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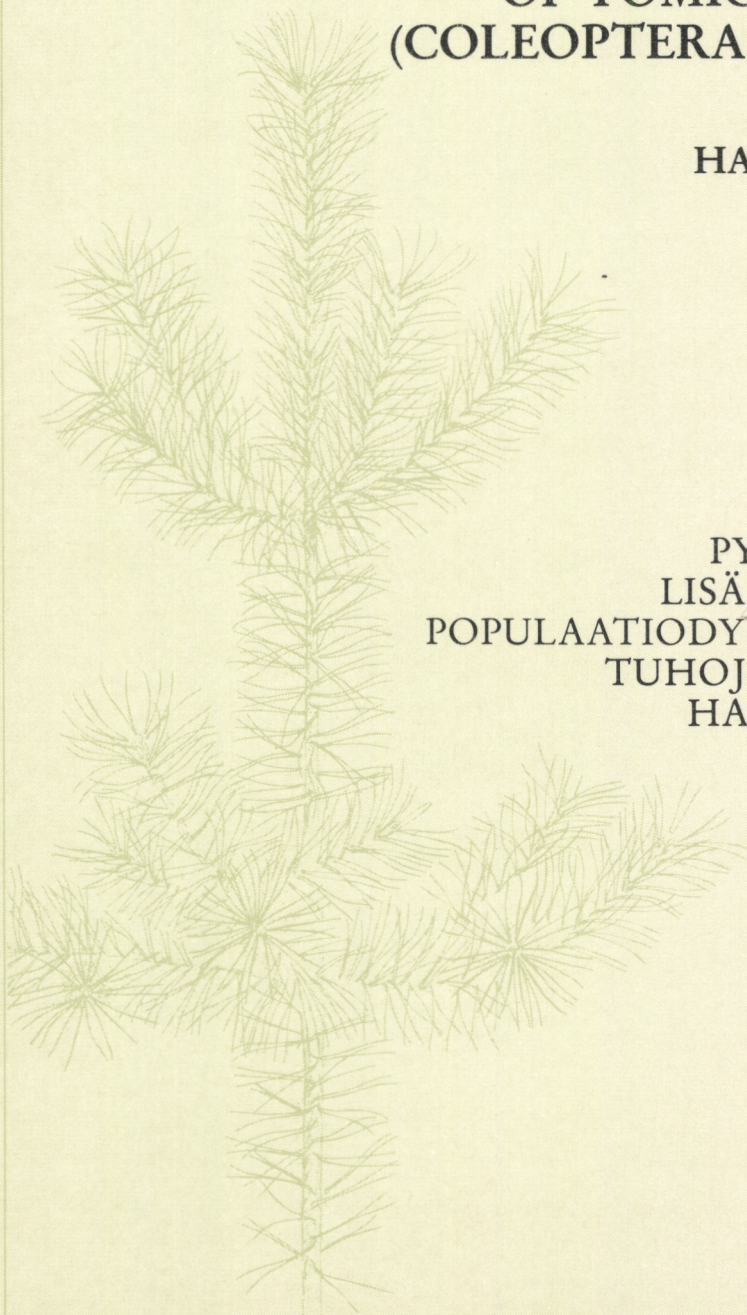
WITHIN-TREE POPULATION DYNAMICS  
MODELS FOR INTEGRATED MANAGEMENT  
OF TOMICUS PINIPERDA  
(COLEOPTERA, SCOLYTIDAE)

HANNU SAARENMAA

SELOSTE

PYSTYNÄVERTÄJÄN  
LISÄÄNTYMISKAUDEN  
POPULAATIODYNAMIIKKAMALLIT  
TUHOJEN INTEGROITUA  
HALLINTAA VARTEN

HELSINKI 1985



# COMMUNICACIONES INSTITUTI FORESTALIS FENNIAE



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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 mil. 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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Within-tree dynamics of *T. piniperda* are reviewed and subsystems for 1) arrival of the parent beetles, 2) oviposition, 3) reemergence, 4) development and emergence, and 5) survival are identified. Non-linear models are constructed for these. While the arrival submodel uses air temperature, the other submodels are driven by physiological time being based on the absolute reaction rate theory. Besides temperature, another denominator in the submodels is attack density. A dynamic biophysical model predicting the timing and frequency of emergence is constructed by integrating the submodels.

Most of the submodels have been developed using laboratory materials at constant temperatures, and by then validating the models against field data. For this purpose, a large hierarchical data base on the development and survival of pine bark beetles in Lapland was gathered by successive sampling, and at the same time, temperatures were measured at hourly intervals in all the sampling habitats. The data revealed that, in Lapland, *T. piniperda* is suppressed by frequent climatic disturbances rather than by regulatory mechanisms. Cumulative physiological time that was a function of temperature explained these changes satisfactorily, but there was an indication that rainfall may also affect development.

The within-tree population dynamics model is tied into the scheme of IPM. Taking the decision making of the forest manager as the focal point, an outline of bark beetle IPM relying on expert systems and on the total information structure of the forest sector is discussed.

Tutkimuksen tarkoituksena oli kehittää simulointimalli, jonka avulla pystynävertäjän kuoriutumisen ajoittuminen ja määrä pystytään ennustamaan ja jota voidaan käyttää integroidun tuhojen hallinnan päätöksenteon tukena.

Pystynävertäjän lisääntymiskauden populaatiodynamiikka eriteltiin viiteen vaiheeseen: 1) emojen saapuminen puutavaraan, 2) muninta, 3) emojen poistuminen, 4) jälkeläisten kehittyminen ja kuoriutuminen sekä 5) kuolleisuus. Näille muotoiltiin epälineaariset regressiomallit. Emojen saapumisen ajoittuminen riippui ilman lämpötilasta, mutta muita malleja sääтели kaarnan alla vallitsevasta lämpötilasta epälineaarisesti riippuva fysiologisen ajan kumuloituminen. Toinen tärkeäksi osoittautunut tekijä malleissa oli iskeytymistiheys. Osamallit yhdistämällä konstruotoitiin dynaaminen biofyysinen malli koko lisääntymiskauden dynamiikalle.

Useimmat malleista kehitettiin laboratoriokeiden avulla vakioilämpötiloissa, minkä jälkeen mallit testattiin maastoaineistoihin. Tätä varten oli kerätty laaja hierarkkisesti organisoitu tietokanta männyn kaarnakuoriaisten kehitymisestä ja kuolleisuudesta Lapissa. Näytteet kerättiin aikasarjoina, joihin liittyvät tunneittain automaattisesti mitatut lämpötilat. Aineistosta ilmeni, että Lapissa pystynävertäjäkantoja hillitsee enemmän ilmaston epäsuotuisuus kuin säätelevät tekijät. Lämpötilasta riippuva fysiologinen aika selitti kannan vaihtelut tyydyttävästi, mutta myös sateen vaikutuksesta saatiin viitteitä.

Populaatiodynamiikkamallin osuutta integroidussa tuhojen hallinnassa tarkasteltiin ja käytännön päätöksenteon ongelmien ratkaisuksi esitettiin tietokonepohjaista asiantuntijajärjestelmää.

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## PREFACE

Many people have been involved in the project the results of which are summarized in this paper. Having started in the fall of 1980 and ending a mere week ago, the laborious processing of the field samples during the years has been carried out by Matti Ahonen, Anne Immonen, Harri Kesäniemi, Matti Kinnunen, Jaakko Laukka, Ari Nikula, Vesa Nivala, Risto Ollikainen, Hannu Räisänen, Jari Saajo, Sirkka Savonmäki, Juha Siitonen, and Pentti Vitikka. In addition, Ulla Alastalo, Martta Autto, Anne-Mari Ekström, Jaakko Paajanen, and Helmi Saunavaara have been responsible for laboratory procedures and care of the field experiments. Managing of the project would not have been possible without the coordination and supervision of Hannu Räisänen in the laboratory and in the

field. In computing, Erkki Kaila, Markku Taipale, and Carl-Gustav Snellman have been very helpful, and Salme Särestöniemi and Raija Vainio have patiently typed all the data into the machine. Richard Foley checked the language. I wish to express my sincerest thanks to all these persons. The encouragement of professor Paavo Juutinen during the work and the comments of professor Matti Nuorteva and Drs. Erkki Annila, Bo Långström and Veikko I. Pajunen on the manuscript are also gratefully acknowledged.

Rovaniemi, March 18th, 1985

*Hannu Saarenmaa*

# 1. INTRODUCTION

The common pine shoot beetle, *Tomicus piniperda* L., is the primary bark beetle pest on pine in Finland. The beetle causes growth losses to pines due to its shoot feeding (e.g. Långström 1980a, 1980b, 1983) and may sometimes even kill living, weak, or stressed trees (e.g. Kangas 1934a, Räisänen et al. 1985). The significance of the damage is apparent, but no attempts at quantifying it have been made in Finland. In Sweden, an annual growth loss from 2.1 to 5.9 million cubic meters of wood due to pine shoot beetles has been estimated (Skogsskyddsutredningen 1978).

So far, almost all control of *T. piniperda* has been silvicultural and more or less unplanned. Avoiding of storage of fresh unbarked pine timber in the forest through a correct timber transport scheduling has been the major strategy. However, the huge growth losses point out that management is not totally successful; the pest is not below economically tolerable levels. However, the present organizational state of our knowledge permits no alternative management strategies.

From an ecological point of view it can be stated that such effective consumers as *T. piniperda* have their ecological roles in the forest ecosystem, and that they cannot be eradicated, i.e., the forest can tolerate growth losses. This point of view notwithstanding, there are even more disruptive consequences in the systems of man: the decision making of forest managers has become very complicated since the impact of forestry operations on pest populations and eventually on forest resources have not been quantified. While pest management requires monetary investments, its benefits are not known. It becomes apparent that we need a system that supports decision making in the management of *T. piniperda*. Such a system can only be based on the concept of integrated pest management (IPM).

## 11. Integrated management for *Tomicus piniperda*

Two parallel concepts of integrated management of forest insects seem to exist (cf. Safranyik 1981). One, which may be called ecological pest control, emphasizes the use of many simultaneous regulating agents of pest populations: augmentation of natural enemies, silvicultural preventive measures, etc. The approach arises from the philosophy of enlarging the balancing inertia of the natural forest ecosystem. The other approach is based on systems theory and integrates pest management with total forest management and operations (Waters and Cowling 1976, Coster 1980, Safranyik 1981, Coulson and Witter 1984) and uses simulation for decision making (Berryman and Pienaar 1974). This direction has not reached operational status except in recent years (Waters and Stark 1980, Coulson and Witter 1984, Rykiel et al. 1984). For the present forestry community of Finland only the latter approach is feasible because only it can be a solution for the main problem: enhanced decision making.

Before the rise of the computer age in the 1980's, it was not possible to build an operational IPM system for forest pests (cf. Waters and Stark 1980). That is due to the fact that when decision making is the focal point, IPM largely is equivalent to an operational computerized system transferring applicable knowledge from research to practice. As a framework for the system, there must be a total information system where the IPM decision support system should reside and be readily accessible for the end user, who usually is a forest manager and not a pest management specialist. Otherwise it is doubtful whether the system will gain users. A total information system of forestry is now under construction in Finland (see Kaila 1985a). The progress in decision support

systems within IPM (Rykiel et al. 1984) and the recent boom of expert systems supported by artificial intelligence (e.g. Hayes-Roth et al. 1983, Kinnucan 1984) give new tools for implementing an IPM system and for technology transfer from research to practice.

The elements of the suggested IPM system for *T. piniperda* (Fig 1) are essentially the same as those adopted for the other IPM projects on forest insects (Waters and Stark 1980). If we take a constructive point of view, a new addition is the control and dialogue maintenance system (see Rykiel et al. 1984). That is a decision support system or expert system containing the heuristic knowledge of the field in such a form that it can operate the models and discuss with the end user, who can invoke the system among other applications in a menu (see Saarenmaa 1985a). The elements of the system are models describing 1) population dynamics of the pest, 2) treatment tactics, 3) pest/forest impacts, and 4) cost/benefit integration. The stand dynamics component, which was in the original scheme (Waters and Cowling 1976), has been removed from the picture in order to reduce the complexity of the system (as by Williams and Shea 1982), and because it will be available in other applications utilizing the stand database. Originally, the model block (Fig 1) was called "research and development core". This is still the case, but after successful implementation, these items become equivalent. The decision support system for IPM can stand alone, but its efficacy can be greatly enhanced if there are on-line databases for forest stands, forestry operations (timber transport particularly), and weather.

The knowledge base required for the IPM system is great, but largely existent. Sufficient knowledge about stand dynamics (e.g. Pukkala 1984, Kilkki et al. 1984) and treatment tactics (e.g. Ehnström 1976, Långström and Lekander 1976, Dehlén and Långström 1977, Annala & Petäistö 1978, Heikkilä 1978, Löyttyniemi and Uusvaara 1977, Uusvaara and Löyttyniemi 1977, Långström 1979, Dehlén et al. 1982, Lilja 1982, Saarenmaa 1984, Räisänen et al. 1985) are already available. Impact models (Nilsson 1974, Bosatta et al. 1975, Fagerström et al. 1978, Långström 1980a, 1980c, Elfving and Långström 1980, 1984) require much additional work. Cost/benefit integration is

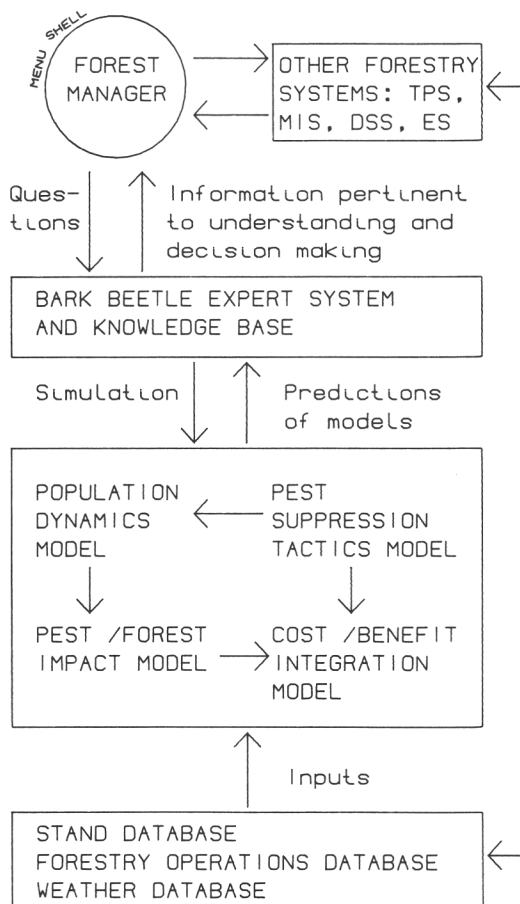


Fig 1. Elements of the suggested integrated pest management system of *Tomicus piniperda*. TPS = transaction processing system, MIS = management information system, DSS = decision support system, and ES = expert system (Rykiel et al. 1984, Saarenmaa 1985a).

non-existent, but can be derived from the other components. Our knowledge about the population dynamics of *T. piniperda* is quite good for making decisions according to rules of thumb, but unfortunately, it is largely useless for quantitative modeling. Therefore, this study has been done.

## 12. Population dynamics of *Tomicus piniperda*

Understanding of the survival mechanisms of a pest is naturally the basis of any management strategy (Coulson and Stark 1982).

Consequently, the biology of *Tomicus piniperda* has been studied on many occasions, most recently by Byers et al. (1985), Jong and Saarenmaa (1985), Saarenmaa (1985b, 1983), Hellqvist (1984), Lekander (1984), Långström (1984, 1983, 1980b), Långström et al. (1984), Nilssen (1978), Galaseva (1976), Beaver (1974), Salonen (1973), Bakke (1968), Eidmann and Nuorteva (1968), and Kangas et al. (1967a, 1967b). The foundation on which the present study relies has been established in the three monographies on *T. piniperda* in Fennoscandia (Bakke 1968, Salonen 1973, Långström 1980b). These sources also give full references to earlier research. Furthermore, two more sources of ideas must be acknowledged: Berryman (1974) and Raffa and Berryman (1983) created a general theory about the effects of density and host resistance on the productivity of bark beetles. On the other hand, the time and temperature factors in the life processes of the southern pine beetle (*Dendroctonus frontalis* Zimmermann) have recently been explored in such a depth (Coulson 1979, Feldman et al. 1981a, 1981b, Wagner et al. 1984a) that the methods are applicable here too.

In this chapter I will review the life cycle of the species from the systems point of view, i.e., by considering the functional responses at each life cycle event. These functional responses are the primary targets in modeling the population dynamics.

In the spring, when the snow has melted around the hibernating sites of *T. piniperda* in the bases of trees and air temperatures first reach 10 to 12°C, swarming begins (Bakke 1968, Salonen 1973, Eidmann 1974). Main swarming occurs during only a few days when maximum air temperature rises up to 14–16°C, and thereafter, only occasional delayers can be observed. The swarming rate thus seems to be a function of the prevailing air temperature above a certain threshold and the sum of these temperatures:

$$\text{SWARMING RATE} = f(\text{AIR TEMPERATURE} > \text{THRESHOLD}, \text{SUM OF AIR TEMPERATURES} > \text{THRESHOLD}) \quad (1)$$

The attack rate of *T. piniperda* on a given piece of breeding material is, of course, a function of swarming rate, but also dependent on a huge array of other factors that are not fully understood. Generally, it is de-

pendent on the size of the local beetle population composed of dispersing beetles originating from a distribution of distances (Johnson and Coster 1978, Gries 1985). The swarming beetles require flight exercise before they react positively to host odors (Kangas et al. 1967a, 1967b). Allocation of the beetles to the breeding material is determined by the physical properties (including accessibility) and suitability of potential hosts (Berryman 1974, 1979). Obviously, the beetles are able to determine the suitability of a host as breeding material. Host selection of *T. piniperda* has been shown to depend heavily on primary attraction by the host volatiles, particularly on (+)- and (—)-alfa-pinene, (+)-3-carene, terpineole, and trans- and cis- carvoneols, but some controversy has arisen as to whether and when certain compounds are attractive or repellent (cf. Kangas et al. 1971, Byers et al. 1985). No aggregation pheromones have been found in *T. piniperda* (Byers et al. 1985), but there are indications of a possible sexual pheromone (Kangas et al. 1971) excreted by the females that initiate the gallery excavation. Odor composition of pine timber changes rapidly due to evaporation and oxidation of compounds changing the suitability of the host. The suitability of a host as breeding material decreases also when it already has been populated. Eventually, a mechanism that shuts off aggregation operates in *T. piniperda*. There is evidence that the stridulation of males during aggregation acts to this end (Nilssen 1978, Saarenmaa 1983), but it is also noteworthy that the evaporation of 3-carene peaks at this time (Lanne et al. 1984). In summary,

$$\text{ATTACK RATE} = f(\text{SWARMING RATE}, \text{LOCAL BEETLE POPULATION}, \text{ATTACK DENSITY}, \text{PHYSICAL PROPERTIES OF THE HOST}, \text{SUITABILITY OF THE HOST}) \quad (2)$$

After a successful attack, reproduction begins. Eggs are laid in niches along the maternal gallery during the excavation. Final egg gallery length and the number of eggs per female have been found to be inversely related to attack density (Nuorteva 1954, 1964, Eidmann and Nuorteva 1968, Salonen 1973, Annala and Petäistö 1978, Saarenmaa 1983). Oviposition rate is dependent on the temperature under the bark; in field

conditions the oviposition period lasts from two to four weeks (Bakke 1968, Salonen 1973). The length of the initial egg-free gallery is inversely related to temperature (Salonen 1973). On the individual level, the oviposition rate slows down in physiological time because the distances between the successive egg niches increase towards the end of egg gallery (Saarenmaa 1983). On the population level, the oviposition rate also decreases when females finish their tasks and reemerge. In some bark beetles, where the functional responses of oviposition have been studied in more detail, its rate has been found to depend also on phloem thickness (Amman and Cole 1983 on *Dendroctonus ponderosae* Hopkins; Haack et al. 1984 on *Ips calligraphus* Germar), and physical and chemical changes in the host (Wagner et al. 1981, 1982 on *D. frontalis*). The following function summarizes the responses above:

$$\text{OVIPOSITION RATE} = f(\text{TEMPERATURE, PHYSIOLOGICAL TIME, ATTACK DENSITY, PHLOEM THICKNESS, PHYSICAL AND CHEMICAL CHANGES IN HOST})(3)$$

When the eggs have been laid, the parent beetles either die or reemerge. The reemerging beetles either fly to the crowns of pines to feed in the shoots or occasionally establish sister broods (Långström 1980b, 1983). Since high attack density prematurely terminates oviposition, the reemergence rate is its variate. Clearly the reemergence rate of a pine shoot beetle population is also a function of temperature and physiological time:

$$\text{REEMERGENCE RATE} = f(\text{TEMPERATURE, PHYSIOLOGICAL TIME, ATTACK DENSITY})(4)$$

The eggs develop into larvae, pupae, callow adults and finally the new insects emerge, unless they have died. Thus, there are two processes active through the rest of the developmental period: development and survival.

Development of poikilotherms has been studied to a great extent since the beginning of the science, and most of the resulting theories and models are more or less applicable also to the present problem. The theories have been reviewed recently by Sharpe and DeMichele (1977), Sharpe et al. (1977), and Wagner et al. (1984b, 1984c). From

these sources it is clear that the "absolute reaction rate" theory is the most suitable for describing the development and physiological time in *T. piniperda* too. This superiority rises from the solid theoretical background of the theory, from its predictive capability, and from the fact that it has been applied successfully in the modeling of the life system of another destructive bark beetle, *Dendroctonus frontalis* (Feldman et al. 1981a, 1981b, Wagner et al. 1984a). The model describes the developmental rate and its variation as a function of temperature.

Are there factors other than temperature — besides mortality that affects the population mean rates — that might affect the developmental rate of the individual larvae? Nutrition of larvae affects their growth and survival, but the nutritional requirements of *T. piniperda* are poorly known. Among bark beetles there are absolute fungivores and phloem-eaters. *T. piniperda*, as all bark beetles, is a vector of several species of blue stain fungi (Käärik 1975). Whether the larvae gain any benefit from them is unknown. Growth and development are not synonymous, although in the long term there is no development without growth. If there is any interaction between these, it is likely to manifest itself in *T. piniperda*, whose larvae regularly suffer from malnutrition due to competition. Thus, we can put forward a model of developmental rate dependent on temperature and on a tentative nutritional component:

$$\text{DEVELOPMENTAL RATE} = f(\text{TEMPERATURE, NUTRITION})(5)$$

Physiological time in *T. piniperda* can be defined as an integral of function (5). For each developmental stage there exists an average physiological transition time which should be constant:

$$\text{TRANSITION TIME (STAGE)} = \text{CONSTANT PHYSIOLOGICAL TIME}(6)$$

These are important from the point of view of systems modeling, in particular when predicting the timing of emergence. Emergence starts about two months after swarming and continues through the rest of the season. This is strongly dependent on temperature and consequently on the latitude (Bakke 1968, Salonen 1973, Långström et al. 1984, Saarenmaa 1985b).

Predicting the production of bark beetles has been very complicated due to the great variation in their breeding results. Even in controlled experiments with *T. piniperda*, beetle production has varied from 1000 to 6000 /m<sup>2</sup> at the same density (Eidmann and Nuorteva 1968, Saarenmaa 1983). In the wild, numbers higher than 2000 /m<sup>2</sup> are very seldom reached although Hanson (1937) reports even 3500 /m<sup>2</sup>. These differences are due to variation in survival.

Bark beetle broods are killed by predators (e.g. Nuorteva 1956b), parasites (Nuorteva 1957, Hedqvist 1963), diseases (Moore 1972, Führer and Purrini 1981), resinosis (Berryman and Ashraf 1970, Raffa and Berryman 1983), interspecific competition (Nuorteva 1962, Coulson et al. 1976a) and intraspecific competition (Nuorteva 1954, 1964, Eidmann and Nuorteva 1968, Beaver 1974, Saarenmaa 1983, Jong and Saarenmaa 1985), drought, heat, moisture (Annala 1969, Safranyik et al. 1975, Webb and Franklin 1978), and frosts (Kangas 1953, Safranyik 1978, Saarenmaa 1985b). The literature is too extensive to be included here; those mentioned above are just examples to get started with. Good reviews on the subject have been made by Nuorteva (1956b), Thalenhorst (1958), and recently by Berisford (1980), Dahlsten (1982), and Amman and Cole (1983). With the exception of vertebrate predators and climatic disasters, survival processes of the species are affected by temperature in the same manner as development. Physiological time is also important since many of the mortality agents have their characteristic arrival patterns. From the systems modeling point of view, we should determine for each mortality agent whether its functional response to *T. piniperda* is dependent on density, age, and/or time, how it interacts with other factors, and how great its absolute significance at each life stage of the host insect is. The relative age (or stage) of a larva is also important, since Jong and Saarenmaa (1985) simulated that the first hatching larvae have about double probability to survive intraspecific competition than their late

hatching siblings. In this context no attempt is made to extract the effects of individual mortality agents; the generalized brood survival rate (cf. Cole 1981) can be expressed:

$$\text{SURVIVAL RATE} = f(\text{TEMPERATURE, PHYSIOLOGICAL TIME, ATTACK DENSITY, STAGE}) \quad (7)$$

Young adults surviving to emergence fly to the crowns of pines for shoot-feeding (Långström 1980a, 1980b, 1983) and join the reemerged adults to form a population that moves to hibernating sites in the bases of trees after the first autumn frosts. Shoot feeding and overwintering beetles are subject to mortality that can be considerable (Butovitsch 1925, Trägårdh and Butovitsch 1935, Salonen 1973).

From the description of the life cycle above, it should be apparent that the basic biology of the species is relatively well-known. Which deficiencies in our knowledge require further studies? Scientifically, dispersal, larval nutrition, and the effects and functional responses of mortality factors are the weak points. Surprisingly, the effect of temperature has not been formulated in a way that would have any use in pest management. From the point of view of knowledge engineering, the present large knowledge is unwieldy, requiring refinement of the rules and facts, quantitative modeling, and integration.

In 1980, The Finnish Forest Research Institute started a project at the Rovaniemi Research Station with the goal of acquiring a data base of the population dynamics of *T. piniperda* that makes modeling possible. The study was designed to be carried out in the north, because in extreme conditions the crucial effects of climate were easiest to establish.

The objective of this study is to construct a within-tree population dynamics model for *T. piniperda* piecewise and integrate the parts into a functioning model that predicts the timing and frequency of emergence, and that can readily be used as a part of an IPM system.

## 2. MATERIAL AND METHODS

Three different types of materials were used in this study: 1) data on laboratory rearings of *Tomicus piniperda*, 2) data on successive sampling of field populations of bark beetles, and 3) weather data related to these two data sets. The general procedure used throughout the study was first to develop the models in the laboratory and then test them in the field. This kind of approach was chosen because it gives maximum applicability of results. If a model is being developed in very different conditions from where it is being (successfully) tested, it has been validated as effectively as possible (Feldman et al. 1981b). Survival, however, cannot be modeled in the laboratory, except for one mortality agent one at a time, since it is practically impossible to assemble the total mortality factor array there.

### 21. Constant temperature rearings in the laboratory

#### 211. Entire developmental period

Beetles were reared at constant temperatures to obtain knowledge about the suitability of the standard degree day concept and to acquire a species-specific developmental rate equation. A total of 44 freshly-cut 0.4 m long pine bolts were placed in plywood cages in six phytotrones in the spring of 1980 and 1981. Parent beetles were collected during swarming in a sawmill and introduced freely into the cages. Emergence was monitored daily by collecting the reared young beetles from glass pots in the walls of the cages.

The constant temperatures prevailing in the cages were measured under the bark 1 to 4 times per day. The temperature regime within a phytotrone was not exactly uniform but ranged within 2°C, because of the location of the cooling and heating units at the bottom. Hence, an almost continuous series of temperatures from 8.2 to 30.1°C was obtained. Table 1 gives data of the material in this experiment. Standard deviations around the "constant" temperatures are less than 1.0°C except for two malfunctioning phytotrones with 12 bolts. Because these are at the middle temperatures where the temperature-response of the beetle is linear, they can be tolerated. Relative air humidity in the phytotrone was set to 70 % but was not monitored.

Median dates have been used throughout this study despite the recommendation that average and

Table 1. Data on the rearings of *Tomicus piniperda* in bolts at constant temperatures. Survival percent is an estimate and based on the mean number of eggs per female 63.6 (Saarenmaa 1983).

Constant temperature (°C)	s.d.	Median development time (days)	Attack density /m <sup>2</sup>	Survival (%)	Number of young beetles emerging in the bolt
8.2	0.56	—	51	0.0	0
8.6	0.31	—	178	0.0	0
9.9	0.27	202	67	17.2	122
9.9	0.27	235	57	2.7	9
10.1	0.48	207	32	14.7	28
10.7	0.47	167	65	36.7	303
10.7	0.47	172	116	17.4	208
11.6	0.46	131	138	28.2	448
11.9	0.44	134	202	28.0	498
14.5	1.03	99	—	39.4	221
15.7	1.03	75	150	16.0	183
17.6	1.06	66	153	34.9	444
17.6	1.06	55	55	42.2	457
18.5	1.28	50	98	33.8	645
18.5	1.28	53	81	40.1	255
18.5	1.28	51	41	40.4	154
19.5	0.75	48	90	52.6	352
19.6	0.95	50	161	44.6	520
19.6	0.82	51	87	44.6	214
19.7	0.88	48	175	30.9	304
19.9	0.68	46	65	80.2	250
20.1	0.67	50	72	30.3	164
20.3	0.99	45	330	26.6	848
23.2	1.83	38	115	28.1	644
23.2	1.83	38	199	34.3	305
23.2	1.83	39	96	42.6	433
23.2	1.83	38	172	42.6	325
23.5	1.99	37	125	47.8	547
24.1	0.40	35	123	41.3	394
24.1	0.40	35	251	34.9	333
24.5	0.69	34	122	52.0	430
24.5	0.69	33	141	85.7	763
24.5	0.69	35	114	41.8	452
26.9	0.40	30	348	19.6	471
27.5	0.31	32	124	40.5	219
28.0	0.29	31	203	8.1	129
28.0	0.36	32	102	23.9	166
28.1	0.27	33	95	33.5	225
28.6	0.38	33	164	27.7	247
29.0	0.77	34	78	16.5	82
29.3	0.32	31	195	4.0	155
29.7	0.30	29	159	3.1	33
29.8	0.29	35	—	2.5	29
30.1	0.45	32	213	2.8	125

standard deviations be used (Shaffer 1983). This has been done purposely to obtain consistency with the field measurements for which average times cannot be always calculated, and because of the strong skew in the emergence distributions.

### 212. Oviposition experiment

Another experiment where the functional responses of oviposition of *T. piniperda* were studied was carried out in the laboratory in spring 1984. A total of 528 freshly-cut randomized sample bolts, averaging 0.1 m in length and 0.14 m in diameter, were placed in 48 cages in the six phytotrones at constant temperatures of 10.1, 13.3, 17.6, 22.7, 26.6 and 29.6°C. These temperatures are averages of data logger measurements made hourly in each cage. Five attack densities, 20, 50, 100, 200, and 300 /m<sup>2</sup> were established by introducing the unsexed parent beetles freely into the cages. The lowest attack density appeared in three and the second lowest in two replications, because of the expected random errors there. Actually, a range of attack densities from 15 to 825 /m<sup>2</sup> was obtained, and eventually attack den-

sity was considered as a continuous variable in the analysis. For each such experiment member, there were 11 bolts (6 temperatures × 8 attack densities × 11 bolts = 528 bolts) which were sampled at regular intervals ranging from 1 to 5 days, depending on temperature. The samples were dissected after deep-freezing and the numbers of egg niches and eggs in each gallery were counted. A total of 3617 egg galleries were studied.

## 22. Field sampling

People sampling bark beetles do not see their objects under the bark until the sample has been taken and processed. While this fact increases the objectivity of a sampling program, it also makes sampling more difficult. Sampling of bark beetle broods is very labor-intensive, at least in the case when dissecting of material is involved. Sampling is therefore subject to severe constraints arising from



Fig 2. Locations of the study sites.

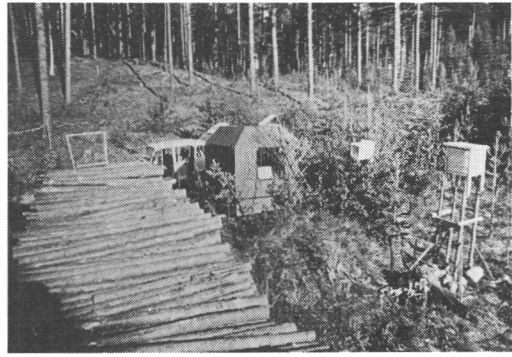


Fig 3. The study site in Rovaniemi mlk. Sheltered from the sun by reflecting screens soon after taking the picture, the cabin houses the measuring equipment. Thermocouples 12 m long have been inserted between the cabin and the stack.

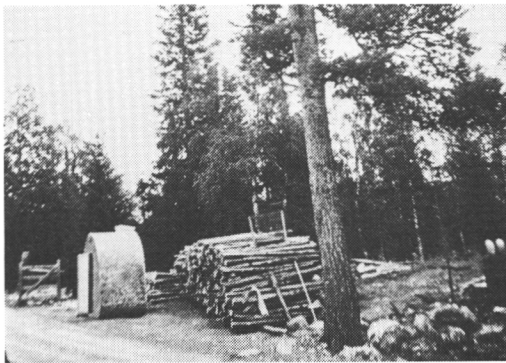


Fig 4. The study stack in Pallasjärvi.

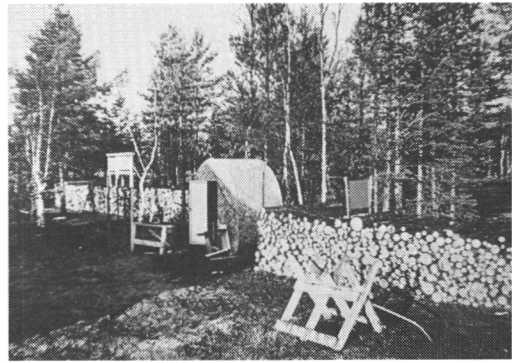


Fig 5. Exposed and shaded stacks in Enontekiö.

the more or less limited resources available. In this light, emergence of an extensive literature describing the sampling of bark beetle populations is not surprising (e.g. Saalas 1919, Kangas 1934b, Beaver 1966, Berryman 1968, Stark and Dahlsten 1970, Coulson et al. 1975, Stephen and Taha 1976, Pulley et al. 1977, 1979, Trofimov 1979, Trofimov et al. 1982). It seems that every study about bark beetle population dynamics requires its own customized sampling schemes. The present study is not an exception to the rule. The goal of acquiring a database on the development and survival of bark beetles led to a successive sampling program, which most closely resembles that employed by Beaver (1966, 1967).

### 221. The successive sampling scheme

Field experiments were carried out in three separate locations in Finnish Lapland (Fig 2) in the hyperboreal coniferous forest region. The main study site was located in the rural commune of Rovaniemi, just below the Arctic Circle. Belonging to the Kivalo Experimental Forest of the Finnish Forest Research Institute, the forests of this area are dominated by Scots pine growing on the sandy soils on the banks of the River Kemijoki. The other study sites were Pallasjärvi in the commune of Kittilä and the village of Enontekiö. Pallasjärvi is located at 270 m a.s.l. and it is surrounded by extensive spruce-dominated forests in the Pallas-Ounastunturi National Park. At 300 m a.s.l., Enontekiö is just 20 km south of the northern timberline. Being north of the timberline of Norway spruce, the study site is characterized by relatively dense and stable pine forests.

Beetle development and survival were monitored from freshly cut pine pulpwood stacks using successive sampling. The stacks were always oriented in an east-west direction. Sampling was stratified according to the levels of the stacks, the sampling interval being one week at the top level (0.0 m) and two weeks at the levels of 0.2, 0.5, 1.0, and 1.5 m from the top of the stack. Sample bolt size ranged from 0.25 to 0.5 m. Samples other than those

from the top level were taken at the southern end of the 2 m long logs. In a preliminary study in Rovaniemi in 1980 and in Pallasjärvi 1981 samples were also taken in the middle of these logs, but, as there were very few insects, this was not repeated in the following years. In Enontekiö, there were two stacks, one in a sunlit opening and the other 20 m away in the shade of trees. Figs 3, 4, and 5 show the experiment stacks at the three sites. The experiment years and the sizes, heights, and average bark thicknesses of the stacks are given in Table 2.

The number of replications per sampling day and level was a compromise between the desired accuracy and work effort. It was adjusted during the study according to the preliminary results as Table 2 shows. The reliability of the data depends on the variation and the number of replications. In forest insect studies, variation is usually large due to the contagious distributions of their occurrence (Waters and Henson 1959). The criteria by which the accuracy of the data can be measured is the standard error about the mean of an attribute in a sampling time. In studying development, we are concerned with the standard error of the proportion of a stage, and in studying survival we deal with the standard errors of the numbers /m<sup>2</sup>. Facing the large variation and contagious distributions, a goal of obtaining a standard error of 1/3 of the estimate was set. Trofimov (1979) recommends to analyze 10–12 trees for 1/5 accuracy and 19–21 trees for 1/10 accuracy. In the absence of previous studies on *T. piniperda*, the number of replications and the accuracy could not be fixed before the third year of the study. In 1982, the goal could be set of obtaining a single standard error less than 7% for the proportion (%) of a particular stage at a particular sampling time and level. This required fewer replications during the spring when all the insects were eggs than in the middle or late summer when there was a mixture of different stages. However, this plan would have caused the trees being sampled to run short in the sampling levels in the middle of the stack before autumn; for this reason, three replications had to be accepted there.

Arrival of parent beetles in the stacks was monitored daily using window traps.

Table 2. Data from the study stacks and sample bolts tabulated according to study site, experiment year and the level of the stack.

Study site	Year	Stack		Sample bolt							
		Volume m <sup>3</sup>	Height m	Average bark thickness mm	Top level			Lower levels			Total n of bolts
					Samp- ling times	Total n of bolts	n of repli- cations	Samp- ling times	Total n of bolts	n of repli- cations	
Rovaniemi	1980	40	2.0	6.0	19	60	3—4	11	89	2	149
—	1981	40	2.2	5.7	20	61	3—4	10	121	3	182
—	1982	40	2.0	6.2	18	91	2—6	10	119	3	210
— *)	1983	40	2.0								
Pallasjärvi	1981	25	1.8	4.7	17	60	3—5	8	94	2—4	154
Enontekiö exposed	1982	20	1.2	5.0	18	85	3—6	9	82	3—4	167
—	1983	20	1.2	5.8	16	78	3—6	8	64	3	142
Enontekiö shaded	1982	20	1.2	4.7	18	87	2—7	9	84	3—4	171
—	1983	20	1.2	5.6	16	87	3—6	8	71	3	158

\*) under preparation

Table 3. Average, minimum, and maximum temperatures (°C) in Rovaniemi Research Station in the autumn and winter 1982–83 with the number of *Tomicus piniperda* that emerged from a bolt taken indoors each day. Temperature conditions are from the interval after the previous sampling day.

Day	Emerged exx	Average	Minimum	Maximum
13.10	40	4.2	-5.5	10.2
15.10	1	-1.8	-2.9	1.8
18.10	0	-4.7	-13.0	-4.5
20.10	0	-6.2	-12.6	-3.2
22.10	0	-2.4	-4.5	0.5
25.10	9	0.9	-3.6	4.1
27.10	5	1.4	-0.9	3.4
29.10	0	-0.8	-3.5	1.6
1.11	0	1.4	-5.8	5.7
3.11	1	-3.0	-8.8	1.3
5.11	0	-7.0	-11.1	-4.0
8.11	1	0.6	-2.8	3.0
10.11	22	1.9	-1.3	3.6
12.11	26	1.8	-0.3	4.6
15.11	0	2.1	-2.3	5.7
17.11	0	1.5	0.4	3.3
19.11	0	0.4	-2.1	2.2
22.11	0	-3.5	-12.0	2.1
24.11	0	0.9	-0.7	2.2
26.11	0	-4.3	-11.7	1.3
29.11	1	-5.8	-9.2	-2.8
1.12	1	-9.0	-15.2	-4.7
3.12	0	-1.9	-10.9	1.9
8.12	0	-4.7	-18.0	0.9
10.12	4	-10.8	-19.8	-6.0
13.12*)	3	-21.8	-31.4	-10.9
17.12	1	-7.3	-26.3	-1.8
20.12	0	-11.3	-22.9	-0.9
22.12	0	-2.2	-4.2	0.2
27.12	2	-6.2	-21.2	-0.5
29.12	2	-5.4	-14.0	-3.8
31.12	9	-6.7	-15.8	0.2
3. 1	0	-1.3	-5.6	2.2
5. 1	0	-3.0	-5.7	-0.1
7. 1	23	-2.2	-5.0	-0.1
10. 1	24	-9.3	-20.9	-0.3
12. 1	18	-7.9	-16.5	1.2
14. 1	0	-6.0	-10.0	-3.9
17. 1	2	-7.7	-18.7	-2.7

\*) Including one day with -29.4 -31.4 -27.5

## 222. Processing of field samples

The samples were taken to the laboratory where they were deep-frozen and dissected during the winter. A small proportion of samples were dissected straight without cold storage in order to provide perspective when determining the health of the larvae. Three sets of data were collected from each sample: 1) bolt data, 2) insect data, and 3) gallery data. Bolt data included measures of the dimensions, bark thickness, fresh and dry weight, etc. Insect data comprised the numbers of all the insects along with their stages (which were determined according to Lekander 1968), health con-

ditions, and causes of death found in the sampling areas within the bolt. The sampling area in a bolt was the bark area where the insects were collected. Normally, it was the entire bolt, but when the amount of *Tomicus piniperda* stages exceeded 200, it was allowable to cut down the dissecting effort and delineate a 0.2 m long sampling area in the middle of the bolt. At the sunlit top level, one sampling area was located on both the upper and undersides of the bolt. Gallery data, finally, was gathered after dissecting by measuring egg gallery lengths and coordinates (Saarenmaa 1983). The laboratory procedures involve considerable know-how which accumulates slowly during the work, and it is not practical to present them here (for details, see Immonen et al. 1985). More details of the data are given in the Section 24.

## 223. Laboratory rearings of frost exposed bolts

The fate of the beetles which had not left their brood logs by winter was studied in two experiments. The first experiment began in October 1982, when 39 bolts of length 0.4 m containing immature *T. piniperda* were randomly sampled from a stack. They were placed outdoors on a shaded but open place and carefully kept free of snow cover. From October 13th to January 17th three times per week, a bolt was taken indoors, and the emerging beetles were counted. Temperatures were recorded 2 m above the ground with a nearby thermograph. It is likely that the temperatures that were recorded are close to those to which the beetles were exposed. Table 3 shows the material of this experiment.

The material for the other experiment originated from Pallasjärvi 100 km south from the northern timberline where, in the middle of winter (February 9th, 1984), 26 bolts were cut of the logs in a thinning experiment where they had been attacked by *T. piniperda* in summer 1983. The felled trees had been in normal outdoor conditions under a snow cover. Eight of the bolts were dissected while the rest were put into rearing cages at room temperature to monitor emergence. To repeat the experiment, another set of 26 bolts was fetched on May 12th, just before swarming. Temperature data for this experiment has been taken from the Muonio weather station 30 km away.

## 23. Climate data

### 231. Measurements

Temperatures were recorded in all the sampling locations under the bark at hourly intervals throughout the entire growing seasons. In Rovaniemi, this was done by a Monitor Labs 9300 datalogger and a Techtran 817A data cassette recorder. The equipment was supplied by 220 V net power and shielded from transient voltage peaks. Using cu-co thermoelements, the datalogger supplies 40 channels with an accuracy of 0.3°C, which was checked regularly

and adjusted when necessary. There was no special protection against induced voltage peaks in the thermocouples, since the data logger was sensitive to such only during the measuring scan which lasted 30 seconds per hour. Nevertheless, during a thunderstorm the thermocouples were detached whenever possible. On the average, there were 6 measuring points at each sampling level in the stack.

In Pallasjärvi and in Enontekiö three Honeywell Versaprint multipoint recorders with cu-co thermoelements were used for the same purpose. As there were only 9 channels available for temperature measurements in each machine, only one channel per sampling level was available. One channel measured air temperature with a Lambrecht thermograph and another one was shortcut so as to show possible jumps of the entire scale. Calibration and decoding of the printer sheets was a laborious task. The level of the recorded data was checked at least once a day. In addition, the entire range of the recorder was checked weekly. After the printer sheets had been interpreted and typed into the computer, the calibration data was built into regression models which were used to transform the recorded %-values into °C. The accuracy of the actual measurements is about 1.0°C. In addition we must count the interpretation inaccuracy and the residual error of the transformation equation. Therefore it was surprising that when the thermal sums from the Lambrecht were compared to the corresponding Versaprint results, the deviations were no more than 20, 25, 20, and 10 dd in the 1982 and 1983 data from Enontekiö stacks. These small deviations were then adjusted from the Versaprint data in order to obtain full consistency between the data sources.

Of course, long measuring periods with delicate instruments involve numerous adversities due to thunderstorms, power outages, equipment failures, human error, etc. Because of the aim of integrating temperature sums over the sampling periods, missing pieces of data — never more than 10 % of all and the longest being 9 days — were estimated as multiple regression of the record of a mechanical thermograph, day, and sine function of hour. The estimated mean square errors in the equations ranged from 1.1 to 4.7 °C<sup>2</sup> between channels. Thus, the differences are tolerable and because these data values are used for summing only, no bias is introduced by this method.

Other climatic variables were not measured directly except for rainfall, which was recorded daily in 1983. Rainfall data for 5 day intervals through the seasons were taken from the closest meteorological stations in Apukka, rural commune of Rovaniemi, and for the northern sites in Muonio. Moisture in trees on the sampling day was measured by weighing and drying them soon after debarking. In addition, in the Rovaniemi stacks through the summers 1981, 1982, five logs were weighed hourly. A special rack was constructed that allowed the logs to hang freely within the stack upon a Kyowa LM-20 load-cell connected to the datalogger. The equipment should be able to detect changes in the weights of the logs within a range of 20 g. Unfortunately, this data is not currently available due to lack of processing time.

Fig 6 shows the distributions of temperatures excluding within-summer variation at all the sampling levels in all the years. It is easy to recognize a general pattern of between-level variation. The higher the level, the wider the range of temperatures is, i.e., the more extreme the microclimate. Temperatures over 30 °C occur only in the sunlit upper sides of level 0 logs, their frequency being highest in 1980. The proportions of those temperatures that contribute most to the development of insects, 20 to 30 °C, are also low except in the uppermost level. It is surprising, how great the proportion of temperatures below 10 °C is in all the experiments. In no case is it less than 30 %, and in the Enontekiö stacks, more than 50 % of the temperatures are in this range.

The course of temperatures at fortnightly intervals within the years in all the study sites is shown in Fig 7. Only the sunlit upside of the level 0 logs is shown to save space. When using sampling days as cutpoints, the data allows discrete summing of all possible temperature sum functions with great efficacy. The pictures are self-explanatory. For example, one can easily recognize the catastrophic cold in June 1982 and the subsequent warm July.

Table 4 shows the degree days in the different sampling locations as well as rainfall and sunshine sums. The warmest year was 1980 and the coldest 1982. The amount of degree days in the air is about 70 % of that in the warmest parts of the stacks, being about equal to that in the coldest lower levels. In summer 1981, it rained nearly twice as much as in summer 1980. In spite of the longer sunshine in 1982, the temperature sum in 1981 is higher. The temperature sums in the shaded Enontekiö stacks are about 20 % lower than in the exposed ones. In the uppermost logs it is about the same as in the air.

## 24. Bark beetle data base BBDB

The main tool of data maintenance, retrieval and analysis was an integrated data base management and applications system called BBDB. By definition, a data base is a collection of interrelated data stored effectively and without redundancy. All the elements in a data base, e.g. variables, codings, and relationships between files, are explicitly defined (Martin 1977). In other words, the computer is not used merely for computing, but for arranging material as well (Saarenmaa et al. 1984, Kaila 1985b). A data base was built because soon after the beginning of the study it became apparent that the huge amount of information gathered in the laboratory and by the automatic equipment could not be managed otherwise.

This approach of using data base management techniques to build an IPM system is not unique. In the decision support system for the management of *Dendroctonus frontalis* (Rykiel et al. 1984), a data base management system (DBMS) is employed. Within agricultural IPM extension delivery systems, it is a common observation that integrated pest

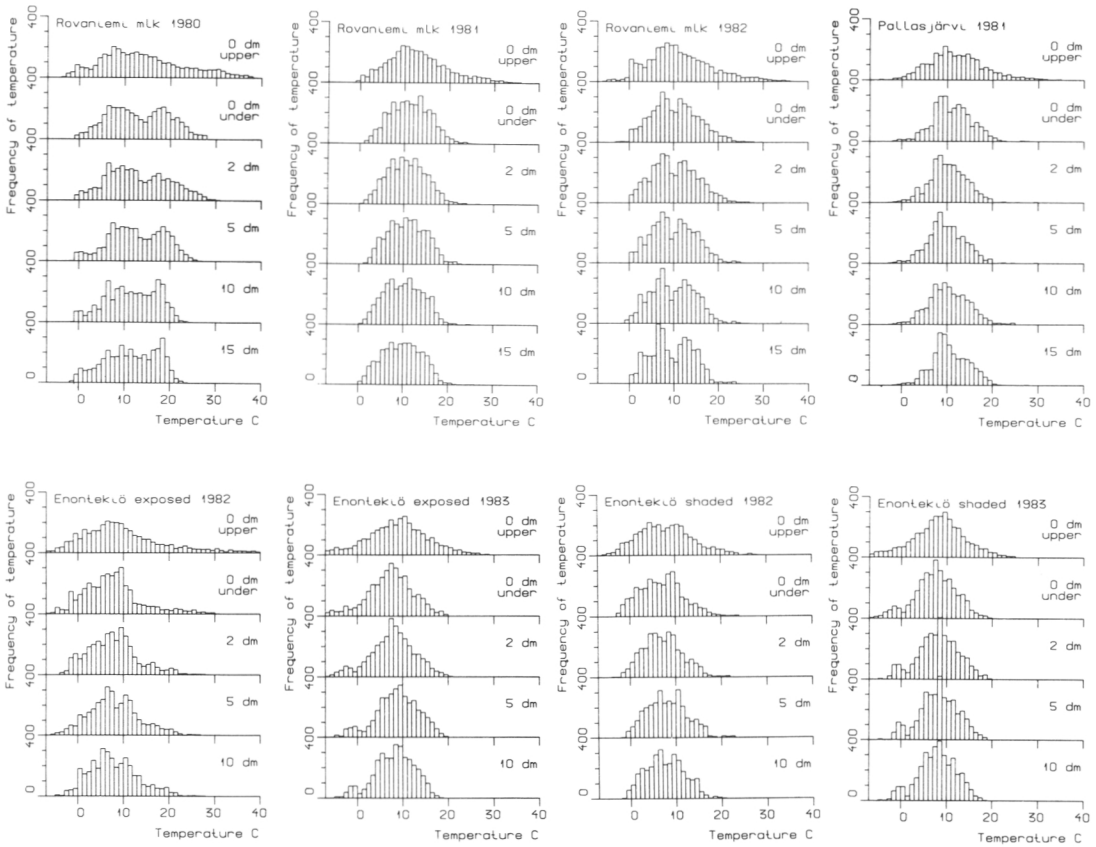


Fig 6. Frequency distributions of hourly temperatures in all the study sites and years at the different stack levels under the bark. For measurement periods, cf. Fig. 7.

Table 4. Final average temperature sums from the air and from the different levels in the stacks. Rain and sunshine hours (Climatological Data) are from the months V—IX.

Level (m from top of stack)	Degree days > 5°C							
	Rovaniemi			Pallasjärvi	Enontekiö exposed			Enontekiö shaded
	1980	1981	1982	1981	1982	1983	1982	1983
Air at 2.0 m	972	801	743	571	560	617	557	611
0.0 m upside	1363	1171	1039	839	856	710	531	601
0.0 m underside	1244	922	892	713	545	481	403	476
0.2 m	1207	825	886	623	541	532	399	553
0.5 m	1077	849	845	591	569	645	485	560
1.0 m	1033	769	833	645	552	549	423	519
1.5 m	946	709	791	680	—	—	—	—
Rain mm	210	410	270	360	310	310	310	310
Sunshine hours	1235	804	1052	—	—	—	—	—

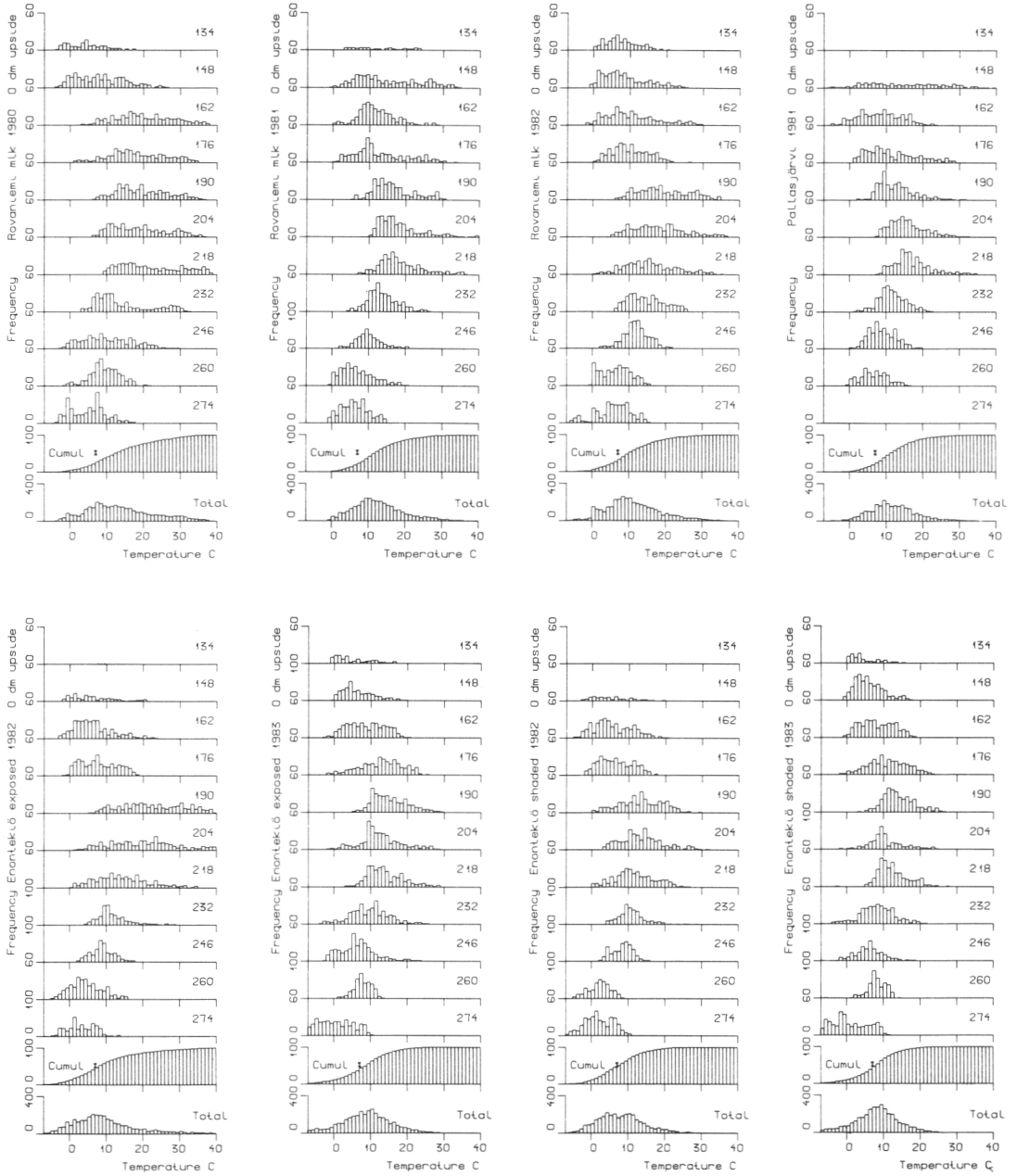


Fig 7. Frequency distributions of temperatures at fortnightly intervals through the summers in all the study sites and years at the upper side of level 0 logs. The numbers to the right of the distribution are the Julian days at the end of each period.

management requires such complex data manipulations that integrated data management needs to be considered (Brown and Lutgardo 1980, Brown et al. 1980, Welch 1984). Building a DBMS for operational IPM extension service is not a trivial

task (Brown et al. 1980). The same applies to research data as well. For arranging ordinary research data files without complex relationships or those that are used only for a short period, the investment required can be too high (cf. Kaila 1985a, 1985b).

Table 5. List of attributes in the BBDB data base.

RECORD TYPE: EXPERIMENT	RECORD TYPE: BOLT	RECORD TYPE: GALLERY
Study site	Bolt number	Bolt number in gallery
N-coordinate	Dissector	Bolt side in gallery
E-coordinate	Sampling time YYMMDD	Gallery number
Experiment year	Cutting time YYMMDD	Gallery species
Vertical level	Codings 1	Number of tunnels
Horizontal level	Codings 2	Position of tunnel
Experiment number	Codings 3	Total length of tunnel
Channels	Tree species	Sample area length of tunnel
Weather data	Sample type	Vertical starting point
	Rearing type	Horizontal starting point
	Vertical location in stack	Vertical ending point
	Horizontal location in stack	Horizontal ending point
	Circumference S-end with bark	Area of gallery
	Circumference N-end with bark	Number of parents
	Circumference S-end wo bark	Number of egg niches in sample
	Circumference N-end wo bark	Number of starting larvae in sample
	Bark thickness	Length of nuptial chamber
	Bark type	Length of sterile end part
	Phloem thickness	Sterility and resinosis
	Bolt length	Vertical 1st intermed point
	Weight before rearing	Horizontal 1st intermed point
	Weight after rearing	Vertical 2nd intermed point
	Weight after unbarking	Horizontal 2nd intermed point
	Dry weight	Vertical 3rd intermed point
	Constant temperature	Horizontal 3rd intermed point
	Daily temperature sum	
	Hourly temperature sum	RECORD TYPE: INSECT
	Blue stain of cover	Bolt number in insect
	Blue stain in S-end	Bolt side in insect
	Blue stain in N-end	Length of sample area
	Tree length	Damaged area
	Lumber length	Insect species
	Length growth	Stage
	Health condition	Health
	Vigor index	Mortality factor or host
	Tree orientation	Amount
	Comment	Amount type
RECORD TYPE: CLIMATE		
Climate time YYDDHHMM		
Air at 2 m thermograph		
Air at 2 m datalogger		
Air in stack at 1 m		
Channel 5		
Channel 6		
.		
.		
Channel 56		
Wind		
Relative humidity		
Rain		
Weight of tree 1		
.		
.		
Weight of tree 5		
RECORD TYPE: EMERGENCE		
Bolt number in emergence		
Beginning of rearing		
Emerging day		
Species emerged		
Reemerged		
Emerged		
Weight of emerged		

### 241. Contents of BBDB

BBDB data is managed by TUTKA DBMS written in VAX-11 FORTRAN. Based on the CODASYL standard, TUTKA supports a hierarchical data structure that is well suited for research applications (Kaila and Taipale 1984). Fig 8 shows the logical schema and status of the data base. The present total size of the data base is about 25 000 blocks, which is equivalent to about two million numbers.

In the database files, EXPERIMENT data contains information about a set of sample bolts that form a successive sampling time series. CLIMATE data comprises microclimatic records that are related to an experiment. BOLT serves as a host for three groups of actual bark beetle data. It also describes a single sample, a bolt, by sampling time, tree dimensions etc. Traces of insects in a bolt have been mapped and stored as GALLERY data. INSECT data contains the numbers of all insect species classified by developmental stage, health

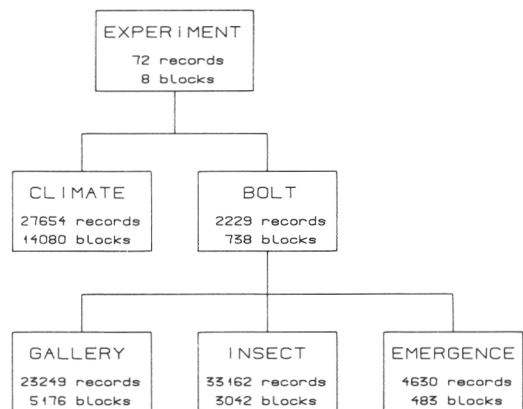


Fig. 8. Logical schema and present status of the BBDB data base.

and mortality factor. EMERGENCE data describes those insects that have come out of a bolt in a time interval. Table 5 shows the attributes of BBDB.

#### 242. BBDB programs

Besides data, BBDB includes a set of data-independent programs written in VAX-11 FORTRAN by the author. They form an integrated system by which one can add data to the data base, search for sample bolts satisfying any criteria, and analyze material with a set of application routines especially made for bark beetle studies. The system is interactive, screen-oriented and menu-driven, but it can also be run in batch mode. I describe its functioning briefly in the following (for operational instructions, see Immonen et al. 1985).

Data can be stored through workfiles created by a typist. While adding data, its minimums, maximums and allowable values are checked and their possible violations reported. Any bugs in the data can be fixed by a data base editor.

Searching for a set of data is a prerequisite for using any of the applications. In order to find a subset of the material, criteria describing it must be given. Criteria can be assigned for any attribute in any except in the CLIMATE group. The system remembers all searches that have been done earlier. Given a set of restrictions that have not been used before, a typical searching time is 3 to 10 minutes. However, if the search has been done before, the material is located within seconds. When an address table of material has been formed by searching, the

material can be analyzed using the applications.

The applications, which all use GPGS-F color graphics (NORSIGD 1980) for illustrating the results, are callable in a menu. Currently available there are routines performing

- data reporting
- drawing of bolt picture with the egg galleries
- calculation of spatial pattern indices (Saarenmaa 1983)
- merging climate data with sample bolts
- forming temperature data distributions
- constructing empirical distributions of development of larvae (Saarenmaa 1985b)
- simulation of intraspecific competition of bark beetle larvae (Jong & Saarenmaa 1985)
- survival analysis and life tables (under development)

As new needs arise and programs are developed to do particular tasks, these can be inserted to BBDB menus. So the system not only manages data, but also programs. The cost of making the system has involved about 8 working months so far.

The field data in this study have been analyzed mainly by the programs described above. Using a separate TUTKA-UTILITY package (Kaila and Taipale 1984), it is also possible to form a general observation matrix out of the data base to be analyzed using standard statistical programs such as BMDP (UCLA 1981). Laboratory data in this study have been analyzed mainly this way. The non-linear regression program BMDPAR has been utilized, in particular.

### 3. MODEL ELEMENTS AND INTEGRATION

A model intended to predict the timing and frequency of emergence of *Tomicus piniperda* can be constructed in at least two different ways. In the first approach, we may construct a mathematical equation, e.g. a regression model, giving the result as a direct function of a list of variables. These variables could be temperature sum, microclimatic classifications of the environment, frequency of logging operations nearby, tree species in the surrounding forests, etc. The other approach takes the functioning of the life system of the beetle into consideration, and results in building biophysical models for the important life cycle events, which can be termed subsystems. This kind of models have been built for *Dendroctonus frontalis* (Feldman et al. 1981a, 1981b, Wagner et al. 1984a). A biophysical model is more applicable to new circumstances than a regression model, which may lack biological foundation (Coulson et al. 1979). In the present study, the latter approach has been chosen because the study of the system is only in its initial stages. After the population dynamics model has been thoroughly tested in the field, we can consider the possibility of building more simple regression models.

The subsystems in the life system of *T. piniperda* were outlined in the introduction. In a working model we must have submodels that simulate 1) arrival of the parent beetles, 2) oviposition, 3) reemergence, 4) development and emergence, and 5) survival. In the following, these model elements are built and the underlying data discussed. Finally, these submodels are tied together.

#### 31. Arrival

Arrival of the parent beetles in the logs is the first component in the model. In the introduction, a swarming model of *Tomicus*

*piniperda* was constructed from the daily maximum air temperature exceeding a particular threshold temperature and from the sum of these temperatures (1). Actually, we are unable to construct a real swarming model, since all data available on swarming have been collected using traps above attractive logs. Thus, our data describes a phase of the life cycle that is intermediate between swarming and attack. Attack was defined to be a result of swarming, beetle population, attack density, and physical properties and suitability of the host (2). The size of the parent beetle population and the subsequent attack density must be taken as given for within-tree dynamics; they are out of the scope of this study, as are the effects of the host attributes. Thus, we can approximate swarming and attack by arrival.

Assuming that the arrival rate is directly related to daily maximum air temperature (AIR MAX TEMP) approaching 100 % asymptotically (see Fig 3 in Långström 1983), and that it is inversely related to the earlier sum of these temperatures above the threshold (AIR MAX TEMP SUM), we can reformulate the swarming equation into an arrival model\*).

$$\text{ARRIVAL \%} = 100 * (1 - \exp(\text{PARAM\_1} * (\text{AIR MAX TEMP} - \text{THRESHOLD}))) / (1 + \text{PARAM\_2} * \text{AIR MAX TEMP SUM}) \quad (8)$$

After the estimation of the three parameters, PARAM\_1, PARAM\_2, and THRESHOLD, the model gives the percentage of arriving parent beetles during a day.

Window trap data from Rovaniemi 1980, 1981, and 1982, and the corresponding daily maximum temperatures were used to esti-

\*) All the equations in this paper have been expressed in a computerized form instead of the usual algebraic notation. This kind of presentation has been chosen for convenience in typing, printing and further use of the equations, and to enhance readability by using English in the expressions instead of symbolic abbreviations.

mate the parameters of the equation with 67 degrees of freedom:

Parameter	Estimate	Asymptotic s.d.
THRESHOLD	10.8003	0.39760
PARAM_1	-0.15721	0.02920
PARAM_2	0.50141	0.15654

$R^2$  is 0.606 and the estimated mean square error 39.27, i.e., 68 % of the predictions were not further than 6.27 % from the real. Projection of the model is shown in Fig 9. It is interesting to see how great an effect the first warm weather above the threshold, 10.8°C, actually has in the spring. If the maximum temperature on the first day reaches

11, 12, 13, 14, 15, 16, 17, 18, 19, or 20°C, then

3, 17, 29, 40, 48, 56, 62, 68, 72, and 76 % of the beetles respectively arrive on that day.

The model was validated against published swarming data. Fig 15 in Bakke (1968) including ten sets of trap catches throughout Norway in spring 1965 and Figs 2 and 3 in Salonen's (1973) study showing window trap data from Rovaniemi in 1962 and Vihti in 1970 were decoded and typed into the computer. The parameters above were estimated from these data with 218 degrees of freedom, and the following values were obtained:

Parameter	Estimate	Asymp. s.d.
THRESHOLD	11.5757	0.16314
PARAM_1	-0.15440	0.01696
PARAM_2	0.29572	0.05346

In the validation material,  $R^2$  is 0.568 and the estimated mean square error 55.94. The threshold temperature differs statistically significantly ( $0.95 < p < 0.99$ ) from the estimated value of 10.8°C. The difference is not great and can be understood as regional variation. PARAM\_1 which describes the accelerating effect of high air temperature on arrival is similar in both materials. PARAM\_2, which is related to the decreasing of the function when the temperature sum above 10.8°C accumulates during the spring, is lower ( $0.95 < p < 0.99$ ) in the validation material than in the material from Rovaniemi. The difference is characteristic of a general feature of northern life: start late and quit early.

Fig 10 shows the observed and simulated arrivals in all the materials on a time axis (see Bakke 1968, Salonen 1973). The

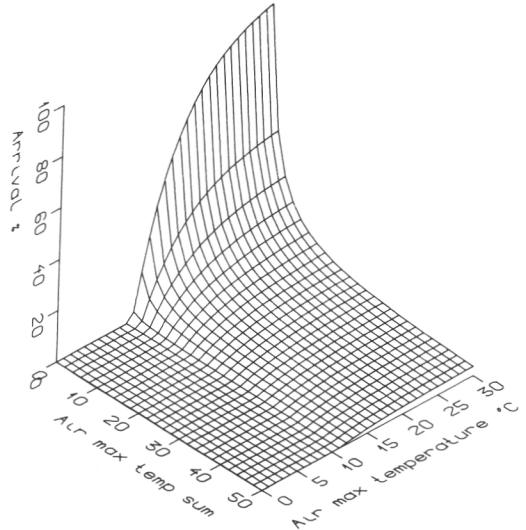


Fig 9. Three dimensional plane of the arrival model (8).

performance of the model can be ranked as good. The only shortcoming is that the model slightly underestimates the first peak of arrival.

#### Discussion of arrival

It was surprising how well the model that was developed using material from a single site in three years could predict arrival. This is an indication of the overriding importance of temperature for the swarming of the species. Nevertheless, the model (8) can still be improved by introducing wind velocity. Such data, however, was not available for the study site which is located in an exceptionally sheltered place. According to Salonen (1973), on a windy day there is not so much arrival as on a calm day with the same temperature, and within a day, the arrival is higher in the calm evening than at noon with a higher air temperature. However, these beetles may have taken off already earlier in the day. Once on the wing, the beetles can fly at temperatures colder than the threshold (Bakke 1968). The efficacy of a window trap is also reduced by wind. Another reason to suppose smaller catches on a windy day is that it is more difficult for the beetles to locate the sources of host odors.

For pest management models, it would be of importance if the time of attack for *T. piniperda* could be predicted beforehand. This time varies by more than 30 days from

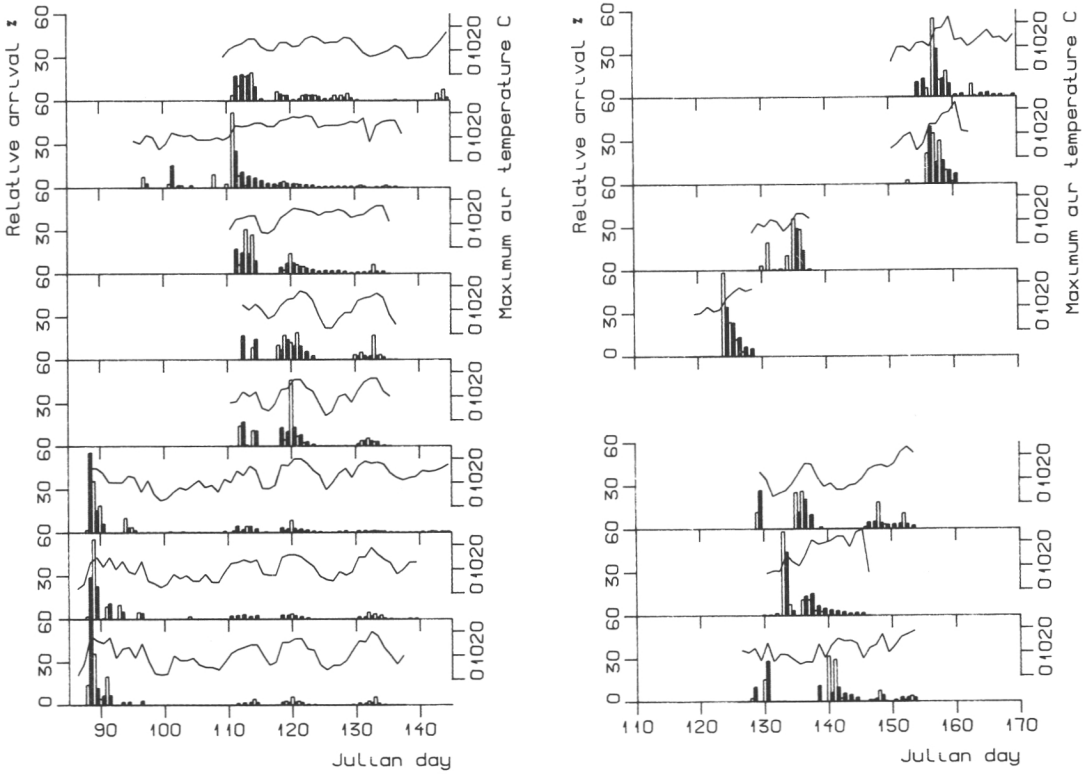


Fig 10. Validation of the arrival model (8) against data of Bakke (1968, Fig 15) on the left and two uppermost diagrams on the right, and Salonen (1973, Figs 2 and 3), third and fourth from above on the right. The calibration material from Rovaniemi in the years 1980, 1981, and 1982 appears in the three lowermost plots on the right. Observed values are shown as open bars and the simulated ones as filled.

year to year (Lekander 1984). An extension of the prediction of the model is possible only after we are able to forecast macro-meteorological changes over such periods. Hence, the present model can function only as a beetle input for the population model.

Timing of attack is not necessarily the same as timing of arrival to window traps. Ehnström (1976) has shown that *T. piniperda* colonizes pulpwood stacks from up to down. Hence, if attack is being approximated by arrival, there can be a time lag in the beginning of development between the stack layers. In particular, those beetles arriving after the most suitable uppermost layers of the stack already have been colonized can have an altered spatial distribution in the breeding material. These items of colonization of the breeding material must be considered when interfacing the population dynamics model with real situations.

### 32. Oviposition

In the introduction, it was suggested that the oviposition rate of *Tomicus piniperda* shows functional responses to temperature, physiological time, attack density, phloem thickness, and physical and chemical changes in the tree (3). In this chapter, we will test these ideas against the oviposition data (see Chapter 212., and formulate those responses that have significant effects on an oviposition model. As the material is standardized, we must ignore the last item; it is also a subject that deals largely with the attack phase and is out of the scope of within-tree dynamics.

It is not self evident how the effect of temperature can be derived from the present successive sampling data without error. A simple comparison of the numbers of eggs laid per day at the different temperatures

yielded a biased result since the sampling interval should in this case be adjusted perfectly to the rate, and this is not known beforehand. Actually, an exact measure of eggs per day per female cannot be calculated from the material directly because doing so we should know whether or not oviposition still continues in the particular egg gallery. Thus, another variable, the average number of days required to establish the nuptial chamber and build 5, 10, 15, 20, 25, 30, 35, and 40 egg niches was calculated for each temperature (Table 6). Egg niches are used as the material rather than eggs, because their number is more accurately determinable through time. Later we will convert egg niche numbers to egg numbers.

From the upper part of Table 6 we can see that oviposition starts most quickly at the middle temperatures, but from 15 to 25 egg niches it proceeds fastest at the highest experiment temperature. 29.6°C is unhealthy for the ovipositing females, since a natality of thirty eggs can hardly be reached at this temperature. Generally, the most rapid oviposition seems to occur a little below 26.6°C, but unfortunately this depends on the criteria used. For this change of pattern over time it is difficult to judge which number of egg niches should be taken as a basis in modeling the oviposition rate. Therefore, the following technique has been used.

It would certainly be valuable if we could use a single measure of physiological time for

all within-tree life processes of *T. piniperda*. Therefore, the applicability of the enzyme inactivation model used as the measure of the rate of development of the entire developmental period and presented earlier (Saarenmaa 1985b (1) ) and here in chapter 341. was tested for describing oviposition. That was done by multiplying the value of function (11) at each temperature by all the numbers of days in Table 6. Thus we obtained the cumulative rate units at the lower part of Table 6. The agreement within columns is not perfect, but again, we can recognize only non-directional variation. The variation gets smaller the larger the number of egg niches we consider. If we are ready to sacrifice a little statistical significance, we can accept the estimator of physiological time of larval development for oviposition, too.

Next we have to consider the decrease of oviposition rate with time and attack density. An examination of a plot of the number of egg niches over time shows that their number hyperbolically reaches a limit, EGG MAX. Oviposition starts after a initialization time, INIT, that is required for boring into the bark and establishing the nuptial chamber. The oviposition rate gradually slows down, and thus is inversely related to time. In the denominator we need a small constant, K. The attack density can be assumed to directly decrease the oviposition rate with a given efficacy, EFFECT OF DENSITY, which, of course, is also related to time.

Table 6. Number of days and cumulative rate units required for *Tomicus piniperda* to establish the nuptial chamber and given number of egg niches at the six experiment temperatures.

Temperature °C	Nuptial chamber	Number of egg niches								
		5	10	15	20	25	30	35	40	45
Days										
10.1	3.45	4.89	6.69	9.02	12.12	16.49	23.08	34.17	56.77	128.11
13.3	3.11	4.03	5.17	6.60	8.47	11.01	14.65	20.34	30.44	53.33
17.6	1.99	2.41	2.93	3.58	4.44	5.61	7.29	9.95	14.72	25.87
22.7	2.31	2.49	2.71	3.01	3.40	3.96	4.83	6.35	9.69	22.88
26.6	2.25	2.44	2.67	2.98	3.39	3.98	4.90	6.50	10.02	24.17
29.6	2.64	2.68	2.74	2.83	3.01	3.51	11.08	—	—	—
Cumulative rate units										
10.1		0.024	0.033	0.045	0.060	0.082	0.114	0.169	0.281	0.634
13.3		0.039	0.050	0.064	0.082	0.107	0.142	0.197	0.295	0.516
17.6		0.040	0.049	0.060	0.075	0.094	0.123	0.167	0.247	0.434
22.7		0.065	0.071	0.079	0.089	0.105	0.126	0.166	0.253	0.598
26.6		0.075	0.083	0.092	0.105	0.123	0.152	0.201	0.310	0.748
29.6		0.084	0.085	0.088	0.094	0.109	0.345	—	—	—

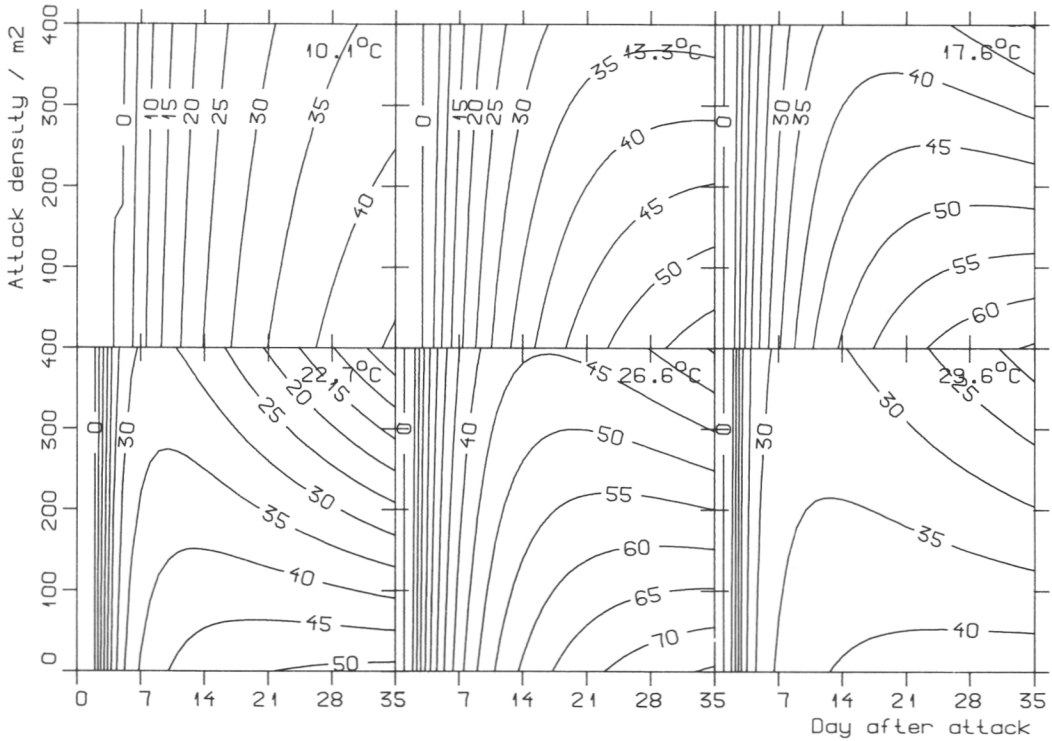


Fig 11. Contour maps of number of egg niches per gallery as a function of time and attack density at the six experiment temperatures. The data is smoothed using equation (9).

Building upon these considerations, we can formulate:

$$\text{NUMBER OF EGG NICHES} = \text{EGG MAX} * \frac{(\text{TIME}-\text{INIT})}{(\text{K} + \text{TIME}-\text{INIT})} - \text{EFFECT OF DENSITY} * \text{ATTACK DENSITY} * \text{TIME} \quad (9)$$

Fig 11 shows contour maps of the model at all the experiment temperatures. It is fascinating to see how a great attack density does not have any effect on the number of egg niches per gallery in the beginning. While oviposition continues, overcrowding becomes apparent, and oviposition is prematurely terminated, especially at densities above 200 egg galleries/m<sup>2</sup>. At 21.3 and 29.6°C, there are some outlying high observations that force the model to decrease the egg niche numbers. After 30 egg niches have been established, the oviposition rate slows down, partially due to a real decrease in oviposition rate, partially because females finish reproduction and start to reemerge.

Absolute time in the model (9) was replaced by physiological time (cumulative rate units as summed from equation (11)),

and then the material at the different temperatures was combined. The parameters of equation (9) obtained the following values:

Parameter	Estimate	Asymp. s.d.
EGG MAX	63.3251	2.2399
INIT	0.02725	0.00386
K	0.09142	0.01056
EFFECT OF DENSITY	0.06881	0.00605

There are 2690 degrees of freedom. The estimated mean square error is 300.4 and R<sup>2</sup> 0.2118. These numbers reveal that there is a large variation in this egg gallery material. Predictions on the bolt level were, however, much more accurate. Figure 12 shows the projection of this model.

A linear term of phloem thickness was introduced to the model, but its regression coefficient was not statistically significant.

To be able to transform the numbers of egg niches into eggs, we need to know the ratio of used egg niches. It was 0.811 (s.d. = 0.166, n = 2554) in the present material. The ratio showed statistically significant correlation with phloem thickness ( $p =$

0.003), attack density ( $p = 0.000$ ), and temperature ( $p = 0.000$ ). However, these can be ignored because their actual combined effect was negligible ( $R^2 = 0.027$ ). In a field material a ratio of 0.873 has been calculated (Saarenmaa 1983).

The model (9) was validated against field material collected in Rovaniemi in the years 1980—82 and retrieved from BBDB. Only such bolts were accepted in which the cumulative rate unit counter was less than 0.5. The average number of egg niches per gallery was calculated for a total of 182 bolts. The parameters of equation (9) were estimated from this data set and the following values were obtained:

Parameter	Estimate	Asymp. s.d.
EGG MAX	63.4986	6.5454
INIT	0.00000	—
K	0.09847	0.02707
EFFECT OF DENSITY	0.15592	0.06099

The two most important factors, EGG MAX and K, are very close to those of the laboratory material. The other two differ statistically significantly from the expected. The difference in INIT is clearly due to the fact that the validation material was dominated by observations at the higher end of the range of cumulative rate units. Thus INIT that operates at the low end of physiological time readily obtains irrelevant values. The cause of the difference in the EFFECT OF DENSITY is less obvious. It might also be a result of higher attack densities in the laboratory material.

There is no statistically significant bias in the predictions of the laboratory model in the validation material. The slope of regression OBSERVED = SLOPE \* PREDICTED was 0.9651 and it did not differ much from unity ( $t = 1.4096$ ). Fig 13 shows the residuals of the regression which do not deviate strongly from normality. (In an independent material it is too much to expect statistically significant normality, and therefore it is not tested). The fit is low ( $R^2 = 0.211$ ).

#### Discussion of oviposition

The material in this study consisted of bolts that are shorter than the maximum length of egg galleries in *T. piniperda*. Short

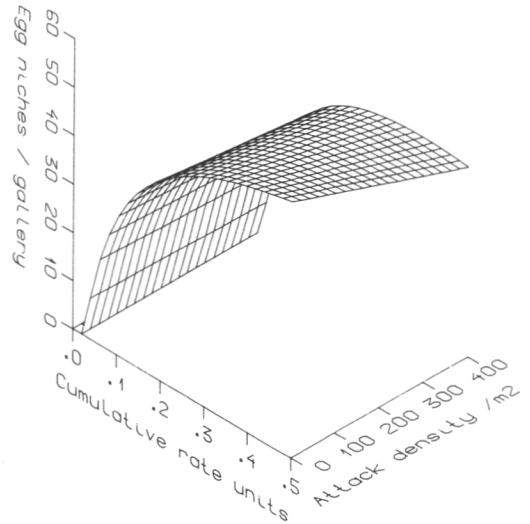


Fig 12. The oviposition model.

bolts were chosen in order to be able to get the desired number of sampling units. Observations on earlier breedings had shown that, when an ovipositing female encounters the bolt end, she turns back and the resulting egg gallery is not shorter than normal. This could have caused errors in larval survival, but it was not studied here. The results obtained in validation also confirmed that the sample size did not introduce an error: the parameter EGG MAX was similar to that in the field material and the one obtained earlier (Saarenmaa 1983).

The effect of temperature on the oviposition rate of *T. piniperda* has been recently studied by Salonen (1973). Generally, the present results are in agreement with his results and those reviewed by him. However, the oviposition rate does not slow down as quickly between 15 and 25°C as indicated in Salonen's study. This is because in the present study the time to lay a given number of eggs was considered instead of the number of eggs laid prior to a given day.

In conclusion, oviposition rate was modeled as a function of temperature, physiological time and attack density. The effect of temperature could not be shown to be different when compared with the entire developmental period. It would be worthwhile to distinguish the two factors that cause the

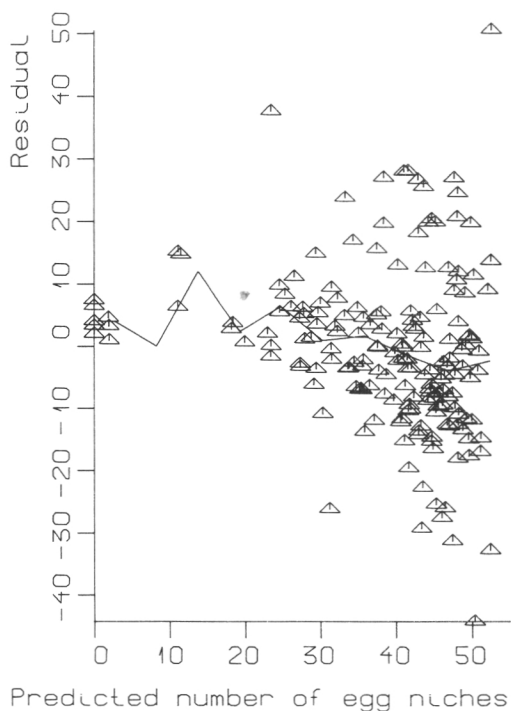


Fig 13. Residuals (observed—predicted number of egg niches) of the oviposition model in the validation material.

oviposition rate to slow down: reemergence and real decelerating of the rate in time. The present material, however, does not allow this. When considering only those galleries where the female is still present, the picture does not change much, an indication that they do stay in the egg gallery after egg laying has ceased (see Långström 1980b). Nevertheless, we can use the model for generating egg births in a population model. Randomly varying developmental rates (Sharpe et al. 1977, Wagner et al. 1984b) were not considered, although the present material would have yielded estimates for them. However, such an estimate would have included also random errors generated during the attack in the cage and maybe also differences in beetle and host quality. If these problems can be solved, the final model could utilize the variation in the ovipositing rate.

High attack density has been shown to decrease the lengths of egg galleries and the

numbers of eggs per gallery in many bark beetles (e.g. Nuorteva 1954, 1964, McMullen and Atkins 1961, Cole 1962, Eidmann and Nuorteva 1968, Salonen 1973). The dynamic change in this effect over time (Fig 11) has also been shown by Wagner et al. (1981). This negative feedback is important especially in those bark beetles that shift from tree to tree during attack and establish sister broods, as well as in the timing of the reemergence of *T. piniperda*.

### 33. Reemergence

Reemergence is a parallel process to oviposition, and we will model it in much the same way. Temperature, physiological time and attack density (4) were suggested as being the factors affecting the reemergence rate. It can be expected that reemergence rate has the same physiological response to temperature as oviposition does. Therefore we do not test it and we accept function (11) as its descriptor. Now, the reemergence rate can be defined as a function of cumulative rate units and attack density. By assuming that cumulative reemergence reaches 100 % asymptotically in time and is linearly related to attack density, we can formulate:

$$\text{REEMERGENCE \%} = \frac{100 * (1 - \exp(\text{PARAM}_1 * \text{PHYSIOLOGICAL TIME} - \text{INIT}))}{\text{EFFECT OF DENSITY} * \text{ATTACK DENSITY} + \text{PHYSIOLOGICAL TIME}} \quad (10)$$

The same laboratory material that was used in the oviposition experiment was classified by cumulative rate units and attack density and the following values for the parameters were obtained:

Parameter	Estimate	Asymp. s.d.
PARAM <sub>1</sub>	-2.2764	0.2024
INIT	0.02084	0.01286
EFFECT OF DENSITY	0.12376	0.03431

There are 212 degrees of freedom and the estimated mean square error is 241.7. Thus, the later the time and the higher the attack density, the more reemergence there is (Fig 14).

This model was then validated against field material collected in Rovaniemi 1980—1982 and extracted from the BBDB data

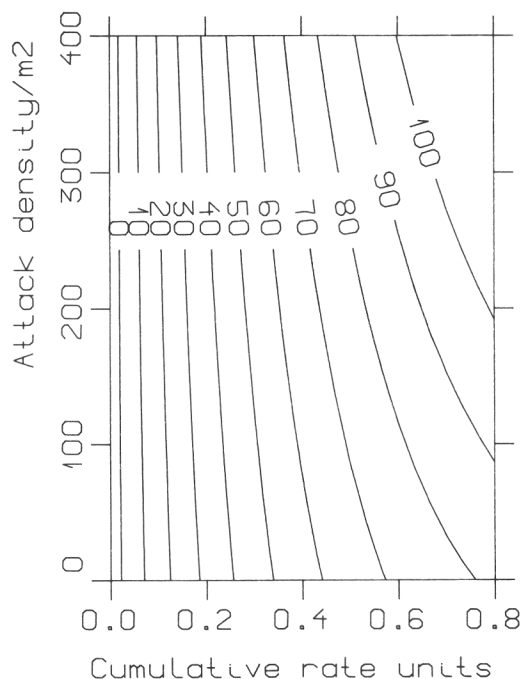


Fig 14. Contour plot of the reemergence model (10).

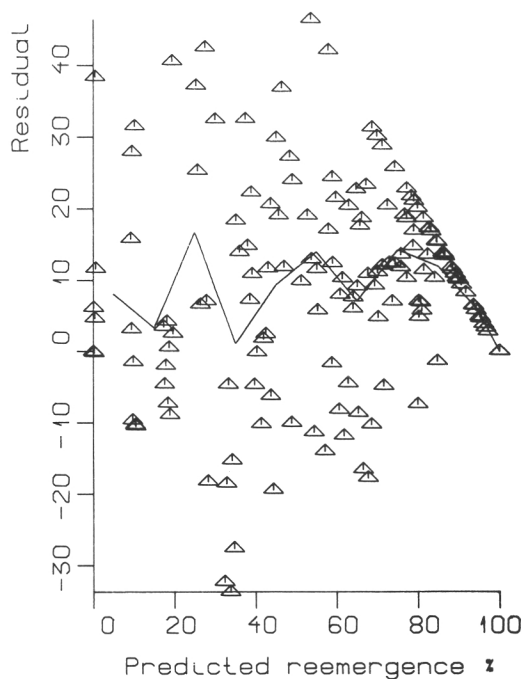


Fig 15. Residuals (observed—predicted cumulative reemergence-%) of the laboratory reemergence model (10) in the validation field material.

base. As above, the following values for the parameters were estimated:

Parameter	Estimate	Asymp. s.d.
PARAM_1	-2.9653	0.1804
INIT	0.00000	—
EFFECT OF DENSITY	0.11469	0.02829

Now there are 157 degrees of freedom and the estimated mean square error is 270.1. The EFFECT OF DENSITY does not differ in the two materials, but the other parameters do. INIT is obviously distorted by the weighing of the material towards late physiological times, and in reality there is not necessarily a difference. What the statistically significant difference in PARAM\_1 does mean can be seen in Fig 15. When observed—predicted reemergence-% of the validation material is plotted against the prediction of the laboratory model, we can see that reemergence in the field is on the average about 10 % ahead of the laboratory reemergence.

#### Discussion of reemergence

The reason for the difference between laboratory and field reemergence is not totally clear. There are no methodological differences: both materials are egg galleries with deep-frozen insects. Because oviposition was similar in the laboratory and in the field, it is evident that the reason for the difference lies in the behavior of the parent beetles rather than in experiment failure. It is not possible to compare the results with those obtained by Långström (1980b, 1983) because of the different time axes. One possible explanation is that, because the laboratory bolts were held in cages in darkness, the parent beetles did not come out of egg galleries. In any case, the parameter values obtained for the laboratory reemergence cannot be applied in the field.

In principle, there is the inherent variability of poikilotherm development present in the reemergence process of *T. piniperda*. This variability has been modeled for *Dendroctonus frontalis* (Gagne et al. 1982). However, the restrictions with regard to oviposition apply here too. Because we have to rely on field data in reemergence, the sequential arrival pattern makes it totally impossible to construct the distribution of

reemergence rates with the present materials.

Sooner or later, all the parent beetles reemerge unless they die (Långström 1980b, 1983). If the population is composed of two-year-old parent beetles, the survival rate of beetles that are expected to reemerge may differ from the normal case. The present materials do not allow determining of the health condition of the parent beetles: in deep-frozen samples dead parents look similar to living ones. Therefore, we have ignored this subject. In *T. piniperda*, the males always leave before the females (Långström 1980b, 1983). Thus, we can expect a two peaked reemergece curve. The present model was not built to show this; with a good imagination one can see the pattern very slightly in the plot of residuals (Fig 15).

### 34. Development

#### 341. Development in the laboratory at constant temperatures

Parent beetles attacked the bolts in cages at all experiment temperatures but development was not successful below 9.9°C (Table 1). The high mortality of larvae at the lower range of temperatures is probably due to fungi because at the end of the experiment, all bolts were more or less covered by fungi under the bark. As the late developing larvae are more affected by them, a bias may occur in the median emerging days, which can be later in reality. Survival was low also at high temperatures above 29.0°C. Any error sources in the timing of emergence are less obvious there.

The rate of development ( $r = 1/\text{median emergence day}$ ) was modeled as a function of temperature using the material in Table 1. The equation developed by Sharpe and DeMichele (1977) and further elaborated by Schoolfield et al. (1981) and reviewed by Wagner et al. (1984c) was chosen for describing this relation. Among bark beetles, this equation has been used earlier in modeling of *Dendroctonus frontalis* reemergence (Gagne et al. 1982) and emergence (Feldman et al. 1981a, Wagner et al. 1984a). The function is:

$$r(T) = \text{SCALE} * T/298 * \exp(\text{DHA}/R * (1/298 - 1/T)) / (1 + \exp(\text{DHL}/R * (1/TL - 1/T))) + \exp(\text{DHH}/R * (1/TH - 1/T)) \quad (11)$$

where  $r(T)$  = mean developmental rate at temperature  $T$  (°K),  $R$  = universal gas constant (1.989 cal/°/mole),  $\text{SCALE}$  = scaling factor, usually the developmental rate at the reference temperature 298°K,  $\text{DHA}$  = enthalpy of metabolic activation of the process catalyzed by the rate-limiting enzyme,  $TL$  = Kelvin temperature at which the rate-limiting metabolic enzyme is ½ active and ½ low-temperature inactive,  $\text{DHL}$  = change in enthalpy associated with low-temperature inactivation of the enzyme,  $TH$  = Kelvin temperature at which the rate-limiting metabolic enzyme is ½ active and ½ high-temperature inactive,  $\text{DHH}$  = change in enthalpy associated with high-temperature inactivation of the enzyme (according to Schoolfield et al. 1981 and Gagne et al. 1982).

Using the non-linear regression program BMDPAR (for alternate techniques, see Wagner et al. 1984c) with 36 degrees of freedom, the parameters got the following preliminary values:

Parameter	Estimate	Asymp. s.d.
SCALE	0.03665	0.01685
DHA	14358.7	17659.1
DHL	-46559.8	52743.2
DHH	44684.9	26380.1
TL	282.9	7.6
TH	303.9	8.3

The parameter values are somewhat interdependent and thus vague, which can be seen also from their high standard deviations. The estimated mean square error of the model is 1.4339E-06 and  $R^2$  0.9852, which represent a very good fit.

Nutrition was also hypothesized as affecting the developmental rate (5). The present material was highly standardized and is thus not good for pointing up this relation. The amount of food available for larvae is dependent on phloem thickness (Amman and Cole 1983). Phloem thickness was not measured directly here, but bark thickness, ranging from 4 to 14 mm and including phloem, was. When the product of bark thickness and temperature was introduced into the model (11),  $R^2$  grew statistically ( $p = 0.9667$ ) to 0.9868. The correlation was a positive one, but the real significance of the effect is negligible.

The same applies to attack density which increased ( $p = 0.9797$ )  $R^2$  up to 0.9871 with a positive sign. This can be understood as an effect of mortality: larvae hatching later do have a lesser probability of surviving to emergence. Surviving larvae are those that have started earlier than the average. On the other hand, Amman and Cole (1983) have suggested that crowding may stimulate feeding. However, also this effect can be disregarded in the applications of the model, but must be kept in mind in examining the further results.

When comparing the range of observations of the data behind the present model with the field temperature distributions (Figs 6 and 7), we see that the range where the model was developed covers less than half of the temperatures occurring. Although these temperatures are those that contribute most to the development, we need further evidence about the validity of the model outside its calibration range. Therefore, the development of larvae and pupae was monitored at temperatures below 10°C. These were dissected from bolts on 30–31.7.1984 and put in phytotrones at five low constant temperatures. The insects were kept in petri dishes as in Annala's (1969) experiment. Development and survival were inspected after 64 days in 1.10.1984 and the results in Table 7 were obtained. After having fixed 100 % for 8°C and calculating the rate of development at that temperature as being 0.002909/day (corresponding to 343 days theoretical developmental time) according to the preliminary parameter values of the equation (11), the developmental

rates and theoretical times were obtained also for the other low temperatures and are given in Table 7.

Fig 16 illustrates the rate of development as a function of temperature, with plots of material from Tables 1 and 7. New *final* values for the parameters of equation (11) were estimated as shown below. After the material of the low temperature experiment had been included, the course of the curve changed markedly. Below 10°C the developmental rate became less than half of that without the additional five points. The values of the parameters are of the same magnitude as those established for *D. frontalis* development (Wagner et al. 1984a).

Parameter	Estimate	Asymp. s.d.
SCALE	0.04371	0.01672
DHA	19426.1	7034.7
DHL	-76641.1	37839.0
DHH	39960.6	9945.8
TL	281.6	1.5
TH	301.3	4.7

Variation in the material (Fig 16) gets larger at high temperatures with the result that the predictions of the model are not necessarily reliable at temperatures of 30...40°C, which, however, regularly occur under sunlight in the field.

So far, we have only dealt with the median emergence. Actually, emergence of bark beetles occurs over a relatively long period (Fig 17). At high temperatures, emergence occurs early and quickly; at the colder end of the temperature range, the process is slow and requires weeks. The phenomenon can, however, be understood as a result of a single underlying distribution (Sharpe et al.

Table 7. Development and survival of *Tomicus piniperda* larvae and pupae at certain low temperatures from 30.7. to 1.10.1984.

	Temperature °C				
	2	4	5	6	8
Number of larvae	25	29	25	25	25
Number of pupae	55	51	57	47	55
Mortality %	40	64	57	56	46
Developed % from larva to pupa	0	0	0	12	36
Developed % from pupa to adult	0	0	9	9	62
Relative % overall developmental rate	0	0	7	24	100
Developmental rate	0	0	.0002605	.0006836	.0029090
Theoretical duration of total period of development (days)	—	—	4842	1462	343

1977, Wagner et al. 1984b). This is shown in Table 8. Cumulative rate units from the function (11) at times when 1, 10, 20, . . . , 100 % of the population had emerged (so called "shape ratios", cf. Feldman et al. 1981b, Gagne et al. 1982, Wagner et al. 1984a, 1984c, Anderbrandt 1985) were calculated for each temperature. At 10 and 11°C there is a deviation from the average distribution. At these temperatures, emergence seems to occur earlier than expected. The error clearly is due to the selective mortality at these temperatures. Consequently, without having checked the cold end of the temperature range, the model (11) would have strongly biased values below 11°C. Otherwise, the distributions do not change systematically with temperature, which allows the use of rate units for summation of physiological time.

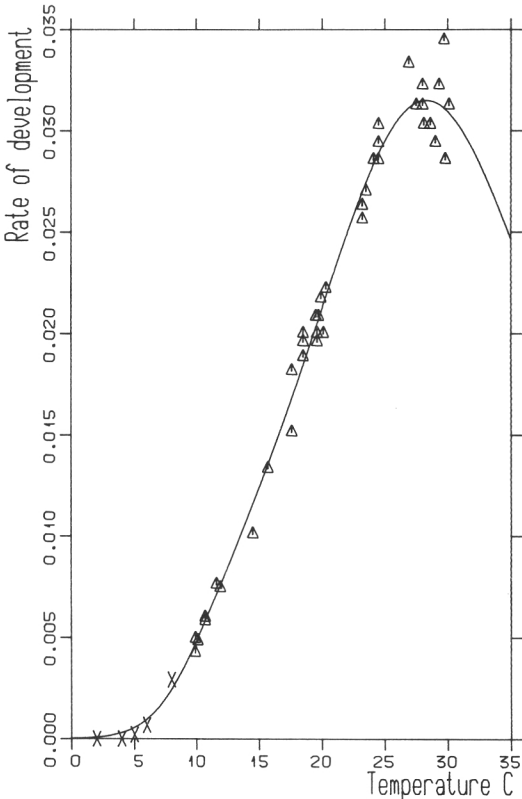


Fig 16. Rate of development in *Tomiscus piniperda* as a function (11) of temperature. Triangles are data from rearing over the entire period of development (Table 1). Crosses are data from the low temperature experiment with larvae and pupae (Table 7).

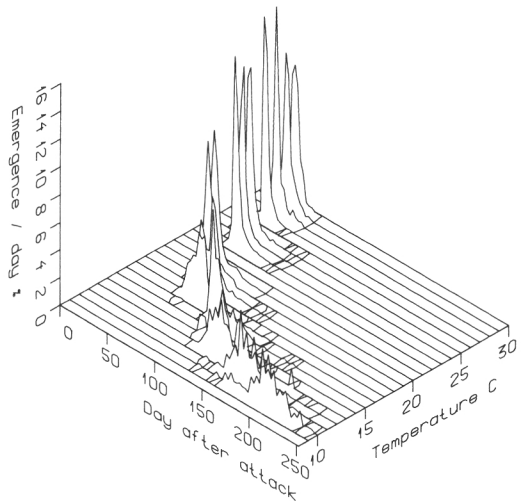


Fig 17. Distributions of *Tomiscus piniperda* emergence days over a range of temperatures.

Fig 18 shows the temperature independent emergence distribution of *T. piniperda*. The following cumulative Weibull model was fitted to it and parameter values below were obtained:

$$\text{EMERGENCE \%} = 100 * (1 - \exp(-(\text{PHYSIOLOGICAL TIME} - \text{START}) / \text{SCALE})^{**} \text{SHAPE})) \quad (12)$$

Parameter	Estimate	Asymp. s.d.
START	0.70833	fixed
SCALE	0.372745	0.003802
SHAPE	2.08689	0.06311

The prediction overestimates emergence by about 3 % between 90 and 96 % emergence. The estimated mean square error is 4.56 and degrees of freedom 30. Although more complicated models predict better (cf. Saarenmaa 1985b), the relatively simple Weibull model is used here to make comparison to field data easier. Due to this convenience, the Weibull model has recently been applied in general models for insect emergence (Wagner et al. 1984b) and tree growth (Krug et al. 1984).

The above variation in emergence times is caused by three factors: 1) Development starts at different times in different broods due to sequential arrival of parent beetles (see Chapter 31.). 2) Eggs of bark beetles are not laid simultaneously but sequentially during the gallery excavation, which means that development starts at different times

Table 8. Distributions of cumulative rate units at different temperatures by the emergence of given proportions of the laboratory population of *T. piniperda*.

Temperature °C	Cumulative rate units by the emergence %										Emerged exx	
	1	10	20	30	40	50	60	70	80	90		100
10	0.572	0.635	0.659	0.676	0.687	0.701	0.720	0.740	0.772	0.810	1.060	570
11	0.593	0.634	0.654	0.671	0.688	0.703	0.721	0.745	0.776	0.832	1.130	1628
13	0.657	0.981	1.098	1.130	1.153	1.184	1.283	1.314	1.430	1.532	1.816	25
14	0.949	0.990	1.000	1.016	1.040	1.060	1.086	1.121	1.187	1.292	1.902	220
15	0.669	0.733	0.782	0.824	0.853	0.887	0.911	0.933	0.971	1.110	1.745	581
17	0.740	0.806	0.842	0.888	0.954	0.993	1.017	1.045	1.075	1.125	1.758	900
18	0.739	0.791	0.824	0.839	0.858	0.880	0.903	0.942	0.981	1.096	1.468	1053
19	0.818	0.851	0.879	0.900	0.919	0.938	0.957	0.985	1.022	1.115	1.751	1723
20	0.871	0.926	0.957	0.992	1.038	1.085	1.154	1.273	1.404	1.575	2.202	4102
22	0.874	0.919	0.934	0.948	0.963	0.978	0.993	1.007	1.023	1.044	1.411	140
23	0.905	0.941	0.960	0.973	0.985	1.012	1.038	1.064	1.113	1.196	1.840	2528
24	0.806	0.841	0.869	0.897	0.925	0.946	0.968	0.994	1.032	1.122	1.893	2762
25	0.802	0.864	0.893	0.923	0.953	0.977	0.988	0.999	1.047	1.153	1.554	171
27	0.815	0.851	0.874	0.893	0.913	0.937	0.963	0.988	1.028	1.121	1.763	760
28	0.855	0.922	0.948	0.971	0.992	1.014	1.041	1.078	1.167	1.291	1.778	789
29	0.792	0.878	0.900	0.930	0.963	0.993	1.020	1.047	1.083	1.176	1.768	357
30	0.736	0.840	0.877	0.913	0.941	0.970	0.999	1.028	1.064	1.127	1.478	125
Average	0.776	0.847	0.879	0.905	0.931	0.956	0.986	1.018	1.069	1.160	1.666	18434

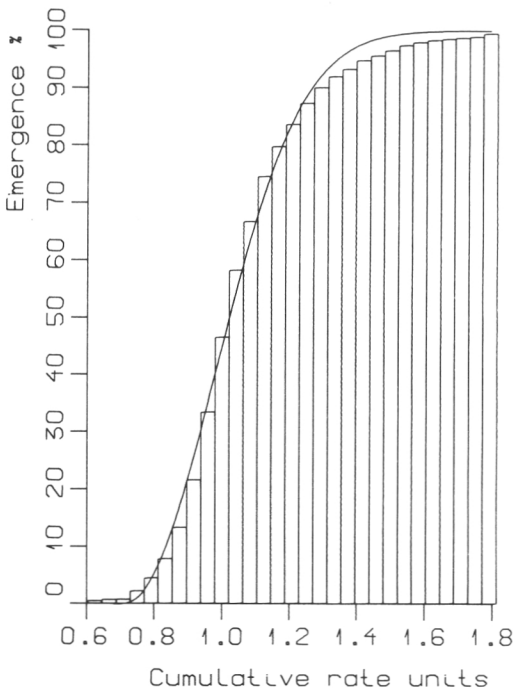


Fig 18. The temperature-independent emergence distribution of *T. piniperda* (histograms) in the laboratory and the cumulative Weibull model (12).

even within a single brood (see Chapter 32.). 3) Development rates vary randomly as in all poikilotherms (Sharpe and DeMichele 1977). Any biophysical simulation model for the emergence of bark beetles has to consider these sources of variation. In Chapters 31. and 32., we already incorporated variation caused by the items 1 and 2 above into the submodels. The third item, randomly varying development times, thus remains. Knowing the oviposition distribution and ignoring the arrival distribution (in the case of the laboratory data) we could estimate the distribution of randomly varying developmental rates under the assumption that survival probabilities of early- and late-hatching larvae are equal. Unfortunately, Jong and Saarenmaa (1985) simulated that the survival probability decreases with age. Therefore, we cannot directly obtain this distribution, but, however, by building on the models of arrival and oviposition and using the successive sampling data it can be iteratively estimated. The job remains to be done in Chapter 362. after all the model elements have been constructed.

Table 9. Density of *T. piniperda* attacks /m<sup>2</sup> (upper part) and production /m<sup>2</sup> (lower part) in the study stacks.

Level (m from top of stack)	Rovaniemi			Pallasjärvi	Enontekiö exposed		Enontekiö shaded	
	1980	1981	1982	1981	1982	1983	1982	1983
	A t t a c k s / m <sup>2</sup>							
0.0 m upside	102	179	99	106	24	52	18	37
0.0 m underside	78	142	71	68	10	12	2	8
0.2 m	70	113	54	17	3	18	0	3
0.5 m	12	54	15	1	0	7	0	2
1.0 m	5	28	7	0	0	6	0	3
1.5 m	2	12	5	0	—	—	—	—
	E x i t h o l e s / m <sup>2</sup>							
0.0 m upside	734	422	656	384	63	631	0	124
0.0 m underside	860	182	305	72	5	175	0	2
0.2 m	716	105	149	17	0	32	0	0
0.5 m	339	188	79	0	0	35	0	5
1.0 m	152	78	36	0	0	78	0	68
1.5 m	136	5	36	0	—	—	—	—

### 342. Development in the field

As background for scrutinizing the field data, attack density and production of *Tomiscus piniperda* in the study stacks are shown in Table 9. It is interesting to see how the density doubled in Rovaniemi from 1980 to 1981, but dropped again thereafter. A similar increase in the local beetle population can be seen in Enontekiö. At the lower layers of the stack, only a small proportion of the beetles are found when compared with the top level. This is because the temperatures inside of the stacks are close to zero at the time of swarming (Saarenmaa 1981). The distribution of *T. piniperda* in the stacks is similar to that reported in previous studies (Ehnström 1976, Heikkilä 1978, Juutinen 1978, Långström et al. 1984).

Usually about 10 % of *T. piniperda* emerge through bark furrows without leaving any visible signs in the bark (e.g. Salonen 1973, Saarenmaa 1983). They may also emerge through the same holes, although this happens in a smaller degree in *T. piniperda* than e.g. in *Ips typographus* (cf. Schlyter et al. 1984). Throughout the rest of this study, exit holes are used as the equivalent of emergence in order to reduce the complexity of calculations. This causes a systematic error, which must be borne in mind in examining the results.

There are several points of view from which the development of a field bark beetle population from egg to adult can be examined in the light of the successive sampling data.

First, the axis against which the data is drawn can be time, degree-days, or physiological time (cumulative rate units). The primary material of calculations, frequencies of the living specimens of the different developmental stages, can be either absolute amounts found in samples, amounts /m<sup>2</sup> bark area, or percentages of sample. Moreover, we may either accept these numbers as such and average the replications within a sampling time, or we may process these means further in order to average the numbers within a stage through time. If numbers within a sampling time are considered, manipulation of the data is not great, sampling error is still visible in the frequencies, and confidence estimators for the means within a sampling day are easy to calculate. In order to show the variability and reliability of the material clearly, this kind of presentation of the development, percentages of sample on a physiological time scale, is shown here in Fig 19 and the standard errors in Fig 20. The other point of view, percentages of stage on a time scale, has already been published (Saarenmaa 1985b). However, this latter method does not permit calculating of any reasonable confidence estimators. All these transformations can be done using the BBDB system.

Differences in the development of *Tomiscus piniperda* between the stack levels, years, and study sites are huge (Fig 19). In Rovaniemi in 1980, emergence starts at the sunlit top level of the stack in the first week of July and is over by the beginning of August. At the lowest levels of the same stack, emer-

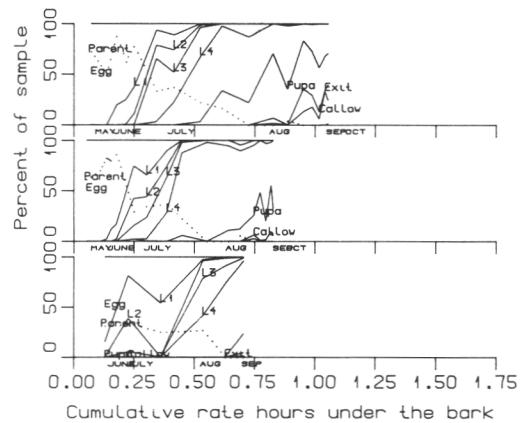
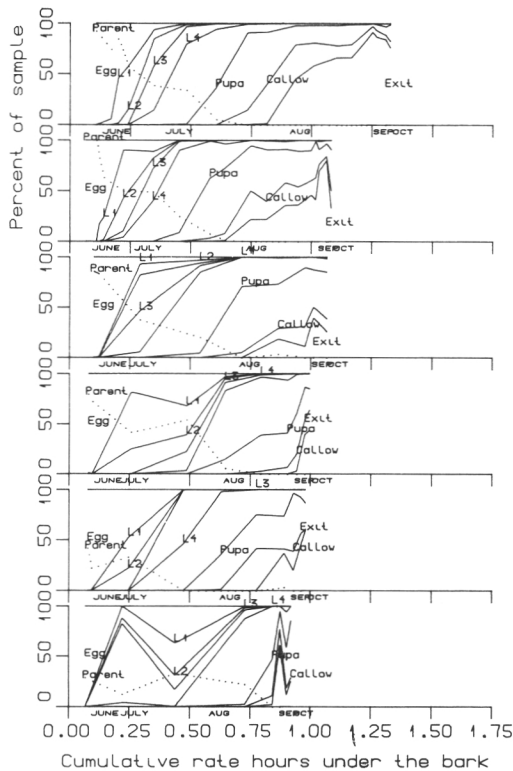
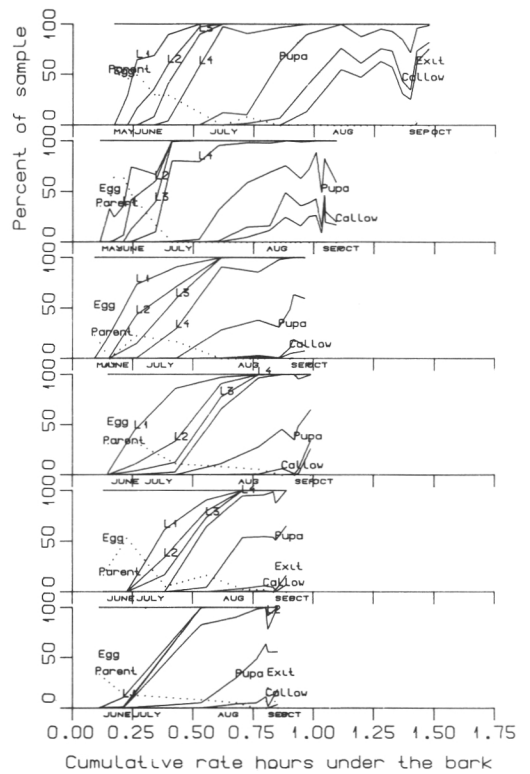
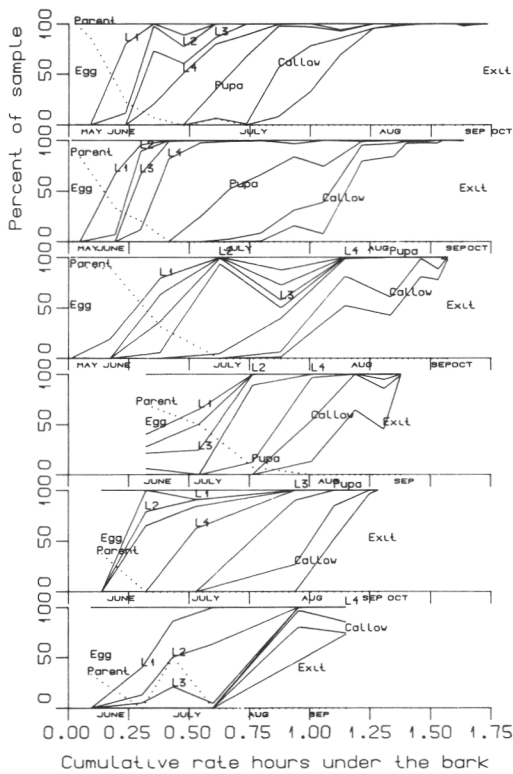


Fig 19. Development of *Tomiscus piniperda* in the field. The data are average proportions (%) of samples. X-axis is cumulative rate units summed up hourly from equation (11). The beginnings of the months are indicated under the axes by the first letter of the abbreviation.

Part I. Rovaniemi 1980 (upper left), 1981 (upper right), 1982 (lower left), Pallasjärvi 1981 (lower right). The stack levels are (top-down) 0.0 m upside, 0.0 m underside, 0.2 m, 0.5 m, 1.0 m, and 1.5 m; in Pallasjärvi only the three first ones.

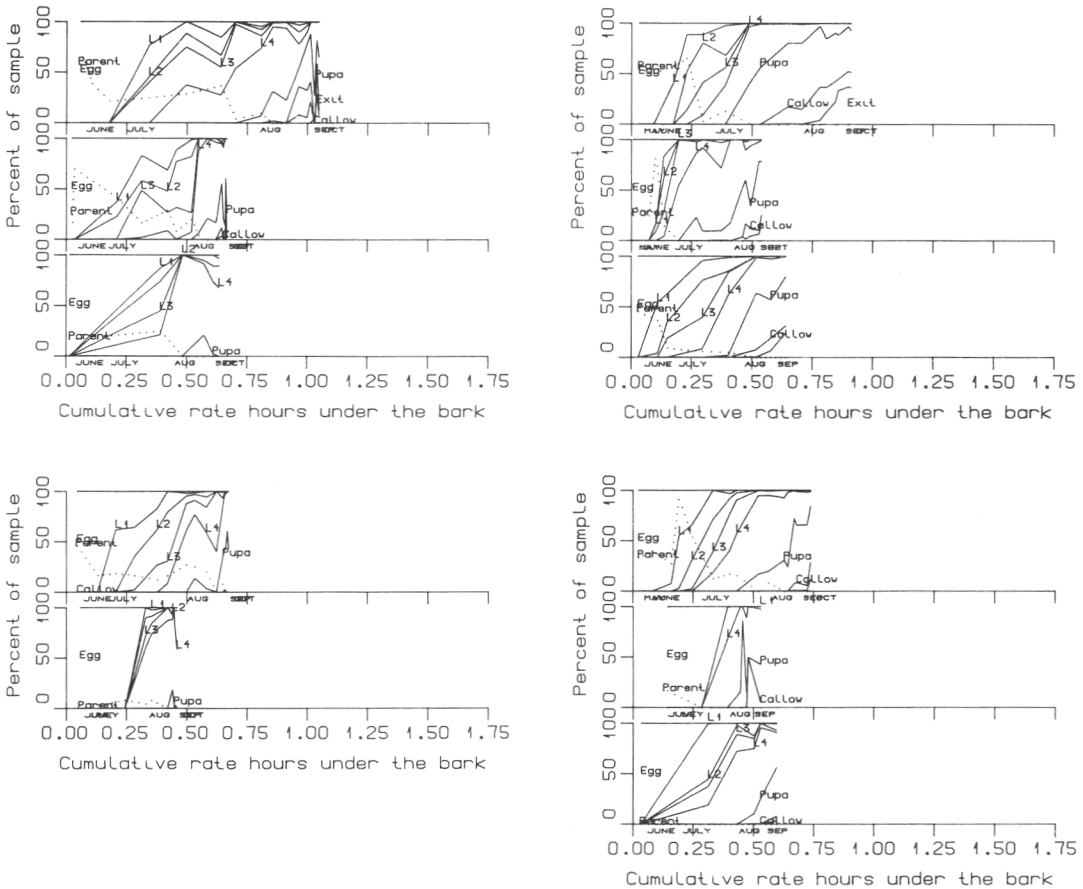


Fig 19, part II. Enontekiö exposed 1982 (upper left), 1983 (upper right), and shaded 1982 (lower left), 1983 (lower right). The three stack levels are 0.0 m upside, 0.0 m underside, and the rest from 0.2 to 1.0 m combined.

gence starts at the same time as it ends at the top level, and is almost over by October. In 1981 at the same site, emergence starts at about the 20th of July, and by the onset of winter, no more than about 2/3 of the sample is exit holes. At the lower stack layers, emergence starts only at the end of August and in September with virtually no results. In 1982 in Rovaniemi, the course of development was slightly more rapid than in the previous year. In Pallasjärvi in the middle of September in 1981, about 1/3 of the sample was exit holes at the sunlit side of the top level with none inside of the stack. Wisely avoiding these conditions, there were no beetles in the lower levels of the stack. In the sunlit stack of Enontekiö in 1982, the final result of development was similar to Pallasjärvi in the previous year, but the

course was entirely different. Due to the coldness of June 1982, the development actually did not start before July. In the shaded stack there was no emergence. In 1983 at the same site, development had again a very different course, but with the same end result. Summarizing, in one out of 8 experiments *T. piniperda* had enough time to go through its development totally before the onset of winter. It is no more surprising that the attack density decreased in the Rovaniemi stack in the third year of experiment (Table 9).

The variation *within* a sampling day between the replications, the number of which varied from 2 to 7 (see Table 2), was considerable. This is not surprising, since the stacks are not uniform; there always are some logs in a stack that are more exposed

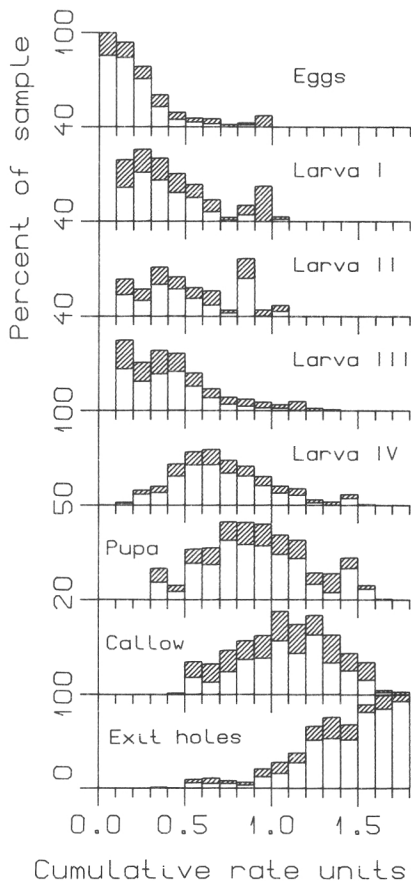


Fig 20. Means (total bars) and single standard errors of the mean (hatched bars) of the proportions of stages within a sampling day. The data are classified and averaged on a cumulative rate unit axis.

than average. Single average standard error of the proportion of a stage generally was about 1/3 of the estimate, as Fig 20 shows. I consider the accuracy of the estimates as varying between satisfactory and hardly tolerable, depending on the material subset.

Most of the variation *between* experiments is clearly due to differences in the accumulation of rate units; the length of the curves on the x-axes of Fig 19 is its pointer. E.g., we can see that in the northernmost sites, the amount of cumulative rate units does not always reach even 0.5 (median emergence occurs at 1.0 according to the laboratory model). Although the cumulative rate unit axis is good in explaining the differences in the development, some extra variation still remains. Most pronounced is the slow de-

velopment in 1981 in both Rovaniemi and Pallasjärvi when compared with the other years. Which factors are responsible for these differences?

The effects of attack density, bark thickness, and water content of the bolt on the development were evaluated. Bark thickness and attack density may affect development through nutrition, although the laboratory data had already indicated that the effects of these factors are negligible. The mechanism by which the moisture of tree can affect development is less obvious, but, because the development was slowest in the wettest summer (Table 4), a possible effect was also examined.

Stepwise regression was used to test the effects of the above factors on the timing of emergence of *T. piniperda*. A base cumulative Weibull model (12) was first constructed for the material from Rovaniemi in Fig 19. A total of 283 bolts (or bolt sides at the top level) was used in the analysis. Linear terms of attack density, bark thickness, and water content were then introduced into the base model, and the significance of the regression coefficient was tested. The following table shows the results:

Model	R <sup>2</sup>	P of increment	Effect on development
Base model	0.5164		
— Attack density	0.5715	1.000	negative
— Bark thickness	0.5215	0.881	none
— Water content	0.5283	0.983	negative

On the basis of these results, we can reject bark thickness from further consideration. The effect of attack density is just the opposite of that observed in the laboratory. Since bark thickness did not have any effect on development, it is not likely that starving resulting from a high attack density has any either. The result obtained here can be interpreted as an intercorrelation between precipitation and attack density: after the favorable summer of 1980 there was a high *T. piniperda* population at the study site, which resulted in a high attack density in the following rainy summer. Thus, only the water content remains to be considered, but its effect in this analysis seems to be too low to have any importance. However, the present data are not necessarily valid for pointing up this relation, since the fact that the moisture of sapwood is much higher than the average

Table 10. Water content (% of dry weight) at the different levels (dm from the top of the stack) in the pine pulpwood stacks in Rovaniemi 1980, 1981, and 1982.

Period	1980			1981			1982		
	0	Level 2-5	10-15	0	Level 2-5	10-15	0	Level 2-5	10-20
20.5-10.6	116	126	110	114	123	130	87	105	94
11.6-30.6	83	106	103	126	113	133	100	95	87
1.7-10.8	69	84	82	99	115	110	83	95	102
10.8-30.9	51	78	90	107	99	96	93	80	86

is ignored. The differences in the water content of the bolts between the years are considerable (Table 10). In the rainy summer of 1981, the water content of the bolts did not decrease through the midsummer as normally. Thus we have circumstantial evidence on the effect of precipitation. It is possible to correct physiological time using rainfall data, but before doing so the underlying mechanism of its effect must be understood.

A test was conducted to determine whether or not the distribution model for the laboratory emergence (12, Fig 18) is sufficient for describing emergence in the field. To achieve this, a series of transformations of the data was necessary. The changes in the frequencies of exit holes /m<sup>2</sup> (= their numerical derivatives) were summed up throughout the seasons in all the study stacks and layers. Then the amounts were divided by the total in order to obtain a relative emergence curve in the experiment. This curve had to be corrected downwards by the proportion of the immature stages found in the last sample in order to take into account the fact that they would have emerged had the winter not set in too early. In order to reduce the sampling error, those samples where the numbers of exit holes diminished from previous sampling day (that is impossible in *T. piniperda*) were combined. As a result, the observation matrix does not indicate merely that e.g. 50 % of the sample is exit holes, but that 50 % of the emergences have occurred. Thus we have emergence curves comparable with those in the laboratory.

Fig 21 shows the fit of the material with the laboratory data. Emergence seems to occur later in the wild; the difference is about 15 %. The worst deficiencies occur in the

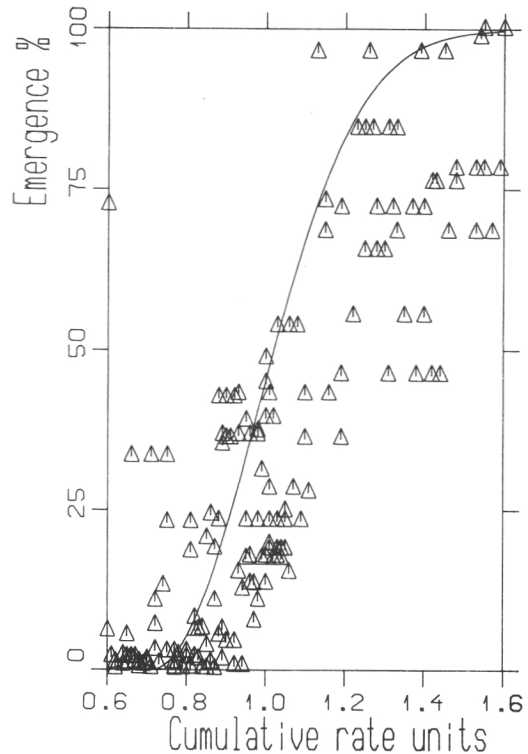


Fig 21. The fit of the laboratory emergence distribution model (cumulative Weibull (12), Fig 18) with the field data. The triangles indicate sampling days.

rainy summer of 1981, and the best fit is in hot 1980 (see also Fig 19). The fact that development is most rapid in the laboratory, where there is no precipitation, supports the hypothesis that rainfall must be present in the physiological time model for *T. piniperda*. Other factors that can be responsible

for the difference are the use of exit holes instead of emergences, sequential attack in the field, and differences in mortality rates between the materials.

The final step in the analysis of development in the field is to estimate the transition times from stage to stage (6). For this purpose, a corresponding transformation from sample averages to stage averages was done for the numbers of all the stages as was done for the exit holes above. The situation is different with other stages, however, since their numbers can and do decrease in time. Hence, the sampling interval should be constant with regard to physiological time, and this, of course is not the case. As a consequence, the numbers late in the season are over-weighted. To overcome this, the numbers were multiplied by the amount of cumulative rate units accumulated between the sampling days. However, this cumbersome series of transformations has not yet been finished. We must consider whether or not the intervals from median to median represent real durations of stages. By considering the factors that cause variation in development times (see the end of Chapter 341) one at a time, it can be shown that they do, provided that the material is detrended for mortality. Using percentages of stages in samples as starting values (on the contrary for using frequencies /m<sup>2</sup> as above for exit holes), this condition is fulfilled. Table 11 shows the result: median cumulative rate units for each stage and the durations of the stages. The 4th and 3rd larval stages are the

longest ones while the young larval stages are quickest over.

### 343. Overwintering of brood

What happens to those immature *Tomicus piniperda* that have not left their growing sites by the onset of winter? Does the slow rate of development act as an indirect mortality factor? Studies about cold-hardiness of *T. piniperda* may give some hint about it. According to Bakke (1968), the super-cooling points of *T. piniperda* larvae is  $-12.5^{\circ}\text{C}$ , and those of older stages about  $-18^{\circ}\text{C}$ . Acclimation to low temperatures enhances cold-hardiness of adults, but  $-10^{\circ}\text{C}$  is fatal in a few days, and at  $-15^{\circ}\text{C}$ , the beetles die in a few hours (Annala and Perttunen 1964). The importance of acclimation in this context has also been emphasized by Ehnström (1963).

The results obtained here indicate that the species, when acclimated to slowly decreasing temperatures, can tolerate much more coldness than the studies above indicate. Table 3 shows emergence of *T. piniperda* in the experiment where bolts were taken indoors at regular intervals during the autumn and winter of 1982. Not all the bolts contained insects, but it seems that there is no decline in survival despite the exposure even to  $-31.4^{\circ}\text{C}$ .

When bolts were taken indoors from the thinning experiment in the middle of winter, only one living callow *T. piniperda* adult was found among hundreds of dead larvae, pupae, and callow adults when the 8 bolts were dissected. Out of the 18 rearing cages, 7 adults emerged. These were put into other cages with fresh shoots and bolts. They fed on the shoots and bred successfully. When the experiment was repeated in May, however, no living *T. piniperda* were found. The temperature regimes to which these beetles were exposed before taking them to the laboratory are not exactly known, but they were exposed for weeks to  $-25^{\circ}\text{C}$ ... $-35^{\circ}\text{C}$  under a snow cover of 5...20 cm during November and December.

These experiments, although incomplete, indicate that *Tomicus piniperda* may survive the winter even in the conditions prevailing in Lapland at an immature stage. Thus a partial two-year generation can occur, although the proportion of survivors is small.

Table 11. Median cumulative rate units for the developmental stages of *Tomicus piniperda*, and the durations of the stages. Material is Rovaniemi 1980, 1981, and 1982. The number of curves decreases towards later stages due to untimely termination of development.

Stage	Median	Standard deviation	Number of curves	Duration
Egg	0.14	0.06	18	0.12
Larva 1	0.26	0.08	18	0.05
Larva 2	0.31	0.11	18	0.06
Larva 3	0.37	0.09	18	0.20
Larva 4	0.57	0.09	17	0.28
Pupa	0.85	0.10	17	0.16
Callow adult	1.01	0.14	11	0.14
Emergence	1.15	0.16	9	—

### 35. Survival

The generalized brood survival rate was expressed as a function of temperature, physiological time and attack density (7). If individual larvae are considered, their age differences must also be taken into account. When mortality agents act during the larval development, survival of the brood diminishes in time. Undoubtedly we can use the cumulative rate unit scale that has been applied for the other life cycle events of *T. piniperda* as well as the physiological time scale for the survival. The effects of the most important mortality agents of *Tomicus piniperda* are positively density-dependent, and consequently, mortality is directly related to density. Taking into account that changes in the numbers of insect populations usually occur on a logarithmic scale (Varley et al. 1980), we can formulate the brood survival as being:

$$\begin{aligned} \text{SURVIVAL \%} = & \text{INITIAL SURVIVAL} \\ & - \text{INITIAL SURVIVAL} * \text{PHYSIOLOGICAL} \\ & \text{TIME} * 24 / (1 + \exp(\text{PARAM\_1} \\ & + \text{PARAM\_2} * \text{PHYSIOLOGICAL} \\ & \text{TIME})) + \text{EFFECT OF DENSITY} * \\ & \ln(\text{ATTACK DENSITY}) * \text{PHYSIOLOGICAL} \\ & \text{TIME} \end{aligned} \quad (13)$$

The material that was used to estimate the parameters was collected in Rovaniemi 1980, 1981, and 1982, and retrieved from BBDB. A total of 622 bolts (or bolt sides at the top level) were present in the analysis. Survival % was calculated as the ratio of live specimens of *T. piniperda* (including exit holes) and the number of egg niches. The number of egg niches is not accurately determinable late in the season. In these cases, comprising about one half of the material, an estimate was used instead. The estimate was calculated as follows:

$$\begin{aligned} \text{NUMBER OF EGG NICHES} = \\ \text{NICHE DENSITY} * (\text{LENGTH OF EGG GALLERY} \\ - \text{LENGTH OF NUPTIAL CHAMBER}) \end{aligned} \quad (14)$$

The estimate for NICHE DENSITY is 0.761/mm (s.d. = 0.268, n = 884), and for the LENGTH OF NUPTIAL CHAMBER 7.7 mm (s.d. = 2.0, n = 884) in the laboratory and Rovaniemi 1980 materials.

The estimates for the parameters of the equation (13) with 618 degrees of freedom, residual mean square 266.1, and R<sup>2</sup> 0.537 are as follows:

Parameter	Estimate	Asymp. s.d.
INITIAL SURVIVAL	82.45	2.57
PARAM_1	3.0052	0.0978
PARAM_2	0.9065	0.1071
EFFECT OF DENSITY	-4.4675	0.7384

INITIAL SURVIVAL includes both the the percentage of empty egg niches and also some egg mortality. In another material (Saarenmaa 1983), an estimate of 87.3 for the percentage of empty egg niches has been obtained. The other parameters do not have direct interpretations. Fig 22 shows the projection of model (13). There is no logistic S-shape in the model, although the model would allow it; survival decreases directly right from the beginning, approaching about 45 % at the lowest density but only about 5 % at the highest by the time of the final emergence.

For the validation of the model, other material, collected at the northern study sites at Pallasjärvi and Enontekiö, was retrieved from the BBDB data base. For this material the parameters got the following values with 480 degrees of freedom:

Parameter	Estimate	Asymp. s.d.
INITIAL SURVIVAL	81.90	2.99
PARAM_1	3.0865	0.1671
PARAM_2	0.5885	0.1911
EFFECT OF DENSITY	0.0000	0.0000

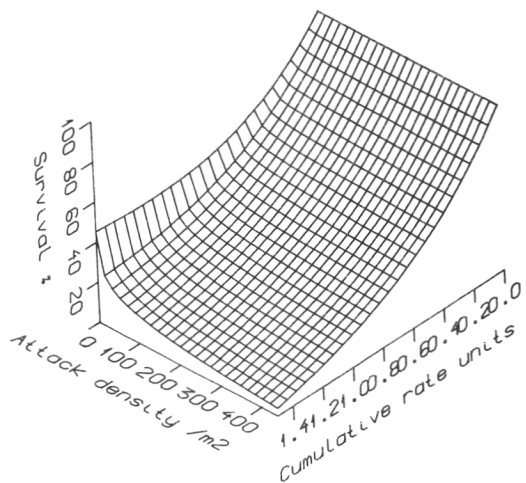


Fig 22. The brood survival model (13).

PARAM\_2 is statistically significantly different ( $0.95 < p < 0.99$ ) from the one of the initial material. At first glance it is striking that attack density does not have any effect in the validation material. However, the balancing of the material was very different when compared with the Rovaniemi data. Only about 10 % of the attack densities were higher than  $100/m^2$ , and, moreover, there were no data beyond the cumulative rate unit of 1.05. Hence, we cannot conclude much about this analysis. What is important, however, is that the prediction of the Rovaniemi parameters is not severely biased in the validation material (Fig 23). Only at the highest survivals does the model overestimate the real survival.

A simulation based only on a brood survival model would yield too prolonged an emergence if individual larvae are considered in the process. For this reason, we must explore the survival process with respect to age distribution of the larvae, too. With the present data from successive sampling and facing the fact that most of the dead larvae have disappeared while the

mortality factors act, it is not an easy task to determine the survival probabilities of larvae in relation to stage. Life-tables or population tables are one possibility. They have been constructed for a small number of bark beetles, e.g. for *Scolytus scolytus* F. (Beaver 1966), *Scolytus ventralis* LeConte (Berryman 1968, 1973), *Dendroctonus brevicornis* Hopkins (DeMars et al. 1970), and *T. pini-perda* (Galaseva 1976). Life-tables are not particularly useful for bark beetles because they ignore the functional responses of mortality factors. Furthermore, estimation of disappearance becomes a major problem. A model has been developed to do that (Jong and Saarenmaa 1985), but its application would lead to an analysis of the entire array of mortality factors, which is out of the scope of the present study.

Two alternate techniques to determine the functional responses of survival of individual larvae were thus developed, and they are reviewed in the following. Ideally, we need a set of models giving the probability of survival for all the stages in given conditions defined by density and physiological time. By summing up the numbers of all stages per unit of area divided by the probability ( $P_{-}$ ) of surviving until the particular stage, an estimate of the number of egg niches is obtained:

$$\begin{aligned} \text{EGG NICHE} = & \text{EGG}/P_{\text{EGG}} \\ & + \text{LARVA 1}/P_{\text{LARVA 1}} + \text{LARVA 2}/P_{\text{LARVA 2}} \\ & + \text{LARVA 3}/P_{\text{LARVA 3}} + \text{LARVA 4}/P_{\text{LARVA 4}} \\ & + \text{PUPA}/P_{\text{PUPA}} + \text{CALLOW}/P_{\text{CALLOW}} \\ & + \text{EMERGED}/P_{\text{EMERGED}} \end{aligned} \quad (15)$$

For example, if there are 500 callow adults and 500 exit holes in the sample, with respective probabilities of 0.17 and 0.15 reaching these stages, there would be 6276 egg niches in the sample. When estimated from the material of Rovaniemi, the probabilities became:

Stage	Probability	Asymp. s.d.
P_EGG	0.68	0.05
P_LARVA 1	1.02	0.24
P_LARVA 2	0.39	0.08
P_LARVA 3	0.53	0.10
P_LARVA 4	0.38	0.02
P_PUPA	0.35	0.03
P_CALLOW	0.14	0.01
P_EMERGED	0.18	0.01

As can be seen, the probability is related to the duration of the stage, and can be even greater than 1, and, due to the nature of the

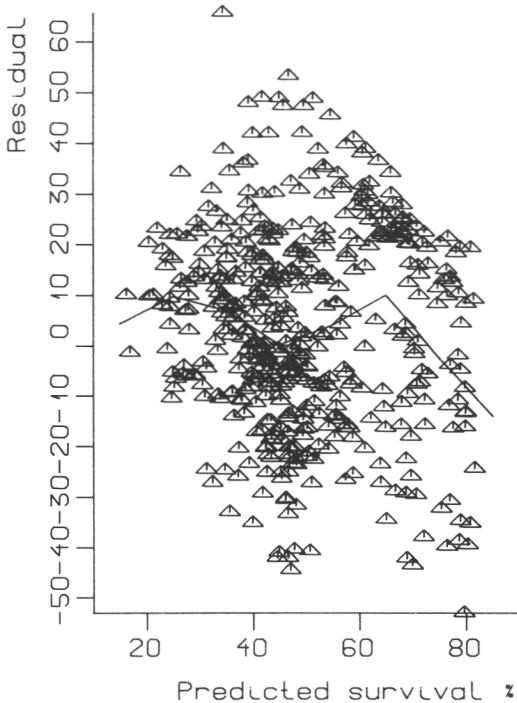


Fig 23. Residuals (observed—predicted survival-%) of the brood survival model (13) in the validation material.

Table 12. An example of the numbers/m<sup>2</sup> of *Tomicus piniperda* stages over a range of summer days (upper part) and the respective survivals (% , lower part) at each stage over the sampling period.

Month	Day	Cumrate	Niche/Born	Egg	L1	L2	L3	L4	Pupa	Callow	Exit	Gallery
6	2	0.109	3255.8	2742.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	116.0
6	9	0.171	4998.9	3050.9	211.4	0.0	0.0	0.0	0.0	0.0	0.0	122.0
6	16	0.201	5234.7	2146.1	1756.0	74.5	0.0	0.0	0.0	0.0	0.0	106.8
6	23	0.242	5063.3	1267.2	1418.5	536.5	9.0	0.0	0.0	0.0	0.0	83.9
6	30	0.348	6097.4	87.0	193.9	651.0	1228.7	440.3	0.0	0.0	0.0	124.2
7	7	0.484	4207.5	0.0	15.2	41.4	313.6	1583.5	15.9	0.0	0.0	78.5
7	14	0.606	4661.3	0.0	0.0	6.3	85.6	851.2	585.6	0.0	0.0	81.9
7	21	0.734	5023.5	0.0	0.0	0.0	3.3	112.2	965.3	199.6	7.4	101.8
7	28	0.816	5518.7	0.0	0.0	0.0	2.6	79.8	483.3	404.2	17.8	109.1
8	4	0.934	5463.7	0.0	0.0	0.0	0.0	30.6	279.8	387.8	420.7	84.0
<hr/>												
6	2	0.109	2742.4	100.0	—	—	—	—	—	—	—	—
6	9	0.171	520.0	100.0	100.0	—	—	—	—	—	—	—
6	16	0.201	714.2	65.3	100.0	100.0	—	—	—	—	—	—
6	23	0.242	0.0	50.3	100.0	100.0	100.0	—	—	—	—	—
6	30	0.348	0.0	0.0	7.8	46.9	100.0	100.0	—	—	—	—
7	7	0.484	0.0	—	10.4	15.3	27.1	96.8	100.0	—	—	—
7	14	0.606	0.0	—	—	0.0	99.8	90.3	93.9	—	—	—
7	21	0.734	0.0	—	—	—	41.4	58.9	91.3	97.4	—	—
7	28	0.816	0.0	—	—	—	61.7	48.2	84.9	95.9	—	—
8	4	0.934	0.0	—	—	—	—	37.3	53.2	29.9	—	—

material, it is also the probability from the middle of a stage to the middle of the next one. Now substituting the probabilities (P<sub>-</sub>) in the function (15) for the function

$$P_{-}(\text{STAGE}) = f(\text{ATTACK DENSITY, PHYSIOLOGICAL TIME}) \quad (16)$$

or even better

$$P_{-}(\text{STAGE}) = f(\text{DENSITY OF ELDER INDIVIDUALS}) \quad (17)$$

these functional responses can be evaluated. However, the result is of little use since the scaling is unknown. It is not convenient to use the durations of stages estimated in the previous chapter to do this, since any possible errors in them would have drastic effects here. Therefore, an alternative technique was used.

Table 12 shows an excerpt of output of the BBDB system, numbers/m<sup>2</sup> of live *T. piniperda* stages through a season. Let us consider a single sampling time, e.g., July 7th. Where have the insects found at that time come from? Obviously they must have been there a week earlier, on June 30th. If we explain the occurrence on July 7th by understanding that the insects have come from the same stage, or one stage younger,

or two stages younger (etc. in this order) from the sample a week earlier, those insects that are not needed for explaining the occurrence have perished. If there are any insects left unexplained after the loops, these obviously have born there, or can be accounted for through the sampling error. Disappearance will be handled automatically, but it can be accounted for a too early stage. By explaining the dead ones that have been found, we can correct the numbers a little bit. By dividing those insects that are not needed for explaining the occurrence at the next stage by the respective total, we get mortality for one stage at a time. The lower part of Table 12 shows the result.

Fig 24 shows the summation of this kind of analysis for all the materials in Rovaniemi 1980, 1981, and 1982. The histograms are probabilities by which an insect survives in a stage over a time interval that is equal to the width of a bar. We can see that the survival of the early stages goes down very quickly. Because a larva goes through the system largely in the same relative position of the distribution, the first ones have very good opportunities to survive while the last ones most probably will die. A shortcoming of this approach is that any possible interaction of time and density is not shown. After constructing Fig 24 as a table against

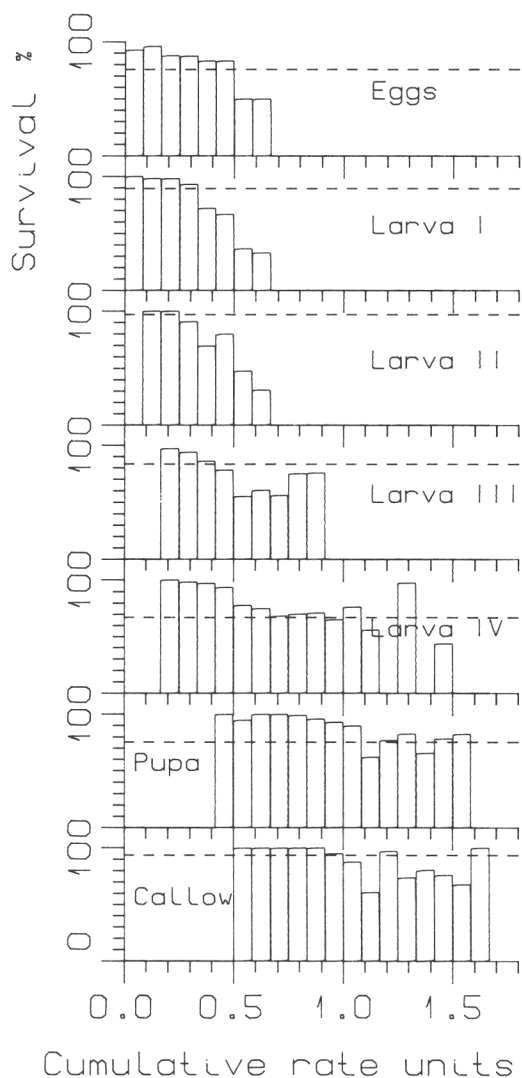


Fig 24. Probabilities (%) by which a *Tomicus piniperda* in an immature stage survives over a physiological time interval. The dashed line is the mean probability of surviving over a stage calculated as the maximum ratio of live specimens and egg niches.

which the brood survival model is corrected during the development and survival simulation of individual larvae, the model elements have now been finished.

#### Discussion of survival

Berryman (1974) reviews the productivity of bark beetles and introduces a survival model including a co-operation curve at low

densities to overcome host resistance and a competition curve that decreases survival at higher densities. In *T. piniperda* the co-operation phase seemingly does not exist, obviously because the species lives in a dead tree material. Coulson et al. (1977) describe the survival as a dynamic process over normalized time in *Dendroctonus frontalis*. The present model (13) is a combination of the ideas above. It is an oversimplification so that it does not bring any understanding to the processes, as the survival probability models for different stages would do. However, survival of *T. piniperda* generally follows the same course, and within a year, it can be predicted without considering the individual mortality agents.

### 36. Model integration

In the five preceding sections, submodels for the pertinent processes in the within-tree population dynamics of *Tomicus piniperda* were built, tested and discussed. Now it is possible to integrate the separate models into a working model that predicts the timing and frequency of emergence.

#### 36.1. Model structure

It is important to notice that all the models use a common physiological time with the exception of arrival (8), which uses daily maximum temperatures. Utilizing this feature, there are two main ways by which the model integration can be done. First, we may project all the models against the common cumulative physiological time axis and take estimates of densities from desired points on it. A corresponding bark beetle population dynamics model, TAMBEETLE, which simulates the life processes of *Dendroctonus frontalis* (Turnbow et al. 1982, Wagner et al. 1984a), operates this way. Using an infested bole or a brood log as the basic unit, the approach is highly effective in computing time. It also facilitates direct use of the brood survival model (13) in simulation.

However, because the model has not been tested yet, and because it is likely that there are dynamic interactions between the sub-models, an individual larva is adopted as the basic unit of the simulation. At this phase of modeling this is even a necessity, since in the

preceding sections we were not able to incorporate the required variability into the development times (Sharpe et al. 1977, Wagner et al. 1984b). However, simulating of the development of individual larvae through the season on hourly steps will be inefficient in the applications of the model, and in future work the model structure must be revised.

The basic unit of the simulation is (quite arbitrarily) one square meter of bark surface. This includes a maximum of 400 egg galleries\* 60 eggs = 24000 larvae. In the model there are four state variables, i.e., vectors with the above number of elements, each containing storage for 1) stage and health of an individual larva, 2) cumulative rate units for it, and 3) its individual relative reaction rate. In addition, there is 4) storage for the cumulative rate units of the ovipositing and reemerging individual parent beetles.

The contents of the above state variables are determined in a loop that simulates the processes in time. The following is a condensed presentation of the program:

```

call get_simulation_target
do time = begin, end
  call get_temperatures_from_database (time,
    temp_under_bark, air_temp, air_temp_sum)
  physiol_time = physiol_time +
    f (temp_under_bark)
  call arrival (air_temp, air_temp_sum)
  call oviposition (physiol_time, attack_density)
  call reemergence (physiol_time, attack_density)
  call development (physiol_time, stage_limits)
  call survival (physiol_time, attack_density,
    stage_weights)
  call output
end do

```

During the early phases of the program execution, arrival, oviposition and reemergence dominate. As in real life, they soon cease and the emphasis shifts to development and survival. The largest effort in computing is required when random larvae are being killed in the survival subroutine. A comprehensive picture of the process can be obtained by examining the submodels in Figs 16, 9, 12, 14, 22, 24, and in Table 11 along with the above program scheme.

### 362. Model calibration

There is a point in the model that needs calibration. With the present data, randomly varying individual reaction rates can only be introduced into the model when all the other

elements are finished. There is no empirical data for this subject for *T. piniperda*.

The data from Rovaniemi in 1980, 1981, and 1982, a total of 18 sets of successive sampling data were used as the material for calibration. The goal of calibration was to achieve unbiased timing of emergence which was attempted by drawing the average curve of percent emergence in the data against physiological time axis. The simulated values were plotted accordingly. If there is no variability in the developmental rates of the larvae, the picture is strongly biased (Fig 25 a).

In other insects studied, the range of the developmental rate is generally about one half of the mean (see e.g. Sharpe et al. 1977, 1981, Barfield et al. 1977, Shaffer 1983, Régnière 1984), which can be used as a starting value for the distance of the displacement in the iterations (i.e., if the mean of the rate is 1, then the range is from 0.75 to 1.25, and the displacement distance 0.25). The distribution about the mean can be described by normal or quadratic distributions (Sharpe et al. 1977, Wagner et al. 1984b),

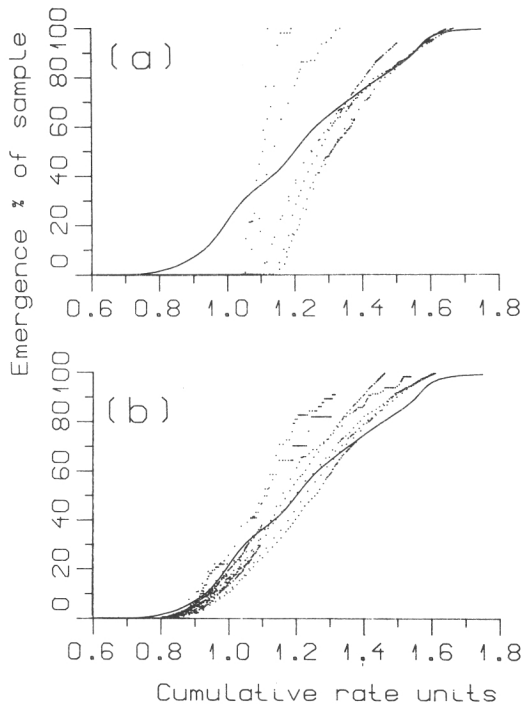


Fig 25. The average real (solid curve) and the simulated (dots) emergence percents of sample. (a) randomly varying developmental rates not included. (b) a randomized rate (see text for distribution) included.

but it may also be asymmetric (see Gagne et al. 1982, Régnière 1984). I have chosen normal distribution due to its convenience in probability estimation. While the the 5 % point of the normal distribution was fixed to the minimum displacement distance, 50 % to the mean, and 95 % to the maximum and the distribution was truncated at the ends beyond the distance, the distance was allowed to loop to obtain the maximum fit, which was found at a distance of 0.33. The result is shown in Fig 25 b.

### 363. Model validation

The result of the calibration was satisfactory, but a slight bias occurs at the end of emergence. There are several possible reasons for this: variation in the oviposition rate was not considered, the distribution of rates may not be symmetric, or mortality may act differently than in the design of the model. The

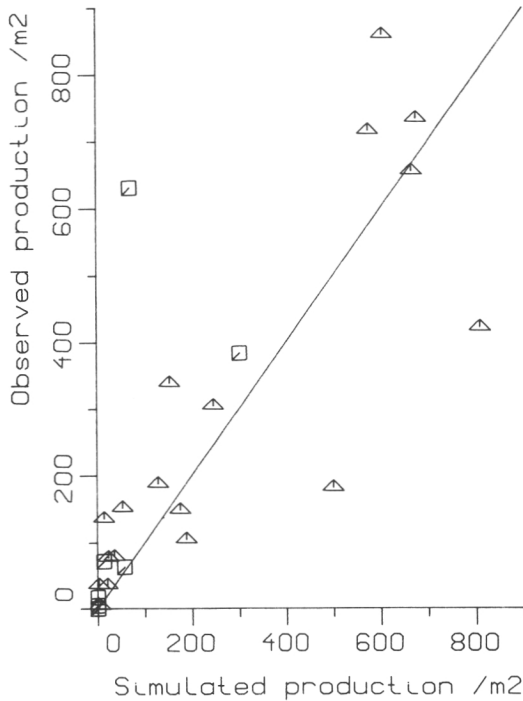


Fig 26. Observed production /m<sup>2</sup> of *Tomiscus piniperda* plotted against the simulated one. The line equals unity. The data are final results from stack layers (an average of 3 to 7 bolts). Triangles are data from Rovaniemi in 1980, 1981, and 1982 that was used for estimating the parameters in the submodels. Squares are independent data from the northern study sites.

present data are not good enough to distinguish between these. It is unavoidable that any estimate of the variability of the developmental rate obtained at this phase of the study is conditioned upon the parameter values of the other submodels in the preceding sections. This is a major weakness of the model. However, the variability of the developmental rate is very similar when compared to those obtained in the studies mentioned above.

There are no adequate statistical methods available for validation of time-dependent population models (Feldman et al. 1984). In the following, only graphical plotting of the observed and simulated values is used. The frequency of the emergence was not an object of calibration. Its prediction is validated by plotting the final observed emergence /m<sup>2</sup> against its simulated pair (Fig 26). The data from Rovaniemi that have been used for estimating of the submodel parameters is shown with different symbols than the independent data from the northern study sites. The productions of *T. piniperda* are relatively low in all the experiments, none of them even reaching 1000 emergences /m<sup>2</sup>. The predictions of the model are fair; the residual mean square is 18284, that is, 95 % of the predictions are not further than 270 exit holes /m<sup>2</sup> from the real values within the range of observations.

The greatest deviations in the prediction of production are caused by a lack of synchrony in the physiological time between the simulation model and reality: a small error in timing becomes multiplied in the frequency. This is shown clearly when the simulated and observed developmental curves were plotted against the physiological time axis (Fig 27). In the materials from Rovaniemi, the predictions are fairly good. The curves in Enontekiö in 1983 are very biased. The durations of the stages (Table 11) may be slightly overestimated. However, this can be a random error in temperature measurements, since those stacks were very heterogeneous and there was only one temperature sensor per sampling layer. The smaller the density of *T. piniperda* larvae, the more prominent the sampling errors become. Another error is visible in the numbers of eggs: it seems that the mortality does not start soon after egg laying, but only after the larvae hatch. The brood survival model (13) does not take this into account.

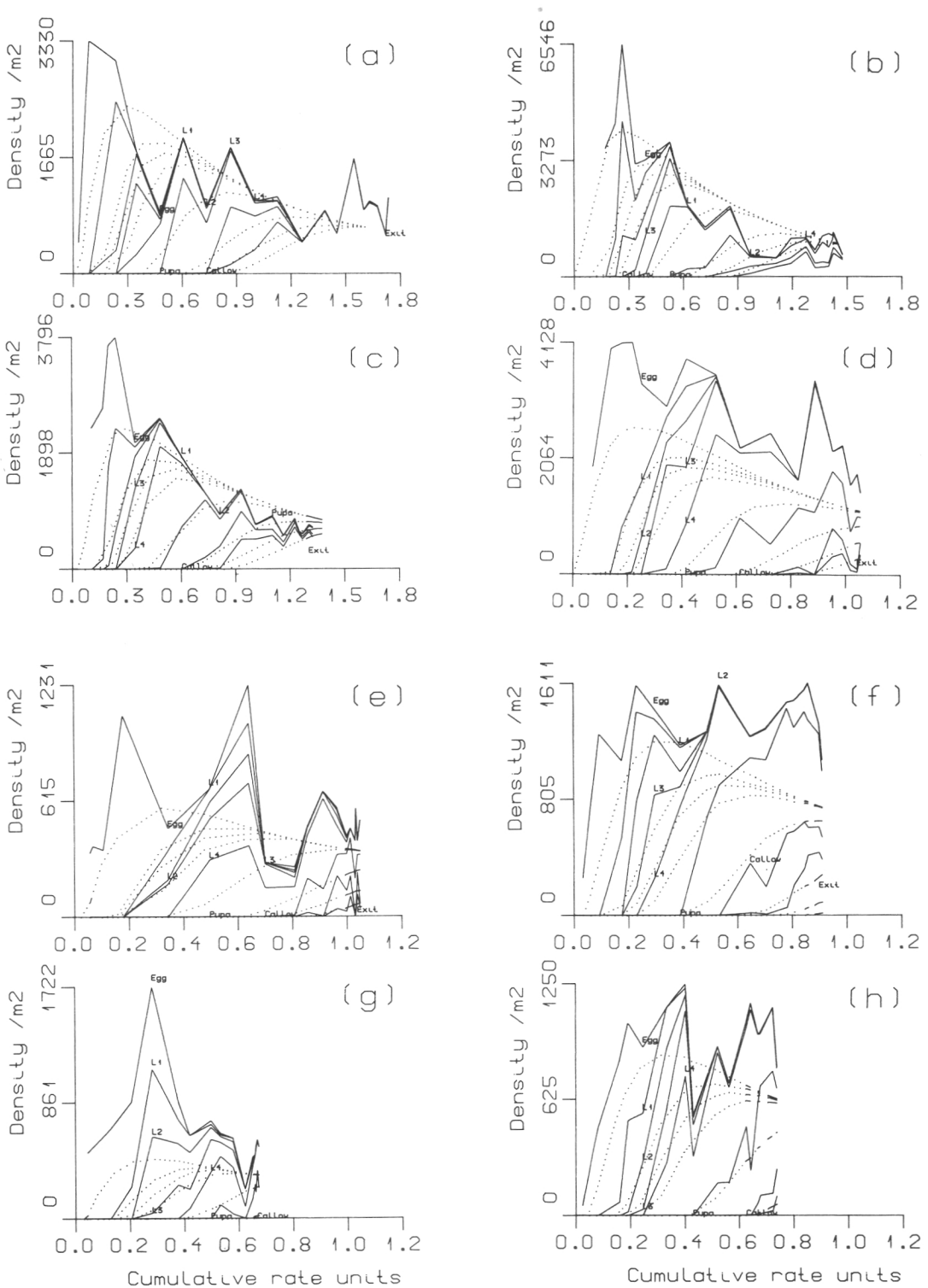


Fig 27. Densities of *Tomicus piniperda* at the sunlit upsides of the top level bolts on a physiological time scale. Solid curves are observed and dotted lines simulated. (a) Rovaniemi 1980, (b) 1981, (c) 1982, (d) Pallasjärvi 1981, (e) Enontekiö exposed 1982, (f) 1983, (g) Enontekiö shaded 1982, (h) 1983.

## 4. DISCUSSION

The different life-cycle events of *Tomicus piniperda* have already been discussed in their specific sections. What are presented here are general remarks about the life system. Following these, we consider the successes and shortcomings of the model as a descriptor of the within-tree dynamics of the species. Inputs for the model, dispersal and attack dynamics and interfacing to real life situations in a variety of environments must also be dealt with. Finally, we will return to the opening theme and framework of this study; how IPM of *T. piniperda* can be implemented.

The present study does not bring much new to our knowledge about the breeding biology of *T. piniperda*. Most of the facts about the different life-cycle events presented here have been known for a long time. However, the goal of the present study is beyond that. Instead of being basic research on a forest insect, this study is more interpretative and technical, more readily to be regarded as a part of the field of bioengineering. After the three recent monographies on *T. piniperda* in the Nordic countries (Bakke 1968, Salonen 1973, Långström 1980), with the huge BBDB database, and the example of a scientific breakthrough in the southern pine beetle project (Thatcher et al. 1980, Coulson 1979, Rykiel et al. 1984), we are now facing a situation where the results of basic research have accumulated to a degree where the next phase of applied entomology, technology transfer from research to practice, has to take place. When this accumulation of knowledge coincides with a revolution in the computer science — the computer is a superior tool for technology transfer (see e.g. Turnbow et al. 1983, Croft and Welch 1984, Rykiel et al. 1984) — this type of studies have to emerge.

### 4.1. Within-tree dynamics and the model

This paper's additions to our basic knowledge on *T. piniperda* are the formulation and use of physiological time and those aspects dealing with the special conditions of the far north (see also Saarenmaa 1985b). There is a single set of data (one out of eight study stacks, and five out of 44 successive sampling series) in the present material where the beetle did have enough time to undergo its development totally before the onset of winter. Total failures were more common, especially in the shaded stacks in Enontekiö. When the production of *T. piniperda* was projected over maps (Saarenmaa 1985b), it was found out that in a normal year, about 90 percent of the *T. piniperda* populations has time to emerge at the uppermost stack layers in Lapland, but less than 30 percent inside the stack (see also Kangas 1953, 1963, Långström et al. 1984, and in Canada for *Dendroctonus ponderosae*, Safranyik et al. 1975, Safranyik 1978, and for *D. obesus* Mannh., Dyer 1969).

As the early onset of winter so often prematurely terminates the development of *T. piniperda*, we may expect advantages in pest management. Accordingly, Långström et al. (1984) have given recommendations on the control tactics of *T. piniperda* utilizing this knowledge. The cost of no action is usually low at high latitudes, but, since the fluctuations in climate between the years are great (Pohtila 1980), the uncertainty in decision making is considerable. This is a special challenge when developing predictive models and decision making tools.

The physiological time in *T. piniperda* was only a cumulative function of temperature (11) in the present study. However, the rate of development was hypothesized as

being a function of nutrition as well (5). The results obtained indicated that there certainly are additional factors that affect development. The most striking differences occurred when the development in the rainy summer 1981 was clearly slower in two independent places than in the other years (Fig 19). The following mechanism by which moisture can affect development in *T. piniperda* can be hypothesized: a high water content — above 120 % — inhibits the growth of symbiotic blue stain fungi (Käärik 1975); if the fungi has any effect on the nutrition of *T. piniperda*, high water content inhibits development. This has been shown to be true for the large fungivorous larvae of *Dendroctonus frontalis* (Wagner et al. 1979). A corresponding mechanism has been suggested by Safranyik et al. (1975) and Webb and Franklin (1978). Unfortunately, there is no evidence on the importance of symbiotic fungi to *T. piniperda*. There are other bark beetles that do not grow successfully without them (Barras 1973, Berisford 1980). Table 10 shows that the water content of the trees indeed was high enough to inhibit fungal growth in 1981. Another explanation might be a physical process; it has been observed that larvae of *Ips typographus* absorb water through osmosis in moist conditions (Annala 1969). This is an interesting subject for further studies.

It could not be shown that bark thickness had any effect on the rate of development. Although there are opposite observations from *Dendroctonus ponderosae* (Amman and Cole 1983, fig. 12) this is not surprising. That growth and development are not synonymous can be seen in the fact that larvae starve due to competition or lack of food emerge as smaller adults at the normal time, or die. This reduction of weight has been observed in many instances (e.g. Beaver 1974, Amman and Cole 1983, Saarenmaa 1983).

With the exception of the normal low level population of *T. piniperda* living endemically in overtopped trees, occasional windfalls, etc., the sizes of *T. piniperda* populations are largely controlled by factors that are disturbances rather than regulating negative feedback mechanisms (cf. Berryman 1981). These disturbances include storms (Trägårdh and Butovitsch 1935, Lekander 1955, Butovitsch 1971, Butovitsch and Ringselle 1968, Annala and Petäistö

1978, Långström 1984, Saarenmaa 1984), activities of man (Nuorteva 1956a, 1968), and hazardous climate in the north (Franz 1948, Kangas 1953, Långström et al. 1984, Saarenmaa 1985b). It would be of importance to analyze the relative significances of disturbances and negative feedback mechanisms in the changes of the populations of more aggressive bark beetles, especially in *Ips typographus* (cf. Bakke 1983).

The different mortality factors were not separated in the present study. It is a general observation that the survival in *T. piniperda* follows the same course from case to case. Within a year, it has not yet been tested whether or not any natural enemies have density dependence in their relation to *T. piniperda*. However, in the light of the results of Beaver (1967) on the regulatory mechanisms of *Scolytus scolytus* F. and the life-tables made for *T. piniperda* (Galaseva 1976), it is likely that at least ectoparasites can show this kind of response. The density-dependent survival (Fig 22) is mainly caused by competition. To gain more insight into the survival process it is necessary to study the effects of different mortality factors in detail. However, it is doubtful whether they will bring any improvement in predictive models and unclear, how their input can be constructed.

Nonetheless, if we can ignore the different mortality factors within years, this is not the case between years. There is circumstantial evidence that natural enemies concentrate in places where bark beetles breed from year to year (Kangas 1963, Annala 1969). This is a factor that has not been dealt with in the model, but must be taken into account in its further development. Although the study site was the same in Rovaniemi for three years, the stack was renewed every winter, and eventually the majority of natural enemies were removed. So there is no possibility of studying this question using the present database.

Once the colonization of the host tree has occurred, within-tree dynamics of most bark beetles are basically similar. The greatest differences are caused by nutrition; those species that are fungivores as larvae, e.g., *Tomiscus minor* Hart. (Långström 1983, 1984) or *Dendroctonus frontalis* (Coulson et al. 1976b), are much more dependent on host suitability and less regulated by competition than phloem-eaters such as *T. piniperda*. We

may conclude that the process of within-tree population dynamics simulation as constructed here is applicable for other similar species where necessary. However, in most of the other harmful bark beetles, the main management strategy is to prevent attack on living trees. For them, predicting of timing and frequency of emergence is not always the focal point. In *Ips typographus*, for instance, it is more important to study dispersal and infestation jumping and develop computerized risk and hazard rating systems.

The present approach resembles the one employed in modeling of the population dynamics of *Dendroctonus frontalis* (Coulson 1979, Feldman et al. 1981a, 1981b, Turnbow et al. 1982, Wagner et al. 1984a). These are biophysical simulation models considering the different life cycle events as subprocesses. The greatest differences between the present and the southern pine beetle models are that the complex allocation and attack models are not yet constructed or are totally unnecessary for such a secondary species as *T. piniperda*. Furthermore, at present the model simulates the process using individual larvae as the basic unit instead of an infested bole, but this may change in the future. Both models use the same type of physiological time, which is standard throughout the life-cycle in *T. piniperda* (except for arrival), but varying between stages in *D. frontalis*. Different zero-points of development have also been found for *D. ponderosae* (Amman and Cole 1983) stages. The developmental processes in *T. piniperda* have not been studied in such depth that any differences in the thermal or other requirements of the stages were apparent. Salonen (1973) gives data indicating differences in the zero-points of development between the stages of *T. piniperda*, but a statistical analysis of his material reveals that this is not the case. Nevertheless, if such differences can be demonstrated, it would improve the model. One basic difference between the *D. frontalis* models and the present one is that while in the former model the processes are affected by the location in the infested bole, in the latter the most important factor after physiological time is attack density. This is a characteristic connected with the different feeding habits of the two species.

The functional responses of the within-tree dynamics of *Dendroctonus ponderosae* have also been studied much in the same

way than here (Amman and Cole 1983). The principal classifiers in that species are phloem thickness and tree diameter. Phloem thickness could not be shown to be of any importance for *T. piniperda*, probably because its variation in the Scots pine is small. Moreover, in the present study, measurements of phloem thickness were available for the oviposition experiment only. The correlation between phloem and bark thickness, which was used elsewhere, is low (Saarenmaa unpubl.). There are also differences in overwintering, and thus in the role of temperature.

The reliability of the estimates of the timing of emergence was adequate. Nevertheless, the estimates can be improved when the causal effects of rainfall on the rate of development have been established. However, predicting of the frequency of emergence succeeded only partially. This is due to the combined errors: a small error in timing in the model is reflected drastically in a situation where emergence is stopped by the autumn cold. The final word about the reliability of the model cannot be said until the model has been tested in the field in a variety of environments. Simulation models never predict real life exactly (Berryman and Pienaar 1974). In the best case, we have probability distributions and eventually the risks calculated for each deviation from the prediction (Welch and Poston 1982). The goal of field testing is to improve the model and estimate the distributions of deviations of the model from the real. The present model is a good starting point for improvements.

## 42. Dispersal dynamics and other inputs

Before the model can be applied, it must be interfaced with the real world. This involves constructing the beetle input for the model, stratifying the breeding material, and transforming the weather information from standard climatic parameters to the physiological time that the model uses.

The results given by the present model are conditioned on our ability to estimate the attack density in the breeding material. In the calibration and validation, we knew the attack density. In a true application situation of the model, however, this is not the case.

We must be able to estimate the number — not only the relative frequency — of arriving beetles and, consequently, the attack density in the different parts of the breeding material.

*T. piniperda* does not create its own dynamics as the more aggressive bark beetles do in epidemic populations. Instead, it is regulated to a very high degree by external factors that provide the necessary breeding material. This makes it relatively easy to construct a between-tree population dynamics model for it. Dispersal dynamics of *T. piniperda* is basically a process of moving from the old breeding site to shoot feeding, to an overwintering site, and in the spring to a new breeding log. The dispersal capabilities of bark beetles are potentially very great (Nilssen 1984), but since the observation holds that we find the highest *T. piniperda* populations near loggings of previous years, we can attempt to construct the necessary beetle input to model by expressing attack as a function of some environmental factors.

Attack can be defined to be a result of swarming (1, 8), the size of the local beetle population (see e.g. Johnson and Coster 1978, Paine et al. 1984), attack density which dynamically shuts off the process (Nilssen 1978, Raffa and Berryman 1983, Saarenmaa 1983), and physical properties and suitability of the host (Berryman 1974). While the last item can be taken as given (e.g. by man) for such a secondary bark beetle as *T. piniperda*, our ability to determine the size of the local beetle population becomes the critical point. It can be suggested as depending to a high degree on the breeding material in the vicinity of a particular site one and two years before. Thus, for a given type of breeding material:

$$\text{ATTACK RATE} = f(\text{RELATIVE ARRIVAL (8),} \\ \text{ATTACK DENSITY,} \\ \text{all (BREEDING MATERIAL} \\ \text{AT A DISTANCE)}) \quad (18)$$

It is easy to formulate this relation further into an equation, i.e. by summing up the breeding materials — the longer the distance, the smaller the amount. Lots of field work is required to estimate the parameters, but presumably it can be done.

Besides the attacking beetles, another type of input must be constructed for the model: the formation of the breeding material, and the physical environment which is a function

thereof, i.e., the microclimate that varies from place to place. The physical form of the breeding material can be a stack (variable in size), timber, windfall, suppressed tree, stump, logging wastes, etc. The qualities of the breeding material also vary as to cutting time, weather, and storage. As a consequence, we may have a very variable beetle input. Moreover, survival of the brood may vary considerably in different types of breeding materials.

The input of temperature (and other climatic factors) is largely determined by the physical location (stratum) of the breeding material. The model uses a physiological time prevailing under the bark which is not directly related to the standard degree-day data readily available. Before the model can find any applications, transformation models for temperature and other factors from the standard weather parameters to the model in each stratum must be constructed. In addition, there is a need for on-line weather data retrieval — even forecasting — in a true application situation. If an updated weather database is not available in the future, the end user of the model must supply the information about climate.

#### 43. Knowledge engineering in IPM of bark beetles

As an applied science, the knowledge base of forest entomology can arbitrarily be divided into four blocks according to the importance of the information on the scientific understanding, and according to the applicability of the knowledge in practice. In the first quarter, we have basic facts about the biology of a pest which a scientist must know and which together form the life-system of the insect. It is a hard job to gather all this information and even harder to base one's understanding about a system's functioning on it. This part of the knowledge base includes, e.g., such information as the lengths of egg galleries of bark beetles, lists of natural enemies, etc. Secondly, there are overriding rules of basic biology by which one can understand the functioning of a system but which are not necessarily suitable for decision making in practice because of the lack of inputs from real world. Bark beetle/host relationships are a good example of this.

The third quarter is the field of bioengineering. It includes those facts about the life system of the pest that lend themselves to modeling and real world interfacing. A scientist working in this field may screen the facts in the first two quarters in order to pick out those that are useful and tries to construct models that might be of help in the practice. Finally, technical questions about the actual operations — understanding the systems of man — are an essential part of applied science. This sector includes developing of the decision making tools, treatment tactics, and cost/benefit integration. Only recently it has been found that it requires a special field of science, knowledge engineering, to organize the essence of this knowledge base in an effective manner for utilization by a human decision maker, who in our case is the forest manager. I suppose that knowledge engineering will be an important part of applied entomology in the near future (see Hayes-Roth et al. 1983).

A forest manager must make plans and decisions about operations in the forest daily. Simultaneously he or she must take into account information dealing with biology, ecology, and development of forests, economical, technical, and legal considerations, land use policies and the needs of the land owner and society. It is not a trivial task to be aware of all this information and to be able to use it. Furthermore, it is not granted that an excess of information makes decision making easier. Decision making is largely dependent on the way information is being handled. The difficulty in human inference is that the amount of factors that can be considered simultaneously is limited and subjectively weighted. There must be a system supporting decision making in this kind of situation (Rykiel et al. 1984, Saarenmaa 1985a). At this moment, decision making within forestry in Finland is supported by the written procedural guides of central forestry boards. Such guides cannot always include all the factors that are of importance in a particular situation. Obviously, computerized decision making tools which can handle all the information available are of high potential use in forestry. The forest manager, who is not an entomology specialist, cannot be blamed if he or she wants a cookbook for pest management instead of or in addition to an ecological insight to pest and forest population dynamics. Now the question arises of

whether a computerized decision making tool can be more than just a cookbook.

At the moment, there are only two such systems available in Finland: VILJO for the comparison of forest regeneration chains (Parviainen et al. 1984) and MELA for stand simulation (Kilkki et al. 1984). Both of these systems fall into the category of management information systems (see Rykiel et al. 1984). In forest pest management, there is a operational decision support system for decision making in unstructured southern pine beetle problems in Texas (Turnbow et al. 1983). In agriculture, the extension service has been on-line for a long time (Croft et al. 1976, Croft and Welch 1984, Welch 1984), but the uncertainties in decision making have not been the focal point as they are in forestry.

Decisions about management operations of bark beetles, or about the forest ecosystem in general, are always made under uncertainty. This uncertainty can be divided into several categories according to its origin:

- unpredictability of the population dynamics of the bark beetles, which partially is a consequence of
- gaps in the scientific knowledge base;
- deficiencies in monitoring and hazard rating (uncertain bark beetle input);
- unpredictability of weather (uncertain weather input);
- frequency of disturbances in the life system of the bark beetle;
- poor technology transfer from research to the actual decision maker;
- limitations of human inference process and deficiencies in the training of forest managers;

These uncertainties make the construction of formalized and structured decision making tools difficult. The problems here lend themselves to the field of artificial intelligence, and specifically to expert systems. An expert system is a computer program driven by artificial intelligence, which means that it utilizes symbolic inference instead of arithmetics during its operation. The system contains the knowledge of an expert (e.g., entomologist) as a knowledge base of rules and facts, including heuristics. Utilizing the knowledge base to judge its operation, it is capable of solving problems (Hayes-Roth et al. 1983). By explaining its reasoning, an expert system may upgrade the numerical predictions of the models, which may not be very informative to the forest manager, to the level of understanding (see Fig 1).

An expert system solving bark beetle problems should utilize the general frame of IPM (Fig 1), because an entomology expert would solve the problem that way. Hence, before we can build an expert system for *T. piniperda*, we must have an adequate heuristic knowledge base and a frame-based simulation system with models for population dynamics, treatment tactics, pest/forest impacts and cost/benefit integration;

all preferably on-line with the pertinent databases. To gather and codify all these information will be a great task. However, the present paper forms a basis for the population dynamics model; the other models will be simpler. There are no expert systems within IPM at the moment, but clearly it promises to be more than just a cookbook of pest management.

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*Total of 165 references*

## SELOSTE

### Pystynävertäjän lisääntymiskauden populaatiodynamiikkamallit tuhojen integroitua hallintaa varten

Pystynävertäjä (*Tomicus piniperda*) on männyn vahingollisin kaarnakuoriainen, jonka aiheuttamien kasvutappioiden arvo on maassamme miljoonia markkoja vuosittain. Tuhojen laajuus on suurelta osin seurausta siitä, että päätöksenteko pystynävertäjä-tuhojen torjunnasta on vaikeaa. Investointeja metsän suojeluun ei ole aina tehty tarpeellisessa määrin, kun näiden hyötyjä ei ole voitu mitata. Tämän ongelman poistamiseksi esitetään tietokonepohjaista asiantuntijajärjestelmää. Perustuen integroidun tuhoistorjunnan teoriaan, matemaattisiin malleihin ja simulointiin, järjestelmän tulee soveltua ei-ekspertin käyttöön ja tulkita simuloinnin numeriset tulokset muotoon, jonka pohjalta päätöksentekijä voi tehdä ekologiseen ymmärtämykseen perustuvan päätöksen torjuntatoimista tai niiden tekemättä jättämisestä. Tällainen järjestelmä voi saada käyttäjiä vain, mikäli se on helposti saavutettavissa metsätalouden tietojärjestelmän käyttäjäliitynnässä (kuva 1).

Järjestelmän tietopohja on suurelta osin olemassa, mutta erityisesti pystynävertäjän populaatiodynamiikasta (= kannan vaihteluista) ei ole ollut riittävän integroitua mallia. Tämän tutkimuksen tarkoituksena on kehittää soveltamiskelpoinen malli kuoriutumisen ajoittumiselle ja määrälle, jotka vaihtelevat tavattomasti vuosien, maantieteellisen sijainnin ja mikroilmaston mukaan (Saarenmaa 1985b).

Aineistoina käytettiin pystynävertäjän laboratorio- kasvatuksia vakioilämpötiloissa sekä Lapissa (kuvat 2, 3, 4 ja 5) säännöllisin välein otettuja maastonäytteitä, joihin liittyvät automaattisesti mitatut lämpötilatiedot kaarnan alta (kuvat 6 ja 7). Aineisto, joka käsittää myös paljon muita kaarnakuoriais-, jäära-, peto-, ja loislajeja, organisoitiin hierarkkiseksi tietokannaksi (kuva 8).

Pystynävertäjän lisääntymiskauden eri vaiheiden toiminnallisia vasteita analysoitiin erottaen siinä viisi eri vaihetta:

- 1) emojen saapuminen lisääntymismateriaaliin (kuva 9);
- 2) muninta (kuva 12);
- 3) emojen poistuminen (kuva 14);
- 4) jälkeläisten kehittyminen kehitysasteelta toiselle (kuva 19, taulukko 11);
- 5) kuolleisuus (kuva 22).

Määrävin tekijöinä eri vaiheissa olivat suurelta osin samat tekijät: lämpötilasta entsyymi-inaktiivumisteorian mukaan riippuva kumulatiivinen fysiologinen aika (kuva 16) ja populaatiosta riippuva tiheys. Ainoastaan ensimmäinen vaihe oli poikkeus, sillä sen ajavina tekijöinä olivat vuorokautinen ilman maksimilämpötila ja tämän summa. Kaikille vaiheille laadittiin epälineaariset mallit pääosin laboratorioaineistojen perusteella minkä lisäksi ne validoitiin maastoaineistoihin. Lopuksi alamallit yhdistettiin ja testattiin (kuvat 26 ja 27).

Aineistosta ilmeni, että Lapissa pystynävertäjäkantaja hillitsee enemmän ilmaston epäsuotuisuus kuin biologiset säätelevät tekijät. Mallin ennustekyky on tyydyttävä; suurimmat poikkeamat ovat seurausta siitä, että fysiologinen aika näyttää lämpötilan lisäksi riippuvan myös kosteudesta. Kuolleisuusosamalli on myös edelleen kehittelyn kohde; tässä tutkimuksessa ei eri kuolleisuustekijöitä lainkaan erotettu. Edelleen, mallin ennusteet ovat riippuvaisia siitä, että myös saapuvien emojen määrä eikä vain ajoittuminen voidaan ennustaa, t.s. tarvitaan myös parveilukauden populaatiodynamiikkamalli. Mallin hyväksikäyttö käytännössä on täysin riippuvaista siitä, että malit tai sääntöpohjainen tietämuskanta myös torjuntatoimille, tuholaisen vaikutukselle metsään ja hyöty/kustannus analyysille kehitetään ja liitetään käyttäjäystävälliseen asiantuntijajärjestelmään. Kaikki nämä seikat on tarpeen selvittää ennenkuin pystynävertäjätuhojen integroitu hallinta on todellisuutta.

Saarenmaa, H. 1985. Within-tree population dynamics models for integrated management of *Tomicus piniperda* (Coleoptera, Scolytidae). Seloste: Pystynävertäjän lisääntymiskauden populaatiodynamiikkamallit tuhojen integroitua hallintaa varten. Commun. Inst. For. Fenn. 128: 1–56.

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Within-tree dynamics of *T. piniperda* are reviewed and subsystems for 1) arrival of the parent beetles, 2) oviposition, 3) reemergence, 4) development and emergence, and 5) survival are identified and modeled. While the arival submodel uses air temperature, the other submodels are driven by physiological time based on the absolute reaction rate theory. Besides temperature, another main denominator in the submodels is attack density. Most of the submodels have been developed using laboratory materials at constant temperatures, whereas they were validated against field data retrieved from a data base. By integrating the submodels, a dynamic biophysical model is constructed. The population dynamics model is tied into the scheme of IPM. An outline of bark beetle IPM relying on expert systems and the total information structure of the forest sector is discussed.

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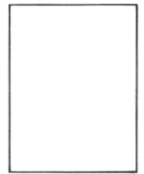
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*Remarks* \_\_\_\_\_

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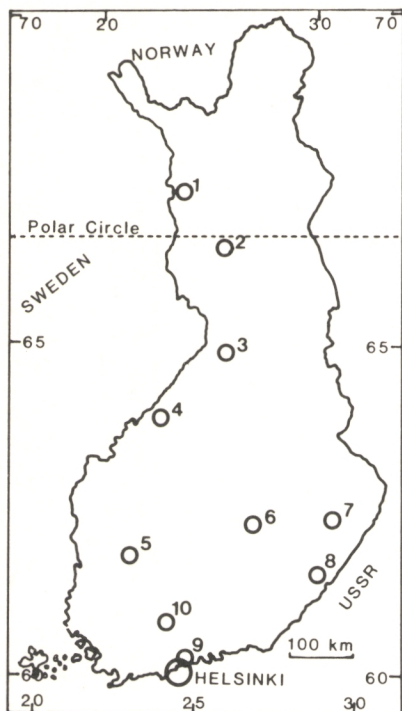
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## THE FINNISH FOREST RESEARCH INSTITUTE

### DEPARTMENTS (Helsinki)

Administration Office  
 Information Office  
 Experimental Forest Office  
 Dept. of Soil Science  
 Dept. of Peatland Forestry  
 Dept. of Silviculture  
 Dept. of Forest Genetics  
 Dept. of Forest Protection  
 Dept. of Forest Technology  
 Dept. of Forest Inventory and Yield  
 Dept. of Forest Economics  
 Dept. of Mathematics

### RESEARCH STATIONS

- 1 Kolari
- 2 Rovaniemi
- 3 Muhos
- 4 Kannus
- 5 Parkano
- 6 Suonenjoki
- 7 Joensuu
- 8 Punkaharju
- 9 Ruotsinkylä
- 10 Ojajoki

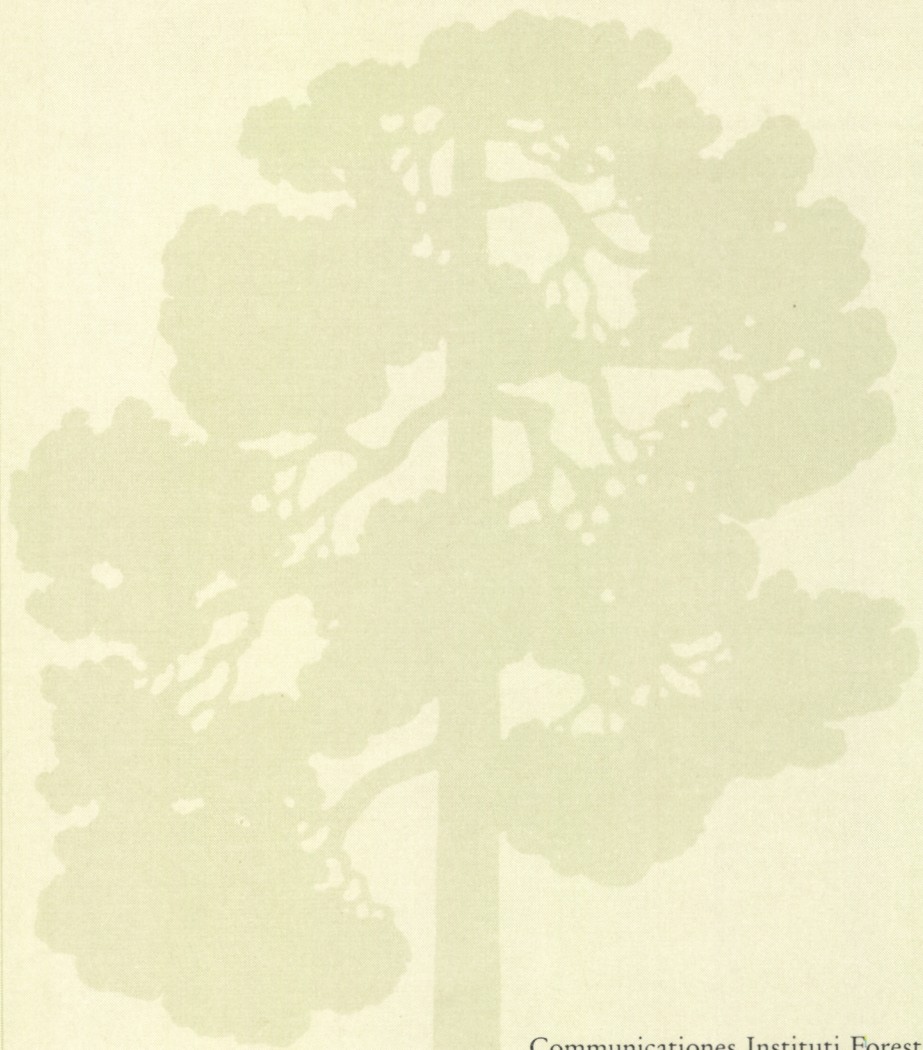
## FACTS ABOUT FINLAND

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*



Communicationes Instituti Forestalis Fenniae

- 125 Lähde, E., Werren, M., Etholén, K. & Silander, V. Ulkomaisten havupuulajien varttuneista viljelmistä Suomessa. Summary: Older forest trials of exotic conifer species in Finland.
- 126 Aalto-Kallonen, T. & Kurkela, T. Gremmeniella disease and site factors affecting the condition and growth of Scots pine. Seloste: Versosyöpätauti ja ympäristö männyn kuntoon ja kasvuun vaikuttavina tekijöinä.
- 127 Tamminen, P. Butt-rot in Norway spruce in southern Finland. Seloste: Kuusen tyvilahoisuus Etelä-Suomessa.
- 128 Saarenmaa, H. Within-tree population dynamics models for integrated management of *Tomicus piniperda* (Coleoptera, Scolytidae). Seloste: Pystynävertäjän lisääntymiskauden populaatiodynamiikkamallit tuhojen integroitua hallintaa varten.
- 129 Sepponen, P. The ecological classification of sorted forest soils of varying genesis in northern Finland. Seloste: Syntyvaltaan erilaisten lajittuneiden kangasmetsämaiden ekologinen luokittelu Pohjois-Suomessa.

