examining the other results. The range of attack density well covers the range that has been observed in *T. piniperda*. However, more observations from the higher densities in the laboratory group, and from the lower densities in the field group, would have balanced the material better. The mean length of the egg galleries is 77 mm in the laboratory bolts and 73 mm in the field ones. These

values do not differ from each other to a statistically significant degree.

Exit hole density is the same in both the laboratory and the field bolts. The ratio of increase is much lower in the field bolts than in the laboratory ones (Table 2). Whether this difference is merely an effect of different attack densities was studied in more detail. The following table shows the mean values of the ratio of increase in different categories of attack density.

Density category, Attacks m <sup>2</sup>	Laboratory			Field		
	mean	s.d.	n	mean	s.d.	n
50—100	13.2	5.7	13	5.7	1.5	6
101—150	10.8	3.7	22	5.8	2.0	9
151—200	9.1	2.9	9	6.5	2.9	7
201—250	6.5	2.0	2	5.2	2.6	9
251—	6.4	2.6	3	4.9	2.2	13

A two-way analysis of variance was carried out over this table. The sums of the squares of both grouping variables were significant at the  $p < 0.05$  level. This means that the greater ratio of increase in the laboratory bolts is not merely an effect of attack density. The two groups will therefore be considered separately in further analyses.

#### 32. Models for attack

##### 321. The dependence of attack density on bark properties

Only the field attack bolts ( $n = 58$ ) are used in this analysis. Attack density is directly but not linearly dependent on bark thickness (Fig 6). The model suggested by Safranyik and Vithayasai (1971) was fitted

$$A = 279.3 (1.0 - 10.0^{-0.1545 B - 0.04925}) \quad (32-1)$$

where A is the density of egg galleries /m<sup>2</sup> and B the bark thickness in mm. This model is asymptotic and does not exceed the



Table 2. Review of material and a comparison of the laboratory and the field bolts with ANOVA. Transformation needed to achieve normality is indicated, except "YES" when not needed, and "NO" when not achieved by any of the transformations SQRT, LN, LOG<sub>10</sub>.  
 Taulukko 2. Katsaus aineistoon sekä laboratorio- ja maastopölkkyjen vertailu varianssianalyysillä. Normaalisuuden saavuttamiseksi tarvittu muunnos on merkitty lyhenteillä SQRT, LN tai LOG<sub>10</sub>, tai "YES" jos muunnosta ei lainkaan tarvittu, tai "NO" jos normaalisuutta ei saatu aikaan millään luetelluista muunnoksista.

Variable Muuttuja	Laboratory bolts — Laboratoriopölkkyt				Field bolts — Maastopölkkyt				F-probability % F-todennäköisyys %		
	$\bar{x}$	Range Vaihteluväli	S.d. Keskiahjonta	n	Normality Normaalisuus	$\bar{x}$	Range Vaihteluväli	S.d. Keskiahjonta		n	Normality Normaalisuus
Bark thickness mm	4.5	1.0—15.0	2.2	83	SQRT	4.6	1.3—10.1	2.1	58	YES	22.18
Kaarnan paksuus mm											
Variance of bark thickness mm <sup>2</sup>	3.8	1.5—8.5	1.8	47	NO	3.4	0.5—19.4	3.0	58	LOG	63.69
Kaarnan paksuuden varianssi mm <sup>2</sup>											
Attack density/m <sup>2</sup>	90.1	6.0—348.0	72.8	83	NO	206.5	57.0—432.0	85.0	58	YES	100.00
Iskeytymistiheys/m <sup>2</sup>											
Production/m <sup>2</sup>	1966.0	133.0—5784.0	1269.6	83	SQRT	2159.6	606.0—5264.0	1260.3	44	NO	58.96
Jälkeläistuotos/m <sup>2</sup>											
Ratio of increase	13.9	3.6—29.0	6.2	83	LOG	5.5	1.2—11.2	2.2	44	YES	100.00
Lisäänymiskerroin											
Egg gallery length mm	77	43—132	16	83	YES	73	51—114	14	58	LOG	82.40
Emokäytävien pituus mm											

Table 3. Relative  $\alpha$  for gallery entrance holes, ending points and exit holes. Notation as in Table 2.  
 Taulukko 3. Iskeytymisreikien, emokäytävien loppupisteiden ja kuoriutumisreikien subteollinen  $\alpha$ . Muut merkinmät kuten taulukossa 2.

Variable Muuttuja	Laboratory bolts — Laboratoriopölkkyt				Field bolts — Maastopölkkyt				F-probability % F-todennäköisyys %				
	$\bar{x}$	Probability (%) of $\alpha = 1$ Todennäköisyys (%) $\alpha = 1$	Range Vaihteluväli	S.d. Keskiahjonta	n	Normality Normaalisuus	$\bar{x}$	Probability (%) of $\alpha = 1$ Todennäköisyys (%) $\alpha = 1$		Range Vaihteluväli	S.d. Keskiahjonta	n	Normality Normaalisuus
Entrance holes	1.093	3.73	0.6—2.0	0.320	54	YES	0.940	3.62	0.5—1.9	0.213	58	YES	99.65
Iskeytymisreitit													
Ending points	1.133	0.32	0.6—2.6	0.320	55	YES	1.060	13.07	0.7—2.3	0.298	58	YES	78.96
Emokäytävien loppupisteet													
Exit holes	4.390	0.00	1.1—14.5	3.412	47	NO	1.465	0.00	1.1—2.5	0.297	21	NO	99.98
Kuoriutumisreitit													

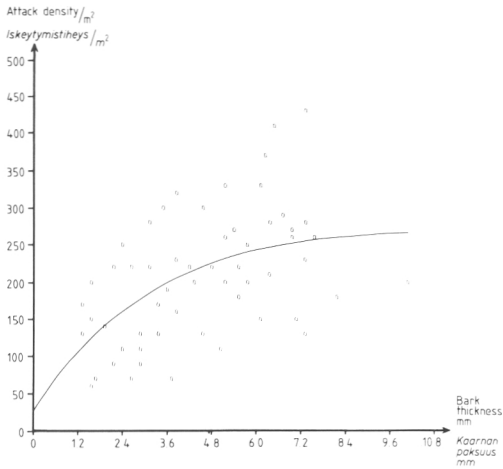


Fig 6. The dependence of attack density on bark thickness in the field material. The model fitted is

$$A = 279.3 (1.0 - 10.0 - 0.1345 B - 0.04925) \quad (32-1)$$

Kuva 6. Iskeitymistihetyden riippuvuus kaarnan paksuudesta luonnonpölkkyissä. Malli on

$$A = 279.3 (1.0 - 10.0 - 0.1345 B - 0.04925) \quad (32-1)$$

maximum attack density of 279.3 /m<sup>2</sup> at any bark thickness. It gives zero attack density at a bark thickness of -0.37 mm. In the model  $r = 0.505$  and  $p < 0.000$ . It is interesting to see that there were galleries even at the thinnest bark thicknesses down to 1.3 mm, which is thinner than *T. piniperda* normally uses. This is probably caused by overcrowding. It is likely that logs with even thinner bark are no longer attacked by *T. piniperda*, and the estimated zero attack density should be about 1 mm.

A linear model performed not as well in this material ( $r = 0.469$ ,  $p < 0.000$ , linearity  $p = 0.255$ ). Theoretically it is not acceptable, since attack density cannot increase infinitely.

The variance of bark thickness has no effect ( $r = 0.206$ ,  $p = 0.121$ ) on the attack density. Neither does it give any additional information to the model where the bark thickness is already present.

### 323. Spatial pattern of egg galleries

The general tendency in the spatial pattern was such that the egg galleries were randomly or slightly regularly distributed. A

review of the results is presented in Table 3. It should be noted that the lowest attack densities are missing, because one bolt with an area of only 0.16 m<sup>2</sup> does not permit the calculation of  $\alpha$  at low densities of up to 32 galleries /m<sup>2</sup>. The distributions of  $\alpha$  for the entrance holes and the end points do not differ from the normal distribution.

The mean value of  $\alpha$  in the laboratory bolts 1.093 is statistically significantly ( $p = 0.037$ ) aggregated. However, only 3 out of the 55 individual cases could be classified as aggregated, 2 as regular while the rest of them were random. The low number of galleries in the bolts makes it difficult to detect significant deviations from randomness in individual bolts. In the field bolts, the mean value of 0.940 for  $\alpha$  points to significant ( $p = 0.036$ ) regularity. Out of the 58 cases, 8 were classified as regular and none of them as aggregated.

The end points of the galleries are randomly distributed in the field bolts, but aggregated in the laboratory bolts. Out of the 55 laboratory bolts, 4 were classified as being aggregated and the rest of them as random. Out of the 58 field bolts, 2 aggregated and 2 regular cases were detected. It thus seems that the end points are slightly more aggregated than the entrance points.

In order to test the hypothesis that sunshine and the cortical temperature are the factors which determine the spatial pattern of the attacks of the parent beetles, the field bolts were placed in different degrees of shading as described in Section 21. One-way analysis of variance was carried out on the 5 shading groups. Table 4 shows the results and the statistical significance of the differences. The results were confusing. There were no differences in the means of  $\alpha$  between the shading groups. On the other hand, the attack density varied significantly within the groups. There was a slight tendency to increasing attack density with increasing sunshine. The number of exit holes is correlated with the attack density and it is largest where there is no shading, as is the ratio of increase. The unshaded bolts reach the production level of the laboratory bolts. The galleries were the longer, the more the bolts were shaded. This indicates that the beetles were suffering from cool microclimate in the shaded bolts.

The regularity of the entrance holes is

Table 4. The effect of shading of bolts on attack density, production, egg gallery length and spatial pattern. Comparison with ANOVA. The shading classes are the multiplications of green mosquito netting.  
 Taulukko 4. Pölkkyjen varjostamisen vaikutus iskeytymistiheyteen, emokäytävän pituuteen, jälkeläistuotokseen ja tilajärjestykseen. Vertailu varianssianalyysillä. Varjostusluokat ovat vihreän sääskiverkon moninkertoja.

Variable Muuttuja	No shade Ei varjoa	1-fold 1-kertainen	2-fold 2-kertainen	4-fold 4-kertainen	Cloth Kangas	F-probability % F-todennäköisyys %
n	8	10	9	10	7	18.13
Bark thickness mm Kaarnan paksuus mm	4.26	4.25	5.14	4.73	4.85	18.13
Bark thickness variance mm <sup>2</sup> Kaarnan paksuuden varianssi mm <sup>2</sup>	2.34	2.73	6.82	3.22	3.11	99.78
Attack density/m <sup>2</sup> Iskeytymistiheys/m <sup>2</sup>	226.7	245.1	146.4	254.3	135.9	99.95
Production/m <sup>2</sup> Jälkeläistuotos/m <sup>2</sup>	3682.2	1299.5	1517.8	2934.3	1149.1	100.00
Ratio of increase Lisääntymiskerroin	8.11	2.93	5.38	5.81	5.57	100.00
Mean length of galleries mm Emokäytävien keskipituus mm	63.5	73.7	78.1	68.9	90.2	100.00
Relative $\alpha$ for entrance holes Iskeytymisreikien suhteellinen $\alpha$	0.903	0.949	0.936	0.967	0.978	9.41
Relative $\alpha$ for exit holes Kuoriutumisreikien suhteellinen $\alpha$	1.637	1.308	1.563	1.463	1.271	58.46

directly related to the logarithm of the attack density ( $r = -0.579$ ,  $p < 0.001$ ) in the field bolt group (Fig 7). At the lowest densities below about 100 galleries /m<sup>2</sup>, the attack pattern is aggregated. In the mean range from 100 to 200 galleries /m<sup>2</sup> the pattern is mainly random. In the highest densities, there is a tendency towards regularity. In the laboratory bolt group the tendency is the same, although statistically not significant ( $r = -0.226$ ,  $p = 0.092$ ).

No significant correlation could be found between the aggregation of entrance holes and bark thickness or the variance of thickness.

### 33. Models for multiplication

The mean length of egg galleries (L; mm) decreases with increasing attack density (A; galleries /m<sup>2</sup>) according to the equation

$$L = 80.79 - 0.0411A \quad (33-1)$$

Both the field and laboratory bolts are used in this analysis ( $n = 127$ ), in which  $r = 0.265$  and  $p = 0.999$  (Fig 8). The relationship is linear ( $p = 0.086$ ).

The mean density of egg niches per mm of egg gallery wall (one side) was 0.380

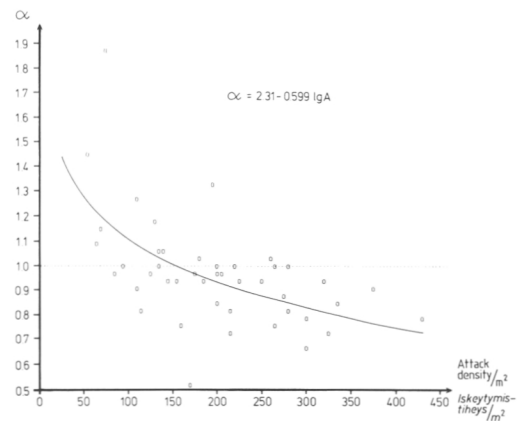


Fig 7. Relative  $\alpha$  of entrance holes as a function of the attack density in the field material.

Kuva 7. Iskeytymisreikien suhteellinen  $\alpha$  iskeytymistiheyden funktiona maastopölkkyissä.

(s.d. = 0.134 mm,  $n = 884$ ). This has been calculated from the material in the data base. The material comprises 884 galleries in 94 bolts at the study site and in the laboratory in 1980. Only 87.3 % of the egg niches actually contained an egg when examined prior to hatching. This proportion is dependent on the examiner's interpretation whether a particular cavity (often unclear) is an egg niche or not. Thus a mean value of

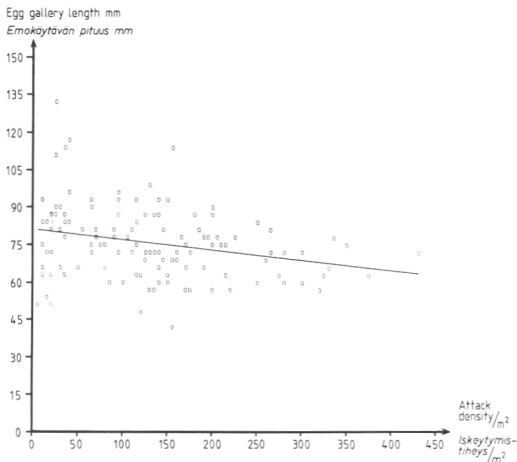


Fig 8. The mean length of egg galleries as a function of the attack density.  
 Kuva 8. Keskimääräinen emokäytäväpituus iskeytymistiheyden funktiona.

0.332 eggs per mm of egg gallery wall is obtained. The density of the egg niches was found to depend neither on the attack density ( $r = -0.102$ ,  $n=94$ ), nor on the mean gallery length ( $r = 0.034$ ,  $n=94$ ). However, according to uncalculated observations, the egg density may be negatively correlated with temperature, although at present no facts to support this can be presented. There is a nuptial chamber at the beginning of each egg gallery. No eggs are laid in the walls of this chamber. Its mean length was 7.7 mm (s.d. = 2.0 mm,  $n=884$ ), which was subtracted from the egg-gallery length when the egg density was calculated. The sterile part of the egg gallery at the end is more vague. Its mean length was 15.3 mm (s.d. = 7.0 mm,  $n=39$ ) in the small material studied.

The spatial pattern of the egg niches in the walls of the egg gallery can be studied by means of the distribution of the distances between successive egg niches. The histogram (Fig 9) is strongly skewed and no theoretical distribution with a biological meaning could be fitted to it. The pattern suggests that the distance is regular, but there are longer intervals where there are no egg niches at all. The mean distance is 1.62 mm (s.d. = 1.49,  $n=3509$ ), which is significantly lower than the mean density of 2.63 mm ( $=1.0/0.380$  egg niches/mm) would suggest. The difference is due to the fact that the mean distance between suc-

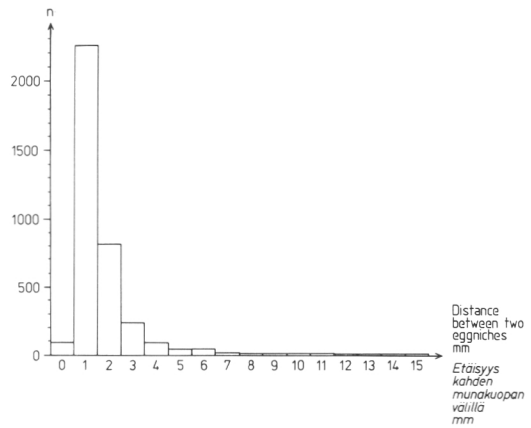


Fig 9. The distribution of the distances between successive egg niches in the egg gallery wall.  
 Kuva 9. Emokäytävän seinällä sijaitsevien kahden peräkkäisen munakuopan välisen etäisyyden jakauma.

cessive egg niches increases towards the end of the egg galleries ( $r = 0.128$ ,  $p < 0.001$ ,  $n = 3509$ ), that the sample comprises mainly unfinished egg galleries, and that the sterile end part was included in the egg gallery length from which the egg density was calculated. If the distance from the last egg to the end of the egg gallery is included in the material, then the distance increases to 1.97 mm (s.d. = 2.36 mm,  $n = 3766$ ).

For describing the multiplication of bark beetles Berryman (1974) suggests the exponential decay function

$$E = Me^{-\epsilon \sqrt{A}} \quad (33-2)$$

where  $E$  is the number of eggs deposited per attack,  $M$  the mean maximum oviposition rate,  $\epsilon$  a rate parameter, and  $A$  the attack density. This function was fitted to the data using the non-linear regression program BMDPAR (Fig 10). Table 5 shows the statistics related to the model. The mean (bolt average) maximum number of eggs per female is 63.6. It should be noted that in many galleries the mean egg density has been used to estimate the number of eggs because the actual number could not be counted due to the deterioration of the phloem. The lack of fit percentage in Tables 5 . . . 9 is obtained by the method described by Draper and Smith (1969). The residual sum of squares was divided into the components "pure



Table 5. Statistics relating to the fits of the multiplication models.

Taulukko 5. Lisääntymistä kuvaavien mallien tilastolliset tunnusluvut.

$$E = M e^{-\epsilon \sqrt{A}} \quad (33-2)$$

$$E = M - \epsilon A \quad (33-3)$$

E = The mean number of eggs laid/egg gallery  
Keskimääräinen munamäärä/emokäytävä  
M = The mean maximum oviposition rate/female  
Keskimääräinen maksimimunamäärä/emo  
 $\epsilon$  = A rate parameter — Vähennisparametri  
A = Attack density/m<sup>2</sup> — Iskeytymistiheys/m<sup>2</sup>  
s.e. = Standard error — Keskiarvo  
s.d. = Standard deviation — Keskihajonta  
d.f. = Degrees of freedom — Vapausasteet  
r = Correlation coefficient with usual significance notation — Korrelaatiokerroin tavannukaisin merkitsevyymerkinnöin  
res. = Residual — Residuaali  
p = Probability that the residuals are normally distributed — Todennäköisyys residuaalien normaality jakautumiselle

	$E = M e^{-\epsilon \sqrt{A}}$	$E = M - \epsilon A$
M	63.58	54.35
s.e.(M)	3.08	1.88
$\epsilon$	0.03125	0.06191
s.e.( $\epsilon$ )	0.004684	0.01006
d.f.	119	119
r	-0.523***	-0.491***
res. s.d.	10.68	10.93
res. s.d. % of est.	25.89	26.22
lack of fit %	5.73 <sup>ns</sup>	5.92 <sup>ns</sup>
p	0.659 <sup>ns</sup>	0.921 <sup>ns</sup>

error" and "lack of fit" and the significance of their ratio was tested with analysis of variance. This very useful method for evaluating models has been performed with the program REKO (Timonen 1983).

A simple linear model

$$E = M - \epsilon A \quad (33-3)$$

provided almost as good a fit (Table 5, Fig 10). This model gives 54.4 eggs per female for the maximum oviposition rate. If the dependence of the egg gallery length on attack density is linear and the egg density in the egg gallery is independent of the attack density and egg gallery length, then the only sources of non-linearity are the constant length of the pairing chamber and the variation in the spatial pattern of the eggs along the egg gallery.

### 34. Models for survival

For describing the survival of bark beetles from intraspecific competition Berryman

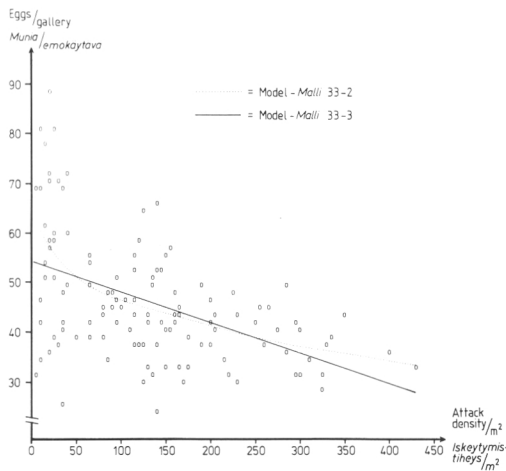


Fig 10. The mean number of eggs/gallery (bolt averages) as a function of the attack density. The models are

$$E = M e^{-\epsilon \sqrt{A}} \quad (33-2) \text{ and } E = M - \epsilon A \quad (33-3). \text{ See also Table 5.}$$

Kuva 10. Keskimääräinen munamäärä /emokäytävä (pölkkeykeskiarvo) iskeytymistiheyden funktiona. Mallit ovat

$$E = M e^{-\epsilon \sqrt{A}} \quad (33-2) \text{ ja } E = M - \epsilon A \quad (33-3). \text{ Ks. myös Taulukkoa 5.}$$

(1974) suggests using the same function as for multiplication

$$S = \gamma e^{-\lambda \sqrt{A}} \quad (34-1)$$

where S is the probability that a larva will survive competition,  $\gamma$  and  $\lambda$  are coefficients and A the attack density. Table 6 and Fig 11 show the fits of this model in both the laboratory and field groups. The model did not have to be constrained below unity, since at the minimum density only 86 % of the larvae survive. The remaining 14 % succumb as a result of intra-gallery competition. The survival in the field bolts is much lower than in the laboratory bolts. There does not seem to be any density dependent mortality in the field bolt group.

The linear model

$$S = \gamma - \lambda A \quad (34-2)$$

again provided as good a fit (Table 6, Fig 11).

The usefulness of the simulation model developed by Jong and Saarenmaa (1984) for predicting survival was also evaluated. The model uses information on the spatial

Table 6. Statistics relating to the fits of the survival models.  
 Taulukko 6. Eloönjäämistodennäköisyyttä kuvaavien mallien tilastolliset tunnusluvut.

$$S = \gamma e^{-\lambda \sqrt{A}} \quad (34-1)$$

$$S = \gamma - \lambda A \quad (34-2)$$

S = Proportion of larva population which survives  
 Toukka populaatiosta eloonjäävä osuus

$\gamma$  = Parameter — Parametri

Other notations as in Table 5. — Muut merkinnät kuten taulukossa 5.

	$S = \gamma e^{-\lambda \sqrt{A}}$		$S = \gamma - \lambda A$	
	Laboratory Laboratorio	Field Maasto	Laboratory Laboratorio	Field Maasto
$\gamma$	0.8625	0.2611	0.7081	0.2440
s.e. ( $\gamma$ )	0.06553	0.09027	0.0293	0.0428
$\lambda$	0.04829	0.01067	0.001482	0.00008979
s.e. ( $\lambda$ )	0.006625	0.02347	0.0002458	0.0001795
df	81	42	81	42
r	-0.536***	-0.071 <sup>ns</sup>	-0.557***	-0.077 <sup>ns</sup>
res. s.d.	0.165	0.102	0.163	0.103
res. s.d. % of est.	29.87	45.99	30.44	45.992
lack of fit %	29.42*	18.96 <sup>ns</sup>	22.02*	27.98 <sup>ns</sup>
p	0.351 <sup>ns</sup>	0.911 <sup>o</sup>	0.649 <sup>ns</sup>	0.911 <sup>o</sup>

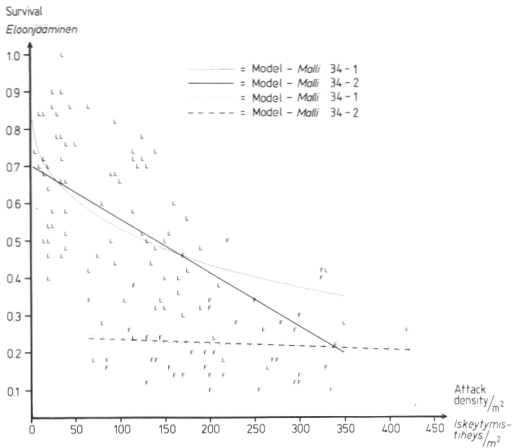


Fig 11. Survival of the larvae as a function of the attack density in the laboratory (L) and field (F) groups. The models are

$$S = \gamma e^{-\lambda \sqrt{A}} \quad (34-1) \text{ and } S = \gamma - \lambda A \quad (34-2).$$

Kuva 11. Eloönjäävien toukkien osuudet iskeytymistiheyden funktiona laboratorio- (L) ja maastopöleissä (F). Mallit ovat

$$S = \gamma e^{-\lambda \sqrt{A}} \quad (34-1) \text{ ja } S = \gamma - \lambda A \quad (34-2).$$

pattern, and will be considered with more detail in the following section. The simulated survivals are shown against the attack density in Fig 12. Table 9 shows the pertinent statistics relating to the fit of the simulation

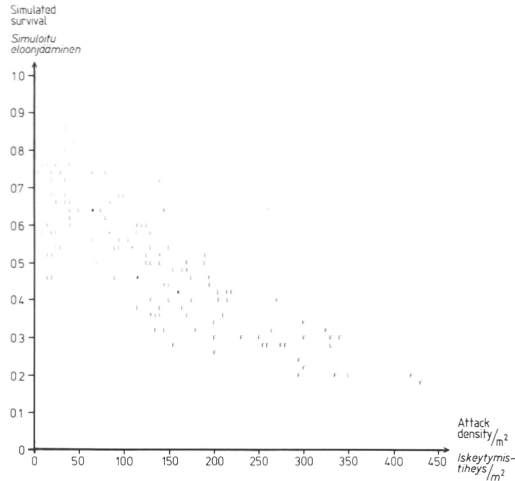


Fig 12. Simulated survival as a function of the attack density. The related statistics are given in Table 9.

Kuva 12. Simuloitu eloonjääminen iskeytymistiheyden funktiona. Mallin tilastolliset tunnusluvut ovat Taulukossa 9.

model. The simulation model is slightly, but not significantly, better than either of the mathematical models in the case of the laboratory group. In the field group it fails, as did the other models.

### 35. Models for emergence

In this section we first take a look at the spatial pattern of the exit holes. Then an attempt is made to develop models for the number of offspring, which is expressed in two different ways: as (i) the ratio of increase, and as (ii) production. The ratio of increase relates the number of offspring to the previous generation, whereas production is defined as the number of offspring per bark area. The two estimators are different also in the condition that the variation of the ratio of increase is largest at low attack densities, but that of production largest at high attack densities.

Several models which predict and describe the ratio of increase and production will be examined:

- 1) Descriptive nonlinear regression of attack density based on the models proposed by Berryman (1974).
- 2) Predictive linear regression of attack density.
- 3) Descriptive multiple linear regression of attack density and spatial pattern indices.
- 4) The four mean minimum distances to the nearest egg galleries.
- 5) Simulation model proposed by Jong and Saarenmaa (1984).

In the first hand the effect of mere attack density is studied (1 and 2). Then the aggregation index  $\alpha$  is introduced (3). The larvae can be supposed to have the greater survival probabilities the greater is the regularity of attacks or larvae. This is the test hypothesis ( $H_1$ ). The fourth approach is different in such a way that it combines the attack density and spatial pattern to minimum distances between egg galleries. The simulation approach (5) does not use regression techniques at all, but it is supposed to use all the information available about spatial pattern.

#### 351. Spatial pattern of exit holes

In contrast to the egg galleries, which were randomly or slightly regularly distributed (Section 323), the exit holes showed strong aggregation in both of the groups. The results are presented in Table 3 together with those for the egg galleries. The exit holes were randomly distributed in only one of the 47 laboratory bolts. In the field group,

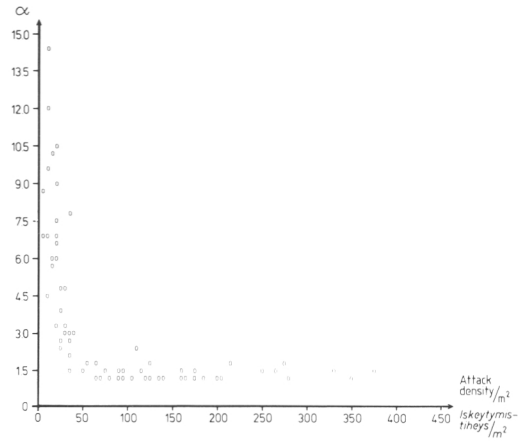


Fig 13. Relative  $\alpha$  of exit holes as a function of the attack density in the entire material.

Kuva 13. Kuoriutumisreikiän subteollinen  $\alpha$  iskeytymistheyden funktiona koko aineistossa.

where there were 21 bolts, the exit holes were randomly distributed in two of them. The distributions of the values of  $\alpha$  for the exit holes did not achieve normality with any of the transformation used. The aggregation of the exit holes is not dependent on the aggregation of the gallery entrance holes (Table 1).

The aggregation of exit holes increases with decreasing attack density in the laboratory bolt group, but not in the field bolt group. The difference is primarily caused by the lack of observations at low densities in the field bolt group. Above 50 galleries /m<sup>2</sup> the aggregation is constant, but below this limit the slope is very steep (Fig 13). This is the point where the broods start to interfere with each other, the exit holes from different galleries mix, and clumpness diminishes.

#### 352. Ratio of increase

The ratio of increase (RI) is best understood as a product of the multiplication and survival models

$$RI = E S \quad (352-1)$$

or

$$RI = (Me^{-\varepsilon \sqrt{A}}) (\gamma e^{-\lambda \sqrt{A}}) \quad (352-2)$$

This model was fitted to the material (Table 7, Fig 14) and it provided an ade-

Table 7. Statistics relating to the fits of models of the ratio of increase

	RI = (Me <sup>-ε√A</sup> ) (γe <sup>-λ√A</sup> )		P = A (Me <sup>-ε√A</sup> ) (γe <sup>-λ√A</sup> )	
	Laboratory	Field	Laboratory	Field
	Laboratorio	Maasto	Laboratorio	Maasto
M	59.50	46.57	62.34	63.85
s.e. (M)	5.00	not obtained	9.71	28.50
ε	0.02905	0.01918	0.03351	0.03304
s.e. (ε)	0.01086	0.02100	0.01257	0.02732
γ	0.445	0.1693	0.847	0.2947
s.e. (γ)	0.03499	0.05118	0.129	0.1320
λ	0.04829	0.01067	0.04829	0.01067
s.e. (λ)	fixed	fixed	fixed	fixed
d.f.	81	42	81	42
r	-0.655**	-0.218ns	0.801***	0.512***
res. s.d.	4.575	2.121	775.3	1047.3
res. s.d. % of est.	31.99	41.72	34.46	45.53
lack of fit %	9.86ns	23.13ns	13.36ns	15.83ns
p	0.117ns	0.897ns	0.030ns	0.995ns

quate fit. The parameter  $\lambda$  was kept fixed at the value obtained in the analysis for survival, and the least square curve was found by changing the other parameters. The values are not exactly the same as in the survival model because the unknown actual number of eggs was in many cases replaced by the estimated number. The differences come, however, within the confidence limits. The product  $M \gamma$  is the mean maximum ratio of increase at the minimum density. It has the value of 26.5 in the laboratory group. Although the variance is correlated with the mean, the model is unbiased according to the distribution of residuals; only at the lowest densities there is some uncertainty about the fit due to the great variance. The model explains 43 % of the variance in the ratio of increase in the laboratory group. However, it does not work in the field group. This strange result can be partly attributed to the fact that the observations at the lowest densities, where the response is clearest, are lacking in the field group. However, this explanation is not exhaustive, because there appears to be a level difference between the groups, too. Obviously the field group includes mortality which is not only due to competition.

The previous model is a descriptive model based on attack density. The material can also be described by a simpler predictive model

$$RI = a - b \log_{10} A \quad (352-3)$$

The fits of this model are of the same magnitude as those of the more complicated predictive model (Table 8, Fig 14). It is easily solved using linear regression. In principle, the coefficient of  $a$ , which is the mean maximum ratio of increase, is equal to  $M \gamma$  of the explanatory model. It gives a value of 31.2 for the laboratory bolt group.

Neither of the two previous models accounts for the possible effect of spatial pattern on the ratio of increase. Whether or not the residual variation of model 352-3 is due to the spatial pattern was tested using multiple regression by introducing  $\alpha$  as an independent variable in the model. First the model had to be recalculated excluding bolts with low attack densities of up to 32 galleries /m<sup>2</sup>. This was necessary because the low attack densities did not permit  $\alpha$  to be calculated with the small bolt size used. The number of observations decreased from 127 to 98. The relative residual variation also increased since the part of the material in



Table 8. Statistics relating to the fits of the models of the ratio of increase  
 $RI = a - \log A$  (352—3)  
and production  
 $P = aA - bA^2$  (353—3)  
a and b are regression coefficients, other notation as in Tables 5 and 6.  
Taulukko 8. Lisääntymiskerrointa kuvaavan mallin  
 $RI = a - \log A$  (352—3)  
ja jälkeläistuotosta kuvaavan mallin  
 $P = aA - bA^2$  (353—3)  
tilastolliset tunnusluvut. a ja b ovat regressiokertoimia, muut merkinnät  
kuten taulukoissa 5 ja 6.

	RI = a—logA		P = aA—bA <sup>2</sup>	
	Laboratory Laboratorio	Field Maasto	Laboratory Laboratorio	Field Maasto
a	31.20	10.76	26.97	15.64
s.e. (a)	2.24	3.63	1.77	2.30
b	9.58	2.44	0.04387	0.02071
s.e. (b)	1.28	1.73	0.008451	0.008103
n	83	44	83	44
r	—0.638***	—0.213 <sup>ns</sup>	0.788***	0.530***
res. s.d.	4.85	2.25	776.7	995.1
res. s.d. % of est.	33.12	41.32	43.59	40.75
lack of fit %	5.93 <sup>ns</sup>	31.75 <sup>ns</sup>	13.79 <sup>ns</sup>	41.76°
p	0.322 <sup>ns</sup>	0.874 <sup>ns</sup>	0.813 <sup>ns</sup>	0.834 <sup>ns</sup>

Table 9. Statistics related to the fit of the simulation model with parameter values  
MINFOO = 46 mm, ICROSS = 10 mm, SOUND = 8 mm, PYX = 0.95, EGGDEN  
= 0.332/mm, DELAY = 0.35 (the parameters are explained in Jong and Saarenmaa  
1984). The model fitted is observed = slope × simulated.

Taulukko 9. Simulointimallin aineistoon sopivuutta kuvaavat tunnusluvut. Simuloinnit  
ajettu parametrien arvoilla MINFOO = 46 mm, ICROSS = 10 mm, SOUND =  
8 mm, PYX = 0.95, EGGDEN = 0.322/mm, DELAY = 0.35, jotka on selitetty toi-  
sessa artikkelissa (Jong ja Saarenmaa 1984). Sovitettu malli on havaittu = slope ×  
simuloitu.

	Survival Eloinjääminen		Ratio of increase Lisääntymiskerroin		Production Jälkeläistuotos	
	Laboratory Laboratorio	Field Maasto	Laboratory Laboratorio	Field Maasto	Laboratory Laboratorio	Field Maasto
n	83	44	83	44	83	44
slope	0.992	0.563	0.986	0.547	1.007	0.683
p that slope = 1	1.000	0.000	1.000	0.000	1.000	0.000
r	0.619***	0.162 <sup>ns</sup>	0.767***	0.126 <sup>ns</sup>	0.836***	0.517***
res. s.d.	0.155	0.115	3.927	2.556	696.4	1085.6
res. s.d. % of est.	29.06	58.27	29.30	60.06	28.69	48.16
lack of fit %	20.75°	14.25 <sup>ns</sup>	30.43*	30.89 <sup>ns</sup>	22.02 <sup>ns</sup>	48.54*
p	0.310 <sup>ns</sup>	0.999***	0.242 <sup>ns</sup>	1.000***	0.251 <sup>ns</sup>	0.998**

which the effect of the attack density on the ratio of increase was clearest was omitted. The distribution of  $\alpha$  for the entrance holes was about normal, but that for the exit holes, or that for the attack density in laboratory group was not (Tables 2 and 3). This could cause poor fit in predictive models, but is not important in descriptive models such as these.

The independent variables in descriptive models are not allowed to be correlated with each other (Draper and Smith 1969). If multicollinearity exists, the t-values of the

independent variables do not describe the pure effect of this variable, and moreover, the regression coefficients may have wrong sign, which strongly affects the interpretation of a descriptive model. There is multicollinearity between  $\alpha$  of entrance holes and the attack density in the field material (see Section 323, Fig 7), and between  $\alpha$  of exit holes and the attack density in the laboratory material (see Section 351, Fig 13). The ridge regression technique as described by Bare and Hann (1981) and programmed by Timonen (1983) was applied in such cases.

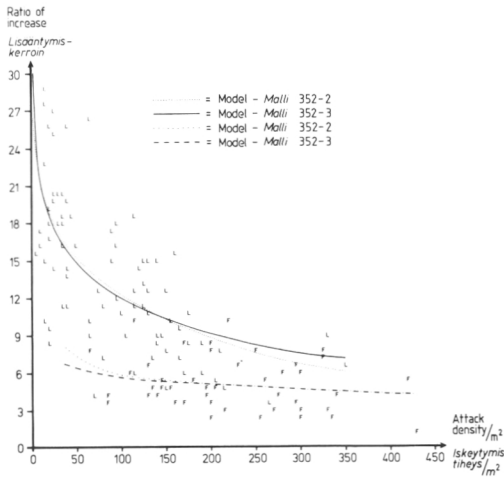


Fig 14. The ratio of increase as a function of the attack density in the laboratory (L) and field (F) groups. The models are

$$RI = (Me - \varepsilon \sqrt{A}) (\gamma e^{-\lambda \sqrt{A}}) \quad (352-2) \text{ and}$$

$$RI = a - b \log_{10} A \quad (352-3).$$

See also Tables 7 and 8.

*Kuva 14. Lisäntymiskerroin iskeytymistiheyden funktiona laboratorio- (L) ja maastopölkkyssä (F). Mallit ovat*

$$RI = (Me - \varepsilon \sqrt{A}) (\gamma e^{-\lambda \sqrt{A}}) \quad (352-2) \text{ ja}$$

$$RI = a - b \log_{10} A \quad (352-3).$$

*Ks. myös Taulukkoja 7 ja 8.*

Ridge regression reveals the real effect of each independent variable in descriptive models, but it introduces bias into the model and thus inflates the multiple correlation square (mcs). Its use in predictive models needs therefore extra care.

The effect of  $\alpha$  calculated on the basis of entrance holes, egg gallery midpoints, and exit holes on the model (352-3) is shown in Table 10. The conclusion concerning the effect of  $\alpha$  is done on the basis of its t-probability. The logical value of  $H_1$  is obtained from the sign of the regression coefficient of  $\alpha$ . The magnitude of the effect can be seen from the increment in mcs. However, the increment is realistic only when no ridge constant has been used. The spatial pattern of the gallery entrance holes as expressed by  $\alpha$  does not have any effect on the ratio of increase in either the laboratory or the field group. Use of the ridge technique did not alter the conclusions here. When  $\alpha$  is calculated on the basis of egg gallery midpoints, it was found to have an almost statistically significant effect ( $p < 0.1$ ) in

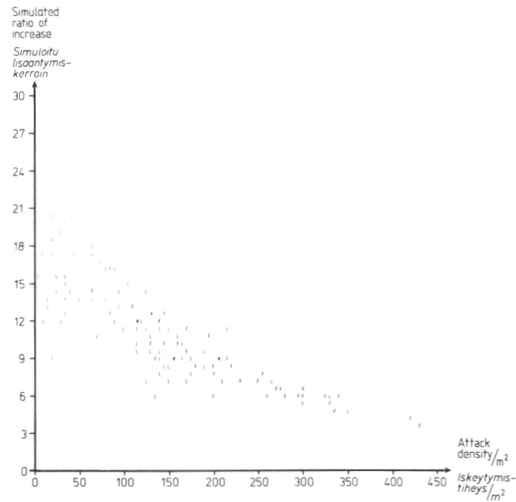


Fig 15. Simulated values of the ratio of increase as a function of attack density. The related statistics are given in Table 9.

*Kuva 15. Simuloitu lisäntymiskerroin iskeytymistiheyden funktiona. Mallin tilastolliset tunnusluvut ovat Taulukossa 9.*

the laboratory group, where  $H_1$  appeared to be true. If the  $\alpha$  of the exit holes is used as an independent variable, then a part of the material must again be rejected because the exit holes were mapped from 68 bolts only. In the laboratory bolts,  $\alpha$  of exit holes does not seem have any effect. If the field bolts only are considered, then  $\alpha$  indicates that  $H_1$  is false, that is, increasing ratio of increase with increasing clumpness.

A model which is based on the four mean minimum distances between the egg galleries was also studied. The model is

$$RI = a_0 + a_1 D_1 + a_2 D_2 + a_3 D_3 + a_4 D_4 \quad (352-4)$$

where  $D_i$  is the mean minimum distance to  $i$ :th neighboring egg gallery. The distances to the 1st, 2nd, 3rd, and 4th nearest galleries were introduced into the model in this order. The distance 120 mm was used to replace the missing distances in the bolts with less than 5 galleries. The results are shown in Table 11. Only the two first distances gave significant increments to mcs in the laboratory group. The final mcs does not exceed the mcs obtained with the pure attack density. In the field group, this model using the two first distances is the only one of all the models which gives any information.

Table 10. The effects of relative  $\alpha$  calculated on the basis of entrance holes, egg gallery midpoints and exit holes on the models for the ratio of increase (RI, 352-3) and production (P, 353-3). Mcs = multiple correlation square.  
 Taulukko 10. Iskeymismreikien, emokäytävien keskipisteiden ja kuoriutumismreikien perusteella lasketun subteellisen  $\alpha$ :n vaikutus lisääntymiskertoimen (RI) malleihin (352-3) ja jälkeläistuotoksen (P) malleihin (353-3).

Material and n	Basic model	$\alpha$ added	Multicollinearity between the regression coefficients of $\alpha$ and other indep. var. at $\lambda = 0.00$	Ridge diagonal constant $\lambda$ applied	t-probability of $\alpha$	Logical value of $H_1$	Basic mcs	Mcs after introducing $\alpha$	Inflated mcs if $\lambda > 0$
Aineisto ja n	Perusmalli	Lisätty $\alpha$	Interkorrelaatio $n$ ja muun selittäjän regressiokerrointen välillä kun $\lambda = 0.00$	Mallin tarvittu harjannevakio $\lambda$	$\alpha$ n t-todennäköisyys	Lohtopäätös $H_1$ :stä	Perusselityksaste	Selityksaste $\alpha$ :n lisäämisen jälkeen	$\lambda$ :n pidoittama selityksaste
Laboratory	$P = aA - bA^2$	$\alpha$ of entrance holes	0.156ns	0.000	0.896ns	none	0.3500	0.3831	0.3831
Laboratorio		Iskeymismreikien $\alpha$							
54	RI = a - blogA	"	0.227°	0.150	0.725ns	none	0.2934	0.3181	0.2721
Field	$P = aA - bA^2$	"	-0.418**	0.300	0.150ns	none	0.3652	0.3810	0.2299
Maasto		"							
44	RI = a - blogA	"	0.580***	1.500	0.424ns	none	0.0434	0.0487	0.0247
Laboratory	$P = aA - bA^2$	$\alpha$ of egg gallery midpoints	-0.202ns	0.000	0.765ns	none	0.3281	0.3482	0.3482
Laboratorio		Emokäytävien keskipisteiden $\alpha$							
53	RI = a - blogA	"	-0.158ns	0.000	0.906°	true	0.3368	0.3734	0.3734
Field	$P = aA - bA^2$	"	0.286°	0.150	0.880ns	none	0.3652	0.3884	0.2961
Maasto		"							
44	RI = a - blogA	"	-0.216°	0.000	0.522ns	none	0.0434	0.0569	0.0569
Laboratory	$P = aA - bA^2$	$\alpha$ of exit holes	0.661***	0.750	0.992**	true	0.8354	0.8483	0.5834
Laboratorio		Kuoriutumismreikien $\alpha$							
47	RI = a - blogA	"	0.759***	1.500	0.503ns	none	0.2094	0.2175	0.0980
Field	$P = aA - bA^2$	"	0.194ns	0.000	0.949°	false	0.5452	0.6338	0.6338
Maasto		"							
21	RI = a - blogA	"	0.101ns	0.000	0.996**	false	0.0309	0.3693	0.3693

The simulated values of the ratio of increase are plotted against the attack density in Fig 15 and the related statistics are in Table 9. The simulation model is significantly lacking in fit at low densities, but in spite of this slight undershooting it has significantly ( $p < 0.001$ ) better predictive force than any of the mathematical models. It explains 58 % of the variance of the ratio of increase. In the field group it is biased, because it is not designed so as to take into account the extra mortality which occurs in the field.

### 353. Production

Production/ $m^2$  (P) can be expressed as the product of the attack density, multiplication, and survival (Berryman 1974)

$$P = A E S \quad (353-1)$$

or

$$P = A (M e^{-\varepsilon \sqrt{A}}) (\gamma e^{-\lambda \sqrt{A}}) \quad (353-2)$$

The results of the regression analysis carried out on this model are presented in Table 7 and Fig 16. The differences between the parameter values of the multiplication and survival models are within the confidence limits. According to these models, maximum production is reached in both groups at attack densities well above 300 galleries / $m^2$ . The variance increased along with the mean. In order to avoid biased models the variables should in principle be normalized by transformation. However, this has not been done for the reasons explained in Section 31. Moreover, the larger number of observations at low densities balances the model and no bias can be seen in the plot of relative residuals. The model explains 64 % of the variance of the production in the laboratory group. In contrast to the models for survival and the ratio of increase, the model for the field group is also significant. It explains 26 % of the variance of the production.

The same material can, as in the case of the ratio of increase, be described with a simpler predictive model

$$P = aA - bA^2 \quad (353-3)$$

It is worth noticing that this is the model we arrive at if the linear models for multiplication and survival are accepted, since

$$P = A (M - \varepsilon A) (\gamma - \lambda A) \quad (353-4)$$

and if further developed with a simplified parameter notation

$$P = aA - bA^2 + cA^3 \quad (353-5)$$

in which the cubic term can be ignored as non-significant. The fits are given in Table 8 and Fig 16. This model gives the maximum production at lower densities than the descriptive model. Anyway, the point of maximum production is very indistinct due to great variation. The square term and curvature are statistically significant at the  $p = 1.000$  level in the laboratory group and at the  $p = 0.986$  level in the field group. This model is unbiased in the laboratory group, but it almost significantly ( $p < 0.1$ ) lacks fit in the field group. Otherwise it performs as well as the nonlinear model.

The result of introducing  $\alpha$  of entrance holes, egg gallery midpoints, and exit holes into the model 353-3 in a similar way as in the case of the ratio of increase, are given in Table 10. Only the  $\alpha$  of exit holes seems to have a statistically significant effect on the production. The effect is, however, contradictory. An increasing regularity of exit holes significantly ( $p = 0.992$ ) seems to increase production in the laboratory group. This result would have been masked below the multicollinearity of  $\alpha$  and attack density without applying the ridge regression technique. In the field group the result is the opposite: increasing regularity decreases production ( $H_1$  is false).

The four mean minimum distances between the egg galleries were less able to explain the production than the attack density in the laboratory group (Table 11). In the field group the result is again the opposite. The reason for this kind of result may be that the laboratory group comprised largely bolts containing less than 5 egg galleries, and therefore many of the distances were lacking.

The simulated productions are shown in Fig 17 and the related statistics in Table 9. The simulation model is equal in performance to the regression models 353-2 and 353-3 in explaining the production, although there is a significant lack of fit and

Table 11. The mean minimum distances to four nearest neighbor egg galleries as independent variables in models for the ratio of increase (352—4) and on analogous model for production. Mcs = multiple correlation square. The statistical significance of the *increment* in mcs in comparison with the previous model is indicated with the usual notation.

Taulukko 11. Keskimääräiset minimietäisyydet neljään lähimpään emokäytävään selittävinä muuttujina mal-  
leissa lisääntymiskertoimelle (352—4) ja vastaavasti jälkeläistuotokselle. Selitysasteen (mcs) lisäyksen  
tilastollinen merkitsevyys on ilmoitettu tavallisin merkinnöin.

Material and n Aineisto ja n	Model for Malli	Mcs with density only (Table 7) Selitysaste tiheyden perusteella (Taulukko 7)	Mcs using the mean minimum distances to galleries Selitysaste käyttäen keskimääräistä minimietäisyyttä käytäviin			
			1	1—2	1—3	1—4
Laboratory Laboratorio 83	Production Jälkeläistuotos	0.6416	0.2332***	0.4309***	0.4802**	0.4807ns
	Ratio of increase Lisäntymiskerroin	0.4290	0.1250**	0.4152***	0.4329ns	0.4422ns
Field Maasto 44	Production Jälkeläistuotos	0.2621	0.3129***	0.3399ns	0.3468ns	0.3509ns
	Ratio of increase Lisäntymiskerroin	0.0475	0.0000	0.1015*	0.1067ns	0.1071ns

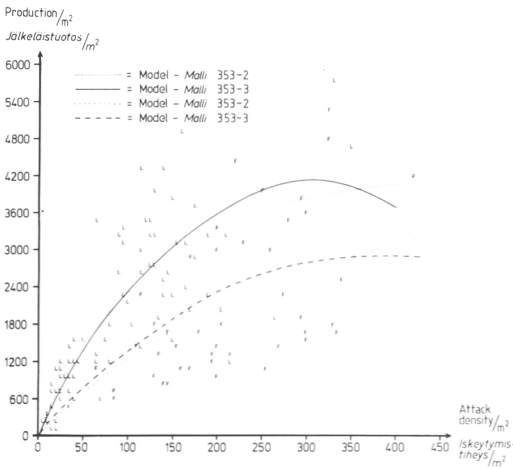


Fig 16. Production of new beetles /m<sup>2</sup> as a function of the attack density in the laboratory (L) and field (F) groups. The models are

$P = A (Me - \epsilon \sqrt{A}) (\gamma e^{-\lambda \sqrt{A}})$  (353—2) and  
 $P = aA - bA^2$  (353—3). Related statistics are given in Tables 7 and 8.

Kuva 16. Jälkeläistuotos /m<sup>2</sup> iskeytymistiheyden funktiona laboratorio- (L) ja maastopölykyissä (F). Mallit ovat

$P = A (Me - \epsilon \sqrt{A}) (\gamma e^{-\lambda \sqrt{A}})$  (353—2 ja  
 $P = aA - bA^2$  (353—3). Mallin tilastolliset tunnusluvut ovat taulukoissa 7 ja 8.

bias, due to the fact that the model was not designed to consider other mortality than that caused by intraspecific competition.

The behavior of the models outside of the range of actual observations gives in-

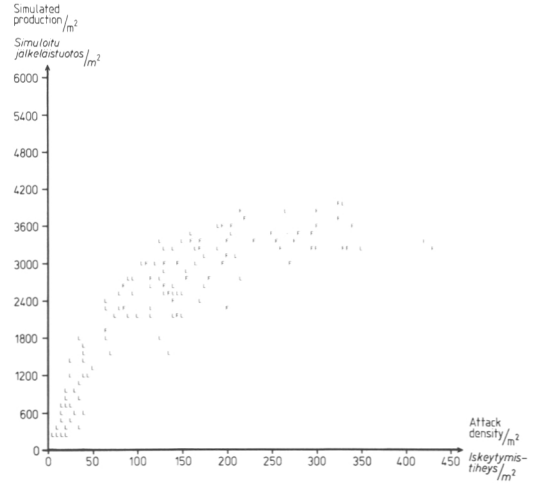


Fig 17. Simulated production as a function of attack density. The related statistics are given in Table 9.

Kuva 17. Simuloitu jälkeläistuotos iskeytymistiheyden funktiona. Mallin tilastolliset tunnusluvut ovat Taulukossa 9.

formation about their intrinsic logic. Fig 18 shows the predicted productions of three models at very high attack densities. The simulated values have been obtained by diminishing the bolt size to one quarter, and then placing the same galleries in a regular pattern. The two regression models behave in very different ways. Intuitively, the most reliable are the simulated predictions.



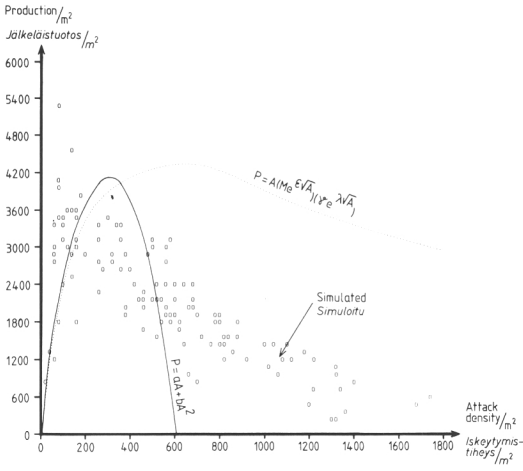


Fig 18. Behavior of the models 353—2 and 353—3 and the simulation model outside the range of observations ( $432 <$ ).

Kuva 18. Mallien 353—2 ja 353—3 ja simulointimallin käyttäytyminen varsinaisen aineiston ulkopuolella.

### 36. The efficiency of the spatial pattern as a regulating mechanism

The potential possibility of beetles enhancing the survival probabilities of their brood by following a more regular attack pattern was studied by means of the simulation model. The very same galleries in each laboratory bolt were placed in a regular configuration, in which the minimum distance to the nearest gallery was iteratively maximized. The distance was typically  $0.5 \times$  the distance expected in the hexagonal regular pattern calculated on the basis of the entrance holes. The results of simulations with the real configuration and the regular configuration are shown in Fig 19. At the

mean range of the attack density a regular pattern would have given an increase of about 1000 new beetles/ $m^2$ , and the maximum production would have been reached at an attack density of 150 egg galleries / $m^2$ . However, at high densities the actual attack pattern is as efficient as can be.

The effect of an artificial purely random attack pattern was also tested in the same way. The outcome was very similar to the actual attack pattern, except at high densities where it gave a slightly lower production. The variance was greater than in the actual pattern.

The effect of the age structure of the larvae was studied by allowing all the larvae to hatch at the same time in the simulation model. The outcome did not differ from the outcome with the real age structure.

### 37. The effect of competition on beetle weight

Competition does not always result in death; it is also manifested in a less severe form as diminished weight and fecundity of the offspring.

The live weight is inversely related to the attack density ( $p < 0.05$ ; Fig 20). The correlation is not very high because there is extra variation arising from the use of five different breeding chambers at different temperatures. The attack density did not vary between breeding chambers, and hence all the material could be combined here.

The live weight of rearing beetles is also inversely related to time (Fig 21). The negative correlation is statistically significant in 4 of the 5 breeding chambers.

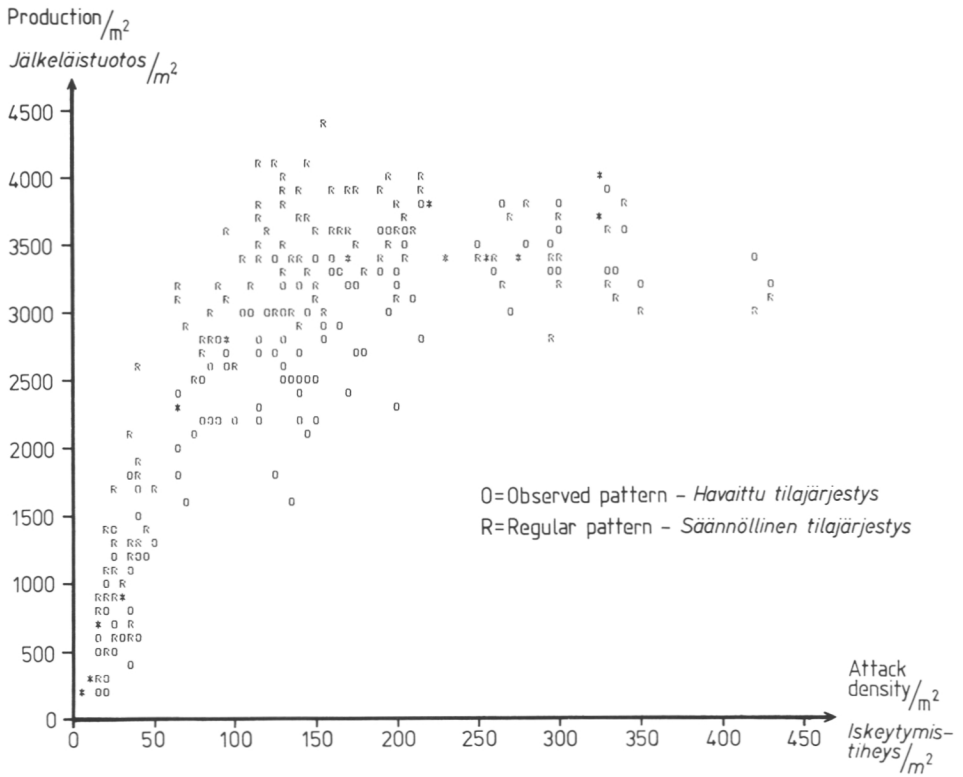


Fig 19. Simulated productions with the observed spatial pattern of egg galleries and with an artificial regular pattern of the same egg galleries.  
 Kuva 19. Simuloidut jälkeläistuotokset havaitulla emokäytävien tilajärjestyksellä ja keinotekoisella tilajärjestyksellä, jossa samat emokäytävät asetettiin säännölliseen tilajärjestykseen.

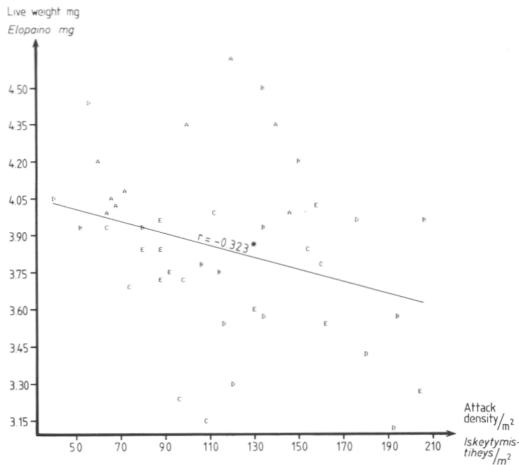


Fig 20. Live weights of young adults as a function of the attack density. The characters A...E indicate different breeding chambers.  
 Kuva 20. Kuoriutuvien nuorten aikuisten elopaino iskeytymistiheyden funktiona. Merkit A...E tarkoittavat eri kasvatuskaappeja.

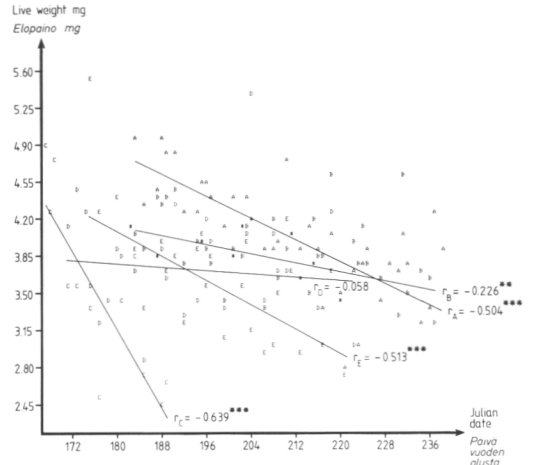


Fig 21. Live weights of young adults as a function of Julian date in five different breeding chambers A...E.  
 Kuva 21. Kuoriutuvien nuorten aikuisten elopaino vuoden alusta lasketun päivän funktiona viidessä eri kasvatuskaapissa A...E.

## 4. DISCUSSION

According to Berryman (1974), a general productivity model for bark beetles is composed of two submodels: multiplication, and survival. As a first step the attack phase is also likely to affect productivity, although it is generally attributed to aggregation and colonization processes.

### 4.1. Attack

Resource partitioning is rather well developed in bark beetles (Coulson 1979). The niche that *Tomicus piniperda* inhabits is freshly fallen or cut, thick-barked pine. In this study the attack density increased linearly with bark thickness; the same result has been obtained in many studies dealing with *T. piniperda* (Trägårdh and Butovitsch 1935, Annala and Petäistö 1978, Nilssen 1978, Långström 1979). The shape of the curve (32—1, Fig 6) is interesting. Attack density approaches the maximum at a bark thickness of about 10 mm. The maximum attack density (279.3 /m<sup>2</sup>) is close to the point where maximum production of progeny is reached. It could therefore be hypothesized that the species has adapted to this maximum attack density level in order to maximize the number of offspring. The asymptotic attack density level seems to depend on the population density, since Annala and Petäistö (1978) obtained a similar shaped curve in spite of the fact that the maximum attack density in their study was only one tenth of the attack density found in this study. This indicates that no conclusions on the species' adaptation cannot be made on the basis of the maximum attack density calculated on the basis of the bark thickness. It only tells, how heavy is the attack.

The roughness of the bark estimated as the variance of bark thickness, was not found to have any effect on the attack density.

The aggregation of *T. piniperda* to its host is guided by the odors of the host tree (Kangas et al. 1967, Perttunen et al. 1970).

Schönherr (1972) suggests that there may be aggregation pheromone exerted by the excavating females, but the evidence is still weak (Nilssen 1978). No evidence for masking repellent pheromones (Rudinsky 1969, Rudinsky et al. 1973), which have been showed to exist in several *Dendroctonus* species, has been presented.

At the whole stand level all bark beetles possess a high degree of aggregative behavior. The behavior within the tree is different; aggregation has to stop so as to avoid overpopulation. The entrance holes of the egg galleries were slightly aggregated in the laboratory material and slightly regular in the field material. The spatial pattern was dependent on the attack density. This is caused by the action of two opposite forces which cancel out each other at the opposite extremes of attack density: (i) Thermokinesis to optimal temperature zones, and (ii) a tendency towards regularity in order to minimize competition.

Bakke (1968) has shown that the temperature which *T. piniperda* prefers for gallery construction is 21.3 °C. This can be seen in the field in that at low densities the egg galleries of *T. piniperda* are concentrated on the sides of the log exposed to direct sunlight. The underside is below and the upper side above the optimum temperature, as could be observed at the time of swarming. This makes the first attacking beetles aggregate in the sides of the log. As the attack continues, overcrowding of the most popular areas becomes apparent and the beetles which attack later have to colonize the less suitable zones. At the highest densities, the beetles seem to maintain a certain minimum distance between each other, which in turn produces a slightly regular pattern at high densities. This kind of significant regression could not be found so clearly in the uniform environment of the laboratory as in the field. Most of the individual cases had to be classified as randomly dispersed due to the small degrees of freedom.

This interpretation of the process fits well to the theory of Taylor (1978). According to him, true randomness in living organisms only exists where an abiotic force, such as a storm, overrules the actions of the organisms. Otherwise randomness occurs only when the populations are changing patterns from one extreme to another.

Nilssen (1978) found a regular pattern of *T. piniperda* attacks in seven out of the eight pieces of log studied. A regular pattern has also been found for *Scolytus ventralis* (Berryman 1968), *Dendroctonus ponderosae* (Shepherd 1965, Safranyik and Vithayasai 1971), and *D. pseudotsugae* (Hedden and Gara 1976). The dependence of the spatial pattern of attack on density has not been analyzed before, but Hedden and Gara (1976) mention that the regular pattern is observed at low densities, where the mean distance between neighbouring attacks was about 26 cm. Safranyik and Vithayasai (1971) report that in standing trees both regularity and attack density were greater on the northern aspect than on the southern aspect. This observation fits well with the results obtained here.

The aggregated pattern at low densities could be interpreted as an effect of temperature. There are several possible explanations for the mechanisms that induce the regular pattern at high densities and shut off the attack at a possible saturation level. They are: (i) the distribution of bark crevices, (ii) sonic interaction, and (iii) repellent pheromones.

It is clear to any observer of a *T. piniperda* attack that the beetles tend to bore in through the crevices in the bark. Shepherd (1965) and Hedden and Gara (1976) suggest that the regularity of attacks is due to the regular pattern of the bark crevices. Safranyik and Vithayasai (1971) have shown in *D. ponderosae* that the beetles attack through artificial holes, even when there is another entrance hole close by, instead of choosing more open areas without holes. Thus there is strong evidence to support the crucial role of the presence of suitable attack sites. However, objections can also arise, since the crevices may be regularly distributed in the horizontal direction, but certainly not in the vertical direction. If no other mechanism were acting, then the pattern would be aggregated especially at high densities. This

is quite the opposite to what has been observed. Furthermore, if we assume that the same mechanism which yields a regular pattern, is due to the aggregation shutoff, then the bark structure cannot be the explanation.

Sonic interaction seems most likely to be the regulatory agent (c.f. Nilssen 1978). The female is the first attacking sex in *T. piniperda*, but only the males stridulate (Schönherr 1970). During the attack they are very noisy, and the stridulation can be heard at distances of up to 30 cm. There are two possible reasons for stridulation, namely competition between males for females, and controlling the spatial pattern of attacks. If the stridulation has an effect on males, it can also affect females which attack later. The attack process of *T. piniperda* should be studied in detail and in respect to short time scale (e.g. Bunt et al. 1980). As the end points of the galleries were slightly more aggregated than the starting points, it can be assumed that the factor which controls the spatial pattern during the attack ceases to operate during gallery elongation. This fits to the cessation of stridulation after the attack phase.

Very high attack densities of over 300 galleries /m<sup>2</sup> have not been found in the field, even with very high *T. piniperda* populations. It is thus obvious that there is a saturation density which the species does not normally exceed. Långström (1980) presents evidence to indicate that the excess part of the population turns to shoot feeding when the attack shutoff density is reached. Other more aggressive bark beetles which produce aggregation pheromones may attack living trees in such conditions. As the tendency to regularity increases with attack density, it is likely that the same mechanism is responsible for both regularity and aggregation shutoff in *T. piniperda*. Thus the tendency to follow a regular spatial pattern with increasing attack density is a very important negative feedback factor.

## 42. Multiplication

The number of eggs laid per female has been shown to depend on a wide range of factors in different bark beetles. These have been reviewed by Berryman (1974). In this

study only the effect of intraspecific competition, that is, effect of attack density on the multiplication was studied.

There are three possible negative feedback mechanisms affecting the number of eggs laid: (i) a change in the length of the egg galleries, (ii) a change in the density of the eggs per unit length of egg gallery, and (iii) a change in the spatial pattern of the eggs.

The length of the egg galleries was found to be linearly inversely correlated with the attack density. Similar results have been found in many studies dealing with *T. piniperda* (Nuorteva 1954, 1964, Salonen 1973, Annala and Petäistö 1978). According to the material of Eidmann and Nuorteva (1968), the dependence is curvilinear. This phenomenon is known in many other bark beetles, too, e.g. *Dendroctonus ponderosae* (Cole 1962), *D. pseudotsugae* (McMullen and Atkins 1961), *D. brevicomis* Le Conte (Dudley 1971), and *Ips typographus* L. (Yamaguchi and Koizumi 1959). There are at least three possible mechanisms, which could induce gallery shortening: (i) the sound produced by gnawing neighbors, (ii) moisture change in the host tree, and (iii) chemical changes in the host tree. Wagner et al. (1982) have hypothesized that these mechanisms all as well as contact to adjacent galleries, are acting in *D. frontalis* Zimmermann. It is likely that only the first has any effect on *T. piniperda*, since the gallery construction takes place during a period lasting for only a couple of weeks and the moisture loss through pure physical evaporation from the cut log ends is much more effective than that through the small beetle entrance holes. The same gallery shortening has been observed also in windfalls (Annala and Petäistö 1978), in which the moisture loss can only be negligible. Chemical changes are not likely either, because in the middle of June when the galleries are almost finished, the phloem between the galleries seems to be completely unaffected. *T. piniperda* is, as all aggressive bark beetles, a vector of blue stain fungi. Whether this affects the host tree so rapidly that excavating neighbors can sense it should be studied. Klomp (1964, p. 31) suggests that changes in the host are the mechanism, and because they cannot be considered as regulatory agents, suspects that there are no negative feedback mechanisms involved

at all in bark beetle reproduction. This view, however, can be disregarded, because after a more careful look negative feedback mechanisms can be found in almost every phase in the life cycles of bark beetles.

The density of eggs per unit length of gallery was independent of the attack density and the length of the egg gallery. The result obtained here can be considered to be rather preliminary, but the same has also been found by Eidmann and Nuorteva (1968). The same is known also in *Dendroctonus ponderosae* (Cole 1962), *D. brevicomis* (Dudley 1971), *Ips typographus* (Yamaguchi and Koizumi 1959). An inverse relationship between egg density in the egg gallery and attack density has been shown in *D. pseudotsugae* (McMullen and Atkins 1961) and *Scolytus ventralis* (Berryman and Pienaar 1973). The egg density in the galleries is directly proportional to the prevailing temperature in *D. frontalis* (Wagner et al. 1981). This was suggested to be the case in *T. piniperda* also by Eidmann and Nuorteva (1968), and similar observations have been made by the author. This may explain why the number of eggs per unit gallery length varies so much between materials. The reason for this may be that at low temperatures the beetles need more food per egg produced.

The spatial pattern of the eggs must have some role in overcoming the host's resistance, as well as in intra-gallery competition at an early developmental stage of the larvae. The spatial pattern of the eggs is of course very aggregated, as far as the entire bolt is concerned. The answer is not as obvious at the gallery level. The question was put: Is the distance between two eggs a random variable? The material analyzed from the subject suggested that the distance between two eggs is rather regular than random, but there are longer intervals where there were no eggs at all. Thus the spatial arrangement in the entire gallery depends on the level of scrutiny. The length of the interval between two eggs increased slowly towards the end of the egg gallery. The spatial arrangement of the eggs can also depend on their location with respect to other galleries. It was not possible to study this relationship because the phloem had deteriorated severely. Other observations of the spatial pattern of the eggs of bark beetles are scarce. In *Dendroctonus pseudotsugae*, the egg density has been found to be

greatest at the beginning of the gallery (Schmitz and Rudinsky 1968). The eggs were laid in clumps along the gallery, but the arrangement of the clumps was not dependent on neighbouring galleries. Avoidance of neighbouring galleries has been found in *Ips perturbatus* (Eichhoff) (Denton 1950 according to Schmitz and Rudinsky 1968).

Berryman (1974) tentatively suggested the exponential decay curve for describing the number of eggs laid per egg gallery. It was found to describe well the multiplication of *T. piniperda*. The effect of several negative feedback mechanisms can be seen clearly in the inverse relationship. The same inhibitory effect of increasing attack density on the number of eggs laid was also observed by Eidmann and Nuorteva (1968) in *T. piniperda*. A similar response is known from *Dendroctonus frontalis* (Coulson et al. 1976).

### 43. Survival

The exponential decay curve was adequate to describe the survival in the laboratory bolts. According to Berryman (1974), the parameters  $\gamma$  and  $\lambda$  are "food quantity coefficients", which may reflect the effect of matrix thickness and the food utilization characteristics of the species. The parameter  $\gamma$  can perhaps be better considered as an intra-gallery competition parameter, since when  $A \rightarrow 0$ ,  $\gamma$  directly determines the survival probability, given that  $\gamma < 1$ . In this material the value of  $\gamma$  was 0.86, which means that the remaining mortality of 14 % is due to host resistance and intra-gallery competition. The host condition was standardized, and it had no effect on survival because attack was successful even at the lowest densities. No humpbacked response to attack density can be seen. Thus only the intraspecific competition needs to be taken into account in the survival function of *T. piniperda* in cut logs. In windfelled trees host resistance may be of importance (c.f. Annala and Petäistö 1978, Fig 8b).

The concurring species, predators, and parasites were excluded in the field material of this study. The larvae were exposed to the effects of weather — heat on the sunlit side, rainfall, night frosts, and diseases — which could destroy part of the larvae. Also

the bolts in the breeding chambers are attacked by fungi due to poor air circulation, but usually too late to harm the larvae. The mortality was much higher in the field than in the laboratory, and even no density dependent response in the survival in the field bolts was found. The result seems strange because the dependence was very clear in the laboratory. It can be explained as an effect of two factors: Firstly, the observations at the lowest densities, where the effect is clearest, are lacking. Secondly, the attack density was greatest in the unshaded field bolts. The mortality due to the effects of rainfall can be assumed to be the greater the more shade there is. According to Annala (1969), the pupae of *Ips typographus* can be killed by an excess of moisture, because the osmotic suction of the pupae leads to their swelling and subsequent bursting. The lack of density dependence is thus only a sampling artefact.

The age structure of the larvae results in the first larvae to hatch having a much greater probability to complete their development than their later hatching siblings. This was also shown by the simulation model. The competing organisms are equally affected only if they have identical competitive abilities (Klomp 1964). Bakker (1961) emphasizes the effect of age structure on the outcome of competition. At the point where the food resources are depleted, the age structure determines the final survival. Those larvae which have gained the minimum weight for pupating, survive, while those below the crucial limit perish. This pattern, observed in *Drosophila*, does not completely fit with Scolytidae, since the spatial pattern of the larvae also affects the survival. There is always survival in *T. piniperda*, even at the highest densities.

Assuming scramble competition (Nicholson 1954), the survival curve should go to zero at high densities. According to the explanatory model, survival is balanced at 20—30 % at high densities and then decreases very slowly. Although the basic nature of the intraspecific competition in *T. piniperda* is a scramble one, this is a pattern we would expect to detect in contest competition. This suggests that cannibalism may be of some importance in *T. piniperda*, although direct observations of it are totally lacking. The wide age differences between larvae may also



have similar effects as cannibalism on the shape of the survival curve.

The exit holes were very aggregated. This is only natural, since the eggs were laid in a very aggregated pattern along the galleries. The spatial pattern of the exit holes is determined by the orientation and moving process of the larvae. The old larvae largely determine the direction, because the larvae avoid crossing each others' paths (Schmitz and Rudinsky 1968). This causes the larvae to consume the phloem systematically and yields an aggregated pattern of exit holes. In *Scolytus ventralis* the clumpness has also been found to increase from attack to emergence (Berryman 1968). According to the author's observations, the larvae tend to prefer longitudinal movement in optimum temperatures, but tangential movement in cold conditions. This may be a response to a search for the optimum temperature. The aggregation of exit holes decreases but is still prevailing above a density of 50 galleries/m<sup>2</sup>. This is the point where the galleries start to interfere with each other. Thus it can be concluded that inter-gallery competition starts only after this density is reached. The limit is distinct. There is no great theoretical difference between intra- and inter-gallery competition. The increase in inter-gallery competition strengthens the intra-gallery competition, too. However, as long as there is only within-brood competition, it has not severe forms.

The results obtained from weighing beetles are very similar to those of Beaver (1974). The live weight of rearing beetles decreased with time and attack density. The weight loss of later rearing beetles could be interpreted to be an effect of deteriorating phloem and bolt drying, and not that of a pure lack of food. The phloem which is broken up into small pieces by excavating larvae may spoil even if it is not eaten. The age structure causes that the larvae hatching later are in fact living in similar conditions as larvae in higher densities. The emerging pattern of *T. piniperda* with respect to time is strongly skewed to the left (Beaver 1974, Långström 1980). The peak is reached after about 1/4 of the total emerging range, and the total period of emergence is about equal to the time from attack to the emergence of the first new adults. The oviposition period is, however, much shorter than the emerging

period. Although this distribution may arise from the stochastic nature of poikilotherm development (Sharpe et al. 1977), here it could also be caused by the delaying of development due to the lack of food. Beaver (1974) noticed that there are always specimens which have much lower weights than the average even at the lowest densities. He suggests that these beetles come from areas of localized competition. Death does not always occur after starving, because the beetles can have 3.4-fold weight differences (Eidmann and Nuorteva 1968, Beaver 1974). The negative correlation between weight and density is a very common phenomenon in insects (Klomp 1964).

To sum up the survival process, it can be concluded that there does not seem to be any negative feedback responses involved in the survival. This is only natural since the larvae are only scrambling for their own survival. All the regulatory activities are those of the parent beetles.

#### 44. Emergence

The productivity of bark beetles can be explained as a product of the attack density, multiplication and survival (Berryman 1974). The model provided an adequate fit in the material, but due to its complexity, the simpler paraboloid model can be used for prediction. However, the residual standard deviations of all the models are too high to be used, for instance, in constructing life-tables. If the residual standard deviation is 30—40 % of the estimate, as it was here, the predictions for individual bolts can be far from real. Furthermore, the regression models apply only in the area from which observations are available. Their extrapolation is not justified, as was apparent in the case of the model for the ratio of increase. The lack of observations at low densities resulted in a totally unrealistic model. The regression models apply only under conditions similar to those that prevailed when the original data was collected. Neither do they take dynamically into account the interaction of the mortality factors. The simulation model, on the other hand, is much safer, because it has intrinsic explanatory force, which the other models largely lack

(see Keulen 1974). If the underlying assumptions of a simulation model are correct, such a model allows predictions outside the range of the original data (Coulson et al. 1979, Hain 1981). Here the simulation model also gave the best fit. Whereas the best regression model explained 43 % of the variance of the ratio of increase, the simulation model explained 58 % in the laboratory. When the simulation model is more elaborated to take into account mortality factors other than intraspecific competition, it is then the most suitable for constructing life-tables and survivorship curves. The simulation model can be considered to be the most powerful model available for studying the effect of spatial pattern, or all within-tree events in bark beetles in general (Jong and Saarenmaa 1984). Its advantage also lies in the possibility to obtain intermediate results and age structures and weights of larvae. Simulation of data obtained with successive sampling thus becomes possible.

The reproduction of *T. piniperda* is much more efficient in the laboratory than in the field. While numbers as high as 5800 new beetles /m<sup>2</sup> can be reached in the laboratory, no more than 1700 new beetles have been observed in normal field conditions (c.f. Butovitsch 1954, Nuorteva 1954, 1964, Salonen 1973, Beaver 1974, Eidmann 1974, Ehnström 1976, Annala and Petäistö 1978, Jutinen 1978, Långström 1979).

The beetle production /m<sup>2</sup> in the laboratory was similar or slightly higher than that in the study of Eidmann and Nuorteva (1968). An exact comparison could not be made, since the equations are not given in that study. The magnitude of the variation seems to fit that presented by Eidmann and Nuorteva (1968). Maximum production is reached at rather high densities. The large variance makes it difficult to trace the point, but it lies at about 300 attacks /m<sup>2</sup>. The decrease in the function is slow, which suggests that contest competition — cannibalism — must occur to some degree. A similar shaped production curve has been found in most bark beetles (Kangas 1953, Thalenhorst 1958, McMullen and Atkins 1961, Cole 1962, Reid 1963, Schmitz and Rudinsky 1968, Berryman 1973, 1974, Berryman and Pienaar 1973).

The curve for the ratio of increase is also similar to those obtained in the previous

studies, except for the fact that the high production in individual cases (even 70x) found by Hanson (1937) and Eidmann and Nuorteva (1968) is not found here. The maximum production is only about 30x. This may be a property of the northern beetle stand, which is smaller in size than those from the more southern regions used in the other studies. The variation in the ratio of increase is greatest at the lowest densities, because the random errors in the experimental design are more pronounced there. The variation may partly be due to differences in the resin flow in the bolts and variation in the parent beetles. At high densities these variation sources are reduced. Thus it is difficult to predict the outcome from a single gallery. The great unexplained variance in the production may be due to differences in the drying process of the bolts. These difficulties associated with the breeding material have been encountered in many artificial experiments with other bark beetles, too (Coulson 1979). The importance of carefully standardizing all rearing conditions, especially phloem thickness, temperature, and moisture, in a study like this thus becomes very apparent.

The effect of spatial pattern on production was not detectable using the aggregation index  $\alpha$  as an independent variable in the multiple regression analysis. The validity of  $\alpha$  as such could be shown with the artificial bolts in which the galleries were randomly dispersed. The most likely explanation is that  $\alpha$  was calculated on the basis of the starting, end, and middle points of the galleries. The competition, however, actually occurs outside the egg gallery where the larvae concentrate, being strongest about 2—4 cm from the gallery. The midpoints of the egg galleries are closest to these areas, but the aggregation of larvae is not necessarily the same as the aggregation of the calculated points. Thus the estimator is not necessarily valid in this application. Another reason is that the small bolt size used meant that just those bolts where the effect of the spatial pattern would have been most detectable, had to be rejected due to missing values for  $\alpha$ . The hypothesis that increasing regularity increases production was not proven to be true, neither was it shown to be false using  $\alpha$ . Moreover, the usefulness of the hypothesis is not self-evident in the case of the exit holes. It may

be that when the larvae are able to move freely, they move in a front, and enter the same regions, thus resulting in clumpness. If they are forced to zigzag due to competition, the result may be more uniform.

The spatial pattern of egg galleries has, however, a small effect on the production. This could be shown with the other methods, multiple regression with the mean minimum distances between the egg galleries, and the simulation model. Both these models use the information available about the spatial pattern. Therefore it can be tentatively concluded that the difference between these models and those which use only the density, is the effect of spatial pattern.

The size of the difference depends on the variable considered. In the case of the ratio of increase it is more detectable, since the unexplained variation is greater at low densities. There is great variation in the spatial pattern at these densities. In some of the bolts the broods do not affect each other at all, whereas in others the galleries almost meet, thus resulting in severe competition. The percentage of the total variance of the ratio of increase, which could be accounted to the spatial pattern, ranged from 1 to 6 % according to the distance model, and from 8 to 15 % according to the simulation model (Tables 7 and 12). In the models for production /m<sup>2</sup> the variation is greater at high densities. There the effect of spatial pattern is not as clear, since the larvae in any case encounter other competitive larvae

from all directions. The proportion of the variance of production per area which was attributable to the spatial pattern, ranged from nought to 9 % according to the distance model, and from 1 to 5 % according to the simulation model. These estimates fit well with the opinion of Kangas (1953) that even 10 % of the larvae may die owing to the effects of a poor spatial pattern.

The simulations showed that the beetles were capable of a considerably higher production especially at the medium densities, if the maximum degree of regularity were reached. At these densities the prevailing spatial pattern is random. At a high density the actual slight degree of regularity is adequate to reach maximum production. The reason for this inefficiency is obvious. In nature the populations are seldom regulated by one factor only, but instead there are usually several pressures acting which the population can respond to in a number of different ways. In the northern conditions, *T. piniperda* populations are frequently suppressed by cold summers, which break the development of the larvae (Kangas 1954, 1963, Juutinen 1978). As a consequence, those individuals which have not emerged will die during the autumn frosts. Thus the importance of searching for the parts of the logs where temperature is optimal becomes clear and the relative inefficiency of the pseudo-random attack pattern at medium densities is understood.

## LITERATURE

- ANNILA, E. 1969. Influence of temperature upon the development and voltinism of *Ips typographus* L. (Coleoptera, Scolytidae). Ann. Zool. Fenn. 6: 161—207.
- & PETAISTÖ, R.-L. 1978. Insect attack on windthrown trees after the December 1975 storm in western Finland. Seloste: Hyönteisten lisääntyminen tuulen kaatamissa puissa Länsi-Suomessa vuoden 1975 joulukuun myrskyn jälkeen. Commun. Inst. For. Fenn. 94(2): 1—24.
- BAKKE, A. 1968. Ecological studies on bark beetles (Coleoptera: Scolytidae) associated with Scots pine (*Pinus sylvestris* L.) in Norway with particular reference to the influence of temperature. Medd. Norske Skogforsöksv. 83, 21(6): 441—602.
- BAKKER, K. 1961. An analysis of factors which determine success in competition for food among larvae of *Drosophila melanogaster*. Arch. Neerl. Zool. 14: 200—281.
- BARE, B. B. & HANN, D. W. 1981. Applications of ridge regression in forestry. For. Sci. 27(2): 339—348.
- BEAVER, R. A. 1966. The development and expression of population tables for the bark beetle *Scolytus scolytus* (F.). J. Anim. Ecol. 35: 27—41.
- 1967. The regulation of population density in the bark beetle *Scolytus scolytus* (F.). J. Anim. Ecol. 35: 435—451.
- 1974. Intraspecific competition among bark beetle larvae (Coleoptera: Scolytidae). J. Anim. Ecol. 43: 455—467.
- BERRYMAN, A. A. 1968. Distributions of *Scolytus ventralis* attacks, emergence, and parasites in grand fir. Can. Ent. 100: 57—68.
- 1973. Population dynamics of the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae). I. Analysis of population behavior and survival from 1964 to 1971. Can. Ent. 105: 1465—1488.
- 1974. Dynamics of bark beetle populations: Towards a general productivity model. Environ. Ent. 3(4): 579—585.
- 1981. Population systems. A general introduction. 222 pp. Plenum Press, New York.
- & PIENAAR, L. V. 1973. Simulation of intraspecific competition and survival of *Scolytus ventralis* broods (Coleoptera: Scolytidae). Environ. Ent. 2: 447—459.
- BONNICKSEN, T. M. & STONE, E. W. 1980. The giant sequoia-mixed conifer forest community characterized through pattern analysis as a mosaic of aggregations. For. Ecol. Manag. 3: 307—328.
- BUNT, W. D., COSTER, J. E. & JOHNSON, P. C. 1980. Behavior of the southern pine beetle on the bark of host trees during mass attack. Ann. Ent. Soc. Amer. 73: 647—652.
- BUTOVITSCH, V. 1954. Die Einwirkung der Läuterungszeit auf die Vermehrung des grossen Waldgärtners, *Blastophagus piniperda*. Berichte des II Kongr. Intern. Verb. Forstl. Forschungsanst. Rom 1953, 645—649.
- CLARK, P. J. & EVANS, F. C. 1954. Distance to nearest neighbor as a measure of spatial relationship in populations. Ecology 35(4): 445—453.
- CLIFF, A. D. & ORD, J. K. 1975. Model building and the analysis of spatial pattern in human geography. J. Royal Stat. Soc. B37: 297—328.
- COLE, W. E. 1962. The effects of intraspecific competition within mountain pine beetle broods under laboratory conditions. USDA, Intermountain For. Range Exp. Stat., Ogden, Utah. Res. Note Int-97: 1—4.
- COULSON, R. N. 1974. Southern pine beetle population dynamics. 26—31. In: Payne, T. L., Coulson, R. N. & Thatcher, R. C. (eds.). Southern pine beetle symposium. March 7—8, 1974, College Station, Texas. Texas Agr. Exp. Stat. and USDA, Southern For. Exp. Stat. 57 pp.
- 1979. Population dynamics of bark beetles. Ann. Rev. Ent. 24: 417—447.
- , MAYYASI, A. M., HAIN, F. P. & MARTIN, W. C. 1976. Resource utilization by the southern pine beetle, *Dendroctonus frontalis* (Coleoptera, Scolytidae). Can. Ent. 108: 353—362.
- , FELDMAN, R. M., FARGO, W. S., SHARPE, P. J. H., CURRY, G. L. & PULLEY, P. E. 1979. Evaluating suppression tactics of *Dendroctonus frontalis* in infestations. pp. 27—44. In: Coster, J. E. & Searcy, J. L. (eds.). Evaluating control tactics for the southern pine beetle: Symposium proceedings. USDA For. Serv. Techn. Bull. 1613., Pineville.
- COX, F. 1971. Dichtebestimmung und Struktur-analyse von Pflanzenpopulationen mit Hilfe von Abstandsmessungen. Ein Beitrag zur methodischen Weiterentwicklung von Verfahren für Verjüngungsinventuren. Mitt. Bundesforschungsanstalt für Forst- u. Holzw. 87: 1—182.
- DE MARS, C. J., DAHLSTEN, D. L. & STARK, R. W. 1970. Survivorship curves for eight generations of the western pine beetle in California, 1962—1965, and a preliminary life table. 134—146. In: Stark, R. W. & Dahlsten, D. L. (eds.). Studies on the population dynamics of the western pine beetle, *Dendroctonus brevicomis* Le Conte (Coleoptera, Scolytidae). Univ. Cal., Div. Agr. Sci. 174 pp.
- DENTON, R. E. 1950. An ecological study of *Ips perturbatus* Eichhoff. Master's Thesis, Ann. Arbor, Univ. Mich. 33 pp.
- DRAPER, N. R. & SMITH, H. 1969. Applied regression analysis. 407 pp. John Wiley & Sons, New York.
- DUDLEY, C. O. 1971. A sampling design for egg and first instar larval populations of the western pine beetle, *Dendroctonus brevicomis*. Can. Ent. 103: 1291—1313.
- EHNSTRÖM, B. 1976. Barkborreangrepp i massa-

- vedsvältor. 146—156. Svenska Skogsvårdsförb., Skogs och Virkeskydd, Konferens 1975.
- EIDMANN, H. H. 1974. Versuche über den Verlauf des Schwärmens von Borkenkäfern und des Insektenbefalls an Kiefernholz in Mittelschweden. Stud. For. Suec. 113: 1—26.
- & NUORTEVA, M. 1968. Der Einfluss der Siedlungsdichte und anderer Faktoren auf die Anzahl der Nachkommen von *Blastophagus piniperda* L. (Col., Scolytidae). Ann. Ent. Fenn. 34(3): 135—148.
- HAIN, F. P. 1980. Sampling and predicting population trends. pp. 107—135. In: Thatcher, R. C., Searcy, J. L., Coster, J. E. & Hertel, G. D. The southern pine beetle. USDA For. Serv. Techn. Bull. 1631, 266 pp.
- HANSON, H. S. 1937. Notes on the ecology and control of pine beetles in Great Britain. Bull. Ent. Res. 28: 185—236.
- HEDDEN, R. L. & GARA, R. I. 1976. Spatial attack pattern of a western Washington Douglas-fir beetle population. For. Sci. 22(1): 100—102.
- JONG, M. C. M. de & SAARENMAA, H. 1984. A mechanistic simulation model for the movement and competition of bark beetle larvae. Ecol. Modelling (in press).
- JUUTINEN, P. 1978. Kuitupuupinot pystynävertäjän (*Tomicus piniperda* L.) lisääntymispaikkoina Pohjois-Suomessa. Summary: Pulpwood stacks as breeding sites for pine shoot beetle (*Tomicus piniperda* L.) in Northern Finland. Folia For. 335: 1—28.
- KANGAS, E. 1934. Tutkimuksia Punkaharjun männiköiden hyönteistuloista. Referat: Untersuchungen über die Insektenhädigungen der Kiefernbestände in Punkaharju. Commun. Inst. For. Fenn. 19(7): 1—68.
- 1953. On population regulation of forest insects living in tree rind, in Finland. Trans. 9th Int. Congr. Ent., Amsterdam. Vol. 2: 224—228.
- 1963. Die Waldwirtschaft im finnischen Lappland und ihre Borkenkäfer-Probleme. Manuscr. 6 pp. IUFRO Discussion Group Population Dynamics 1963.
- , PERTTUNEN, V., OKSANEN, H. & RINNE, M. 1967. Laboratory experiments on the olfactory orientation of *Blastophagus piniperda* L. (Coleoptera, Scolytidae) to substances isolated from pine rind. Acta Ent. Fenn. 22: 1—87.
- KEULEN, H. van 1974. Evaluation of models. 250—252. Proc. 1st Int. Congr. Ecol.
- KLOMP, H. 1964. Intraspecific competition and the regulation of insect numbers. Ann. Rev. Ent. 8: 17—40.
- LÄNGSTRÖM, B. 1979. Märgborrarnas förökning i röjningsavfall och kronskadegörelse på kvarstående träd. Summary: Breeding of pine shoot beetles in cleaning waste of Scots pine and subsequent shoot-damage on remaining trees. Sveriges Lantbruksuniv., Skogsentomol. Rapp. 1: 1—51.
- 1980. Life cycles of the pine shoot beetles with particular reference to their maturation feeding in the shoots of Scots pine. Sveriges Lantbruksuniv., Avd. Skogsentomologi, 123 pp.
- 1983. Life cycles and shoot feeding of the pine shoot beetles. Stud. For. Suec. 163: 1—29.
- MAWSON, J. C. 1968. A Monte Carlo study of distance measures in sampling for spatial distribution in forest stands. For. Sci. 14(2): 127—139.
- McMULLEN, L. H. & ATKINS, M. D. 1961. Intraspecific competition as a factor in the natural control of the Douglas-fir beetle. For. Sci. 7(3): 197—203.
- MOUNTFORD, M. D. 1961. On E.C. Pielou's index of non-randomness. J. Ecol. 49: 271—275.
- NICHOLSON, A. J. 1954. An outline of the dynamics of animal populations. Australian J. Zool. 2: 9—65.
- NILSSEN, A. C. 1978. Spatial attack pattern of the bark beetle *Tomicus piniperda* L. (Col., Scolytidae). Norw. J. Ent. 25: 171—175.
- NUORTEVA, M. 1954. Versuche über den Einfluss der Bevölkerungsdichte auf die Nachkommenzahl des grossen Waldgärtners, *Blastophagus piniperda* L. Ann. Ent. Fenn. 20(4): 184—189.
- 1956. Über den Fichtenstamm-Bastkäfer, *Hylurgops palliatus* Gyll., und seine Insektenfeinde. Selostus: Tutkimuksia vaippanilurista, *Hylurgops palliatus* Gyll., ja sen hyönteisvihollisista. Acta Ent. Fenn. 13: 1—118.
- 1962. Über die Nützlichkeit der Zimmerbocklarven (*Acanthocinus aedelis* L.) im Walde. 171—173. XI. Int. Congr. Ent., Wien 1960, II.
- 1964. Über den Einfluss der Menge des Brutmaterials auf die Vermehrlichkeit und die natürlichen Feinde des grossen Waldgärtners, *Blastophagus piniperda* L. (Col., Scolytidae). Ann. Ent. Fenn. 30(1): 1—17.
- PAYANDEH, B. 1970. Comparison of methods for assessing spatial distribution of trees. For. Sci. 16(3): 312—317.
- PERTTUNEN, V., OKSANEN, H. & KANGAS, E. 1970. Aspects of the external and internal factors affecting the olfactory orientation of *Blastophagus piniperda* (Coleoptera, Scolytidae). Contrib. Boyce Thompson Inst. 24: 293—297.
- PIELOU, E. C. 1959. The use of point-to-plant distances in the study of the pattern of plant populations. J. Ecol. 47: 607—613.
- 1977. Mathematical ecology. 385 pp. John Wiley & Sons, New York.
- POHTILA, E. 1980. Havaintoja taimikoiden ja nuorten metsien tilajärjestyksen kehityksestä Lapissa. Summary: Spatial distribution development in young tree stands in Lapland. Commun. Inst. For. Fenn. 98(1): 1—35.
- PULLEY, P. E., FOLTZ, J. L., MAYYASI, A. M. & COULSON, R. N. 1976. Topological mapping to estimate numbers of bark-inhabiting insects. Environ. Ent. 5(4): 640—643.
- REID, R. W. 1963. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the east Kootenay region of British Columbia. III. Interaction between the beetle and its host, with emphasis on brood mortality and survival. Can. Ent. 95(3): 225—238.
- RUDINSKY, J. A. 1969. Masking of the aggregation pheromone in *Dendroctonus pseudotsugae* Hopk. Sci. 166: 884—885.
- , MORGAN, M., LIBBEY, L. M., & MICHAEL, R. R. 1973. Sound production in Scolytidae: 3-methyl-2-cyclohexen-1-one released by the female Douglas fir beetle in response to male sonic signal. Environ. Ent. 2: 505—509.

- SAARENMAA, H. & RÄISÄNEN, H. 1982. Kaar-nakuoriaisnäytteiden otto- ja käsittelyohjeet. 25 pp. Manuscript.
- SAFRANYIK, L. 1971. Some characteristics of the spatial arrangement of attacks by the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), on lodgepole pine. Vithaya-sai, C. Appendix: Statistical analysis of the "hole-pairs" experiment. *Can. Ent.* 103(11): 1607—1625.
- SALONEN, K. 1973. On the life cycle, especially on the reproduction biology of *Blastophagus piniperda* L. (Col., Scolytidae). *Seloste: Pystynävertäjän (Blastophagus piniperda L., Col., Scolytidae) elämäntyyliä, erityisesti sen lisääntymisbiologiasta.* *Acta For. Fenn.* 127: 1—72.
- SCHMITZ, R. F. & RUDINSKY, J. A. 1968. Effect of competition on survival in western Oregon of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae). *Oregon State Univ., School of For., For. Res. Lab., Res. Paper* 8: 1—42.
- SCHÖNHERR, J. 1970. Stridulation einheimischer Borkenkäfer. *Z. ang. Ent.* 65: 309—312.
- 1972. Pheromon beim Kiefern-Borkenkäfer "Waldgärtner", *Myelophilus piniperda* L. (Coleopt., Scolytidae). *Z. ang. Ent.* 71: 410—413.
- SHARPE, P. J., CURRY, G. L., DEMICHELE, D. W. & COLE, C. L. 1977. Distribution model of organism development times. *J. Theor. Biol.* 66: 21—38.
- SHEPHERD, R. F. 1965. Distribution of attacks by *Dendroctonus ponderosae* Hopk. on *Pinus contorta* Dougl. var. *latifolia* Engelm. *Can. Ent.* 97(2): 207—215.
- TAYLOR, L. R., WOIWOD, I. P. & PERRY, J. N. 1978. The density dependence of spatial behaviour and the rarity of randomness. *J. Anim. Ecol.* 47: 383—406.
- THALENHORST, W. 1958. Grundzüge der Populationsdynamik des grossen Fichtenborkenkäfers *Ips typographus* L. *Schriftenr. Forst. Fak. Univ. Göttingen* 21: 1—126.
- TIMONEN, M. 1983. REKO — Regressio- ja korrelaatioanalyysiohjelma. 68 pp. *Metsäntutkimuslaitos, Rovaniemen tutkimusasema.*
- TRÄGÅRDH, I. & BUTOVITSCH, V. 1935. Redogörelse för barkborrekampanjen efter stormhärjningarna 1931—1932. *Medd. Stat. Skogsforskningsanst.* 18: 1—80.
- WAGNER, T. L., FELDMAN, R. M., GAGNE, J. A., COVER, J. D., COULSON, R. N. & SCHOOLFIELD, R. M. 1981. Factors affecting gallery construction, oviposition, and reemergence of *Dendroctonus frontalis* in the laboratory. *Ann. Ent. Soc. Amer.* 74: 255—273.
- , FARGO, W. S., KEELEY, L. L., COULSON, R. N. & COVER, J. D. 1982. Effects of sequential attack on gallery construction, oviposition, and reemergence by *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Can. Ent.* 114(6): 491—502.
- WENSEL, L. C. 1975 a. Computer generation of points on a plane. *Hilgardia* 43: 130—142.
- 1975 b. Treatment of boundary line overlap in a forest sampling simulator. *Hilgardia* 43: 143—159.
- YAMAGUHI, H. & KOIZUMI, C. 1956. Resume: Ecological researches on the Ezo eight-spined engraver, *Ips typographus* L. f. *japonicus* Nijima, with special reference to its reproduction, behavior and dispersal. I. The relationship between the density of egg galleries and the progeny population. *Government. For. Exp. Stat., Hokkaido Stat., Sapporo. Ann. Rep.* 39—47.

Total of 80 references



## SELOSTE

### Pystynävertäjän tilajärjestystä ja lajinsisäistä kilpailua kuvaavia malleja

Pystynävertäjä (*Tomicus piniperda* L.) on eräs pahimmista männyn tuhohyönteisistä maassamme. Lajin aikuiset parveilevat keväällä, iskeytyvät kuorelliseen mäntypuutavaraan ja munivat kaarnan alle. Kesän aikana toukat kehittyvät ja puutavara sinistyy. Syksyllä kuoriutuvat nuoret aikuiset lentävät mäntyjen latvakasvaimiin syöden ne ontoksi, minkä johdosta kasvaimet putoavat maahan ja syntyy kasvatappioita. Edellä kuvattu elinkierto on todellisuudessa kuitenkin hyvin paljon monimutkaisempi varsinkin toukkien kuolleisuuden kannalta. Siihen vaikuttavat puun vastustuskyky, pihkan määrä, emojen iskeytymistiheys, toukkien kilpailu, kilpailevat lajit, pedot, loiset, taudit, sateet. Pohjois-Suomessa, missä tämä tutkimus on tehty, myös lämpötilalla on suuri merkitys. Lopputuloksena on, että pystynävertäjän lisääntymistä on erittäin vaikea ennustaa määrän ja ajan suhteen. Tällaisen tiedon tarve on kuitenkin suuri puutavaran käsittelyn ja torjuntatoimien suunnittelun kannalta. Niinpä on lähdetty kehittämään pystynävertäjän eloonjäämistä ja kehitysnopeutta kuvaavia malleja.

Pystynävertäjän, kuten myös useimpien muiden kaarnakuoriaisten, lisääntymistä rajoittaa merkittävimmin puute sopivasta lisääntymismateriaalista. Tästä seuraa, että toukkien kilpailu ruoasta kaarnan alla on ankaraa ja lajinsisäinen kilpailu on pystynävertäjän tärkein kuolleisuustekijä. Kilpailun seurauksena kuolleet toukat pilaantuvat nopeasti tai ne tulevat syödyiksi, eikä niiden lukumäärää näinollen voi laskea. Populaatiodynamiikan tutkimuksissa tälle kuolleisuudelle on kuitenkin saatava estimaatti, joten ainoaksi mahdollisuudeksi jää mallin laatiminen. Aikaisemmissa tutkimuksissa on havaittu, että pystynävertäjän lisääntymistulokset ovat äärimmäisen vaihtelevia. Malli ei voi siksi perustua vain iskeytymistiheyteen. Voidaan olettaa, että myös emokäytävien tilajärjestyksellä on vaikutuksensa kuolleisuuteen, sillä havaintojen mukaan emokäytävät sijaitsevat usein niin lähekkäin, että niiden välissä kuoriutuvilla toukilla ei ole juuri eloonjäämismahdollisuuksia. Työn tarkoituksena oli kehittää malli, joka kuvaisi pystynävertäjän jälkeläistuotoksen tiheyden ja tilajärjestyksen funktiona.

Aineisto koostui 40 cm mittaisista näytekölkistä, joista 83:een pystynävertäjien annettiin iskeytyä laboratoriossa ja 44:ään maastossa. Pölkkyt oli suojattu kilpailevilta lajeilta, pedoilta ja loisilta. Keskimäärin yksi pölkky sisälsi 26 emokäytävää ja 235 kuoriutumisreikää. Emokäytävät ja kuoriutumisreitit kartoitettiin mittaamalla niiden koordinaatit. Kuoriutumisreikien koordinaatit, jotka mitattiin kaarnan päältä, muunnettiin kaarnan alle (kuvat 1 ja 2). Kun pölkkyt oli tällä tavoin numerisesti kartoitettu voitiin joustavasti soveltaa erilaisia laskentamenetelmiä. Varsinaisen aineiston tukena käytettiin tietokantaa, johon oli 3 vuoden aikana kerätty tietoja noin tuhannesta vastaavanlaisesta pölkystä erilaisissa luonolosuhteissa.

Kuoriutumisreikien määrän todettiin aliarvioivan

todellisen kuoriutuneiden määrän noin 9 %:lla. Virhe lisääntyi kaarnan paksuuden kasvaessa. Korjauskorrointa ei kuitenkaan käytetty, koska vaihtelu oli suurta ja näkymättömiä kuoriutumisreikiä ei olisi voitu käyttää tilajärjestysindeksejä laskettaessa.

Tilajärjestyksen kuvaamiseen on tarjolla lukuisa joukko erilaisia ryhmittymisindeksejä. Näitä tutkittiin soveliaimman löytämiseksi. Tarkempaan tarkasteluun valittiin Cox'in nollaruutudiagrammaan perustuva  $I_c$ , lähimpään naapuriin mitattuihin etäisyyksiin perustuva  $R$  ja satunnaisesta pisteestä lähimpään kohteeseen mitattuun etäisyyteen perustuva  $\alpha$ . Indeksien harhattomuutta erityisesti tilanteessa, jossa on vähän laskentakohteita, tarkasteltiin.  $I_c$  hylättiin siihen todennäköisesti laskennan tuloksena syntyvän systemaattisen harhan takia (kuva 5). Lähin naapuri indeksi  $R$  täytyi myös hylätä, koska se antoi harhattomia tuloksia vasta, kun yli 12 emokäytävää oli pölkkyssä (kuva 5), ja oli tärkeää saada mukaan myös alhaiset tiheydet. Niinpä jatkossa käytettiin vain  $\alpha$ .

Ns. reunavaikutuksen takia  $\alpha$ :an syntyvän systemaattisen virheen välttämiseksi pölkyn päihin rajattiin alue, johon sattuvia pisteitä ei hyväksytty mitausten alkukohdiksi. Tämän alueen leveys oli 0.75 kertaa satunnaisjakauman edellyttämä minimietäisyys kahden kohteen välillä (kuva 4).

Ennen yksityiskohtaista analyysiä aineistoon tehtiin yleisluontoinen katsaus, jossa mm. kaikkien muuttujien normaalisuutta tarkasteltiin. Mitään muunnosta normaalisuuden saavuttamiseksi ei kuitenkaan tehty, koska saatava hyöty oli kyseenalainen. Kaarnan paksuus, sen varianssi ja emokäytäväpituus olivat yhtä suuret laboratorio- ja maastopölkkyissä. Iskeytymistiheys oli maastopölkkyissä huomattavasti suurempi, mutta jälkeläistuotos /m<sup>2</sup> yhtäsuuri. Niinpä lisääntymiskerroin maastossa oli huomattavasti alhaisempi kuin laboratoriossa (taulukko 2). Tämä ei johtunut pelkästään erilaisesta iskeytymistiheydestä, vaan maastossa ilmeisesti sateista ja kylmyydestä johtuva kuolleisuus oli niin suurta, että se peitti lajinsisäisen kilpailun vaikutuksen lähes täysin.

Iskeytymistiheys riippui kaarnan paksuudesta epälineaarisesti kaavan 32—1 mukaan (kuva 6). Teoreettinen maksimi-iskeytymistiheys 279.3 emokäytävää /m<sup>2</sup> saavutettiin kun kaarnan paksuus oli yli 10 mm. Kaarnan paksuuden varianssilla ei ollut siihen mitään vaikutusta.

Iskeytymisten tilajärjestys riippui tiheydestä (kuva 7). Tiheyksissä alle 100 emokäytävää /m<sup>2</sup> se oli ryhmittäinen, 100—200 satunnainen ja yli 200 emokäytävää /m<sup>2</sup> säännöllinen. Yksittäisistä pölkkyistä johtopäätösten teko oli vaikeaa, koska vähäinen emokäytävämäärä piti vapausasteet pieninä. Emokäytävien loppupäätt olivat hieman enemmän ryhmittäisesti jakautuneet kuin alkupäätt. Kuoriutumisreitit olivat erittäin ryhmittäisesti jakautuneet. Niidenkin ryhmittäisyys väheni eksponentiaalisesti iskeytymistiheyden kasvaessa.

Syyksi tilajärjestyksen tiheydestä riippumiseen arveltiin emojen pyrkimys etsiä optimaalisiin lämpötiloihin. Parveilun aikana optimilämpötila vallitsee auringonpaisteessa sijaitsevan pölkyn sivuilla; yläpinnalla on liian lämmintä ja alapinnalla liian kylmää. Ensiksi iskeytyvät kuoriaiset hakeutuvat parhaisiin paikkoihin ja tuloksena on ryhmittäinen tilajärjestys. Näyttää siltä, että Lapissa lämpötilalla on suuri käyttäytymistä ohjaava merkitys, sillä pystynävertäjä ennemminkin ajautuu jonkinasteiseen ylikansoitukseen kuin hakeutuu lisääntymään optimista poikkeaviin lämpötiloihin. Iskeytymisen jatkuessa vähemmän kelvolliset alueetkin kansoitetaan, ja tilajärjestys muuttuu tasaisemmaksi. Iskeytymistiheydellä on tietty yläraja, jota laji ei ylitä kuin satunnaisesti. Se sijainnee noin 300 emokäytävää /m<sup>2</sup> tiheydessä. Tämä kattotiheys on luultavasti saman mekanismin aikaansaama kuin säännöllinen tilajärjestys. Säännöllinen tilajärjestys on näinollen eräs tärkeä takaisinkytkentämekanismi populaation säätelyssä.

Emokäytäväpituus väheni lineaarisesti iskeytymistiheyden lisääntyessä (kaava 33—1, kuva 8).

Munakuopat olivat jakautuneet tasaisesti munakuopparyhmän sisällä, mutta koska ryhmien välillä oli pidempiä välejä kokonaan ilman munakuoppia, munakuoppien tilajärjestys koko emokäytävän puitteissa oli ryhmittäinen. Keskimääräinen välimatka kahden munakuopan välillä oli 2.63 mm; se lisääntyi hitaasti emokäytävän loppua kohti. Vain 87.3 % munakuopista sisälsi munan. Tämä suhde on riippuvainen havaittujen tulosten tulkinnasta: onko syventymä emokäytävässä todella munakuoppa? Munakuoppien tilajärjestyksellä arveltiin olevan vaikutusta puun pihkanerityksen voittamiseen ja toukkien keskinäiseen kilpailuun nuorella iällä. Munien määrä /emokäytävä väheni iskeytymistiheyden lisääntyessä. Tämä riippuvuus voitiin parhaiten kuvata eksponentiaalisen vähenemisen mallilla (33—2), mutta myös lineaarinen malli (33—3) toimi tyydyttävästi (kuva 10).

Toukkien eloonjääminen oli käänteisesti riippuvainen iskeytymistiheydestä (kuva 11). Tämä riippuvuus voitiin kuvata lähes yhtä hyvin eksponentiaalisen vähenemisen mallilla, yksinkertaisella lineaarisella mallilla ja simulointimallilla. Tilajärjestyksen vaikutusta eloonjäämistodennäköisyyteen ei kuitenkaan tutkittu yksityiskohtaisesti, koska eloonjäämistodennäköisyys oli suurimmassa osassa aineistoa estimoitu keskimääräisestä munamäärästä.

Maastopöleissä eloonjääminen ei riippunut iskeytymistiheydestä. Tämä tulos oli yllättävä, koska laboratoriossa riippuvuus oli tilastollisesti erittäin merkitsevä. Syiksi arveltiin, että maastosta kerättyssä aineistossa alhaiset tiheydet, joissa riippuvuus olisi ollut selvän, puuttuivat. Lisäksi todennäköisesti saateet ja kosteus lisäävät kuolleisuutta varsinkin alhaisissa tiheyksissä, koska nämä pölköt sijaitsivat voimakkaamman varjostuksessa kuin pölköt, joissa oli suuri tiheys.

Lisääntymiskertoimen (kuva 14) ja jälkeläistuotoksen /m<sup>2</sup> (kuva 16) ennustamiseen ja selittämiseen kokeiltiin viittä eri mallia. Ensiksi selittäjä oli pelkkä iskeytymistiheys. Munatiheysmallista ja eloonjäämismallista johdettu eksponentiaalinen malli (352—2 ja 353—2) oli hieman parempi kuin lisääntymiskerrointa kuvaava logaritminen malli (352—3) ja jälkeläistuotosta kuvaava paraboloiden malli (353—3). Jälkimmäisten yksinkertaisuus

oli kuitenkin siksi suuri etu, että niitä käytettiin jatkossa. Iskeytymistiheys selitti 43 % lisääntymiskertoimen varianssista ja 64 % jälkeläistuotoksen varianssista. Kaikki mallit olivat varianssin ja keskiarvon korrelaatiosta huolimatta harhattomia. Selittämätön vaihtelu oli kuitenkin siksi suurta, että näitä malleja ei suositeltu käytettäväksi.

Tämän jälkeen malleihin lisättiin selittäjäksi iskeytymisreikien, emokäytävien keskipisteiden ja kuoriutumisreikien tilajärjestyksestä kuvaava ryhmittymisindeksi  $\alpha$ . Hypoteesina oli, että jos tilajärjestys vaikuttaa jälkeläisten määrään,  $\alpha$  aiheuttaisi merkitsevän lisäyksen selityksasteeseen. Multikollineaarisuuden poistamisesta huolehdittiin nk. ridge regressio-tekniikalla.  $\alpha$ :n lisääminen malleihin ei tuottanut juuri mitään tulosta (taulukko 10). Tämä johtui osaksi siitä, että ne pölköt, joissa vaikutus olisi ollut selvän, jouduttiin vähäisen emokäytävämäärän vuoksi poistamaan aineistosta. Malli, jossa selittäjinä olivat keskimääräiset etäisyydet neljään lähimpään emokäytävään antoi parhaat tulokset maastopölkkyissä, mutta ei toiminut tyydyttävästi laboratoriopölkkyissä (taulukko 11).

Paras tutkituista malleista oli toisessa yhteydessä (Jong ja Saarenmaa 1984) kehitetty simulointimalli, joka perustuu toukkien kuolleisuuteen niiden liikkumisprosessin tuloksena. Tämä malli selitti 58 % lisääntymiskertoimen (kuva 15) ja 70 % jälkeläistuotoksen (kuva 17) varianssista. Simulointimalli osoittautui vertailussa muutenkin laajimmin käyttökelpoiseksi, koska sillä voidaan saada välituloksia kehityksen eri vaiheista ja jos sen perushypoteesit ovat oikeat, sitä voidaan soveltaa myös alkuperäisen aineiston ulkopuolella (vrt. kuva 18). Toisin kuin regressiomallit simulointimalli voi ottaa myös dynaamisesti huomioon muiden kuolleisuustekijöiden vaikutukset, kun ne saadaan sisällytettyä malliin.

Tilajärjestyksen vaikutus kuolleisuuteen arvioitiin vertailemalla tuloksia niistä malleista, jotka eivät käytä informaatiota tilajärjestyksestä sellaisiin malleihin, jotka tätä informaatiota käyttävät. Tämä vertailu ei ole aivan yksinkertaista, koska mallin joustavuus vaikuttaa myös tulokseen. Lisääntymiskertoimen vaihtelu oli suurinta alhaisissa tiheyksissä, jälkeläistuotoksen taas suurissa tiheyksissä. Jälkimmäiselle tehdyissä malleissa eroa tilajärjestyksen huomioiden mallien hyväksi ei juuri tullut. Sen sijaan lisääntymiskertoimelle tehdyissä malleissa ero oli selvempi. Tästä pääteltiin, että alhaisissa tiheyksissä tilajärjestys selittää noin 15 % lisääntymiskertoimen varianssista, mutta suurissa tiheyksissä tilajärjestyksen vaikutus vähittäin lakkaa tuntumasta. Tämä johtuu siitä, että suurissa tiheyksissä kilpailua on joka tapauksessa niin paljon, että sen paikalliset vaihtelut peittyvät. Tähän suuntaan vaikuttaa myös iskeytymien tasaisuuden lisääntyminen tiheyden myötä. Tilajärjestyksen vaikutusta tutkittiin myös simulointimallin avulla asettamalla kaikkien pölkkyjen emokäytävät uuteen, optimaaliseen säännölliseen tilajärjestykseen. Tulos (kuva 19) osoitti, että erityisesti keskitiheyksissä pystynävertäjän lisääntymistulos voisi olla parempi, jos tilajärjestys olisi tasaisempi, mutta suurissa tiheyksissä vallitseva järjestys on kutakuinkin paras mahdollinen.

SAARENMAA, H. 1983. Modeling the spatial pattern and intraspecific competition in *Tomiscus piniperda* (Coleoptera, Scolytidae). Seloste: Pystynävertäjän tilajärjestyksestä ja lajinsisäistä kilpailua kuvaavia malleja. Commun. Inst. For. Fenn. 118:1—40.

ODC 145.7×19.92 *Tomiscus piniperda* +152--015.5+453  
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The spatial pattern of *Tomiscus piniperda* was studied during its developmental period, the emphasis being on the effects of density and spatial pattern on the reproduction and intraspecific competition. The main goal was to develop models for life-table studies in order to explain the mortality and subsequent disappearance of larvae due to intraspecific competition.

The aggregation of the egg galleries was dependent on density. At densities below 100 egg galleries/m<sup>2</sup> the spatial pattern was clumped, above 200 egg galleries/m<sup>2</sup> regular, and in the intermediate densities random. A mechanistic simulation model, which accounted for the effect of spatial pattern, was considered superior to the regression models in describing the effects of intraspecific competition.

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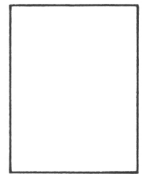
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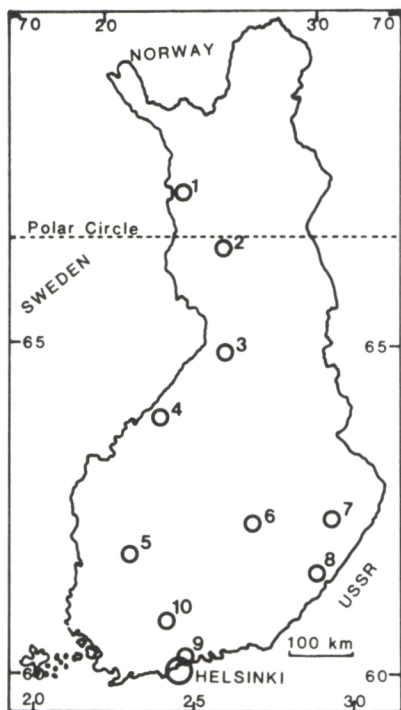
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## FACTS ABOUT FINLAND

Total land area: 304 642 km<sup>2</sup> of which 60—70 per cent is forest land.

Mean temperature, °C:	Helsinki	Joensuu	Rovaniemi
January	-6,8	-10,2	-11,0
July	17,1	17,1	15,3
annual	4,4	2,9	0,8

Thermal winter (mean temp. < 0°C):	20.11.—4.4.	5.11.—10.4.	18.10.—21.4.

Most common tree species: *Pinus sylvestris*, *Picea abies*, *Betula pendula*, *Betula pubescens*





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