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Geographic variation in the life-history of *Aradus cinnamomeus* and a breakdown mechanism of the reproductive isolation of allochronic bugs (Heteroptera, Aradidae)

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Aradus cinnamomeus Panzer, the pine bark bug, is a pest of young Scots pines which exhibits a two-year pattern of periodicity in most parts of Europe. The alternate-year populations live almost exclusively in different geographical areas. Geographical variation in the developmental time, absolute and relative densities of these populations, the densities in environmentally extreme areas and in zones of overlap were studied from the eastern coast of Sweden across the Åland archipelago and Finland up to the Arctic Circle in the north.

The densities of bugs were high everywhere in dry upland forest sites studied in southern Finland and decreased gradually northwards, although spatial variation within localities was great. In the archipelago the absolute densities were low. No decrease in bug density was observed in the narrow transition zone between the alternate-year populations.

Both in the north and in the southern archipelago the bug appeared to have a life cycle of three years. The change in the life cycle strategy seems to be correlated with the long-term means of the highest daily temperatures in mid-summer, roughly with the 21°C isotherm of July. In the area of the three-year life cycle there does not exist such a distinct numerical dominance of one cohort over another as the parapatry of the alternate-year populations, but the three cohorts usually coexist in relatively low densities. One of them usually slightly predominates, resulting in a temporally changing mosaic-like biogeographical pattern. It is suggested that the change in the life-cycle period itself can cause the breakdown of the dominance of one generation. Computer simulations using a deterministic model lead to a conclusion that in the system of three competitive cohorts the rate of disappearance of a smaller cohort or cohorts is substantially lower than in the system of two competitive cohorts, although the intensity of competition would be the same.

A possible breakdown mechanism of the reproductive isolation of sympatric but allochronic bugs is described. Gene exchange between even/odd-year populations is suggested as happening via mutual contact with the three-year life-cycle.

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1. Introduction

Allochronic populations have been recorded from several perennial insects, of which the best known examples are the North American 13- and 17-year cicadas (Homoptera, Cicadidae, *Magicicada* spp.). The regular 17-year developmental period of a periodical cicada nymph is the longest known for any insect (Lloyd & Dybas 1966a, b, White & Lloyd 1975). In this particular case there are 17 possible years for reproductively isolated allochronic populations, which are usually called broods, to emerge, but not all the years are occupied. The broods have different distributions so that in a given locality only a certain number of broods is found. For instance, broods one year out of phase never exist sympatrically in the same woods (Simon & Lloyd 1982).

In Europe, the May beetles or cockchafers, *Melolontha melolontha* (L.) and *M. hippocastani* Fabricius (Coleoptera, Scarabaeidae) exhibit a complicated periodicity (Hurpin 1962, Niklas 1974, Bulmer 1977). Roughly speaking, both species have a life cycle of three years in western Europe, four years in Central Europe, and five to six years in eastern Europe and the USSR. Lengthening of life cycles can also be observed at higher altitudes. Adults emerge synchronously every third to sixth year, depending on the geographical area. Whenever the two species coexist they tend to have the same flight years. Transition zones between areas of different flight years seem to be abrupt.

A great constancy in the time of pupation and of adult emergence can be observed in periodical species, which may indicate the ability to synchronize, for instance, the moment of mating with the variations in the external conditions. In some cases the mechanism controlling the developmental rhythm has been suggested as being based on photoperiod and temperature induced diapause (Gejspits 1965) but in periodical cicadas the physiological machinery by which these insects can count 17 or 13 years is still a mystery (Simon & Lloyd 1982). In the European cockchafers climatic factors are said to be partially responsible for the differences in the duration of life cycles, but basic mechanisms in the control of periodicity are poorly known (Niklas 1974).

The pine bark bug, *Aradus cinnamomeus* Panzer (Heteroptera, Aradidae), the target of the present study, has two or three allochronic sympatric 2-year or 3-year populations, depending on the geographical area in Europe. The bug resembles the periodical cicadas and the May beetles in having sympatric but temporally totally isolated populations or broods which function as ecological species. According to the model of geographic speciation, new species arise in geographically isolated populations through the gradual accumulation of genetic differences (Mayr 1963, Dobzhansky 1970). However, it seems obvious that speciation events do not always conform to this pattern (Bush 1975, White 1978). One of the alternative models is the model of sympatric speciation with temporal isolation (Alexander & Bigelow 1960, Bush 1974, 1975, Tauber & Tauber 1977a, b, Tauber et al. 1977, Masaki 1978). We have previously found that the sympatric populations of the pine bark bug are genetically differentiated, indicating reproductive isolation (Heliövaara, Väisänen, Hantula, Lokki & Saura, unpubl.). However, the degree of differentiation is very small suggesting, as one explanation, that there is a mechanism breaking down the isolation.

In the present study we investigate the possibility that the reproductive isolation of the allochronic bugs could be broken down by the geographical variation in the life-history traits of the bug, which would make the gene exchange possible among broods. Variation in insect life cycles has usually been recorded along latitudinal and altitudinal transects, where it is supposed to represent a response to climatic gradients (Masaki 1961, 1965, 1967, 1978, Gejspits 1965, Danilevsky et al. 1970, Niklas 1974, Harrison 1978, 1985). Latitudinal differentiation in life history characteristics can apparently develop in the course of relatively few generations, since it has been observed in recently introduced species (Beck & Apple 1961, Sparks et al. 1966).

The ultimate aim of the present study is to determine the key factors controlling the biogeographical variation in the life history traits of the pine bark bug. The densities of *Aradus cinnamomeus* and the relative proportions of different cohorts were investigated in different parts of northern Europe in relation to spatial heterogeneity, climatic conditions, and number of coexisting cohorts. The term cohort is here used for the temporally isolated sympatric bugs. A cohort may consist of bugs in different nymphal instars which, however, become adults and reproduce in the same year.

The analysis of the biogeographical patterns for the pine bark bug was extended by examining the structure and location of transition zones between the alternate-year generations, and between 2-year and 3-year generations, and the densities of the bug in these transition zones. Comparison of both absolute and relative densities in the areas of alternate-year populations, 3-year populations, and in both types of transition zones may throw more light on the origin and dynamics of this peculiar distributional pattern.

2. The natural history of *Aradus cinnamomeus*

During recent decades the pine bark bug *Aradus cinnamomeus* Panzer (Heteroptera, Aradidae) has increased in abundance and become an expensive primary pest of young Scots pines (*Pinus sylvestris* L.) in Eurasia. The species seems to favour areas characterized by poor soil and sparse undergrowth. In light, dry upland forests hundreds or even thousands of bugs can be found on a single stem

(Tropin 1949, Brammanis 1975). The increase in number and probably the expansion in the distribution of the pine bark bug is apparently a result of supplementary planting in under-stocked pine plantations, favouring the Scots pine in the regeneration of forests, construction of highways, pollution, and many other kinds of human activities (Heliövaara & Väisänen 1983, 1986a).

Long life cycles are characteristic of many insect species living on trees, and especially those feeding on the dilute diet of xylem fluid (Cheung & Marshall 1973, White & Strehl 1978). The flat, reddish bugs, both nymphs and adults, live in crevices in the bark on the trunks of pines. They suck sap from the trunks with their long stylets, which may penetrate into phloem, cambium and xylem layers, thus disturbing the growth of the host tree (Heliövaara 1982). In general, the life span of the pine bark bug is two years, but in northern Europe close to the tree limit it is three years (Brammanis 1975). The eggs of *A. cinnamomeus* are laid in May, and nymphs hatch in June. In the area of the two year life span the nymphs reach the fourth instar during the first summer. After hibernation, they become full-grown in July-August, after which they hibernate as adults. It is not until the following spring that the bugs mate and begin egg-laying. In the area of the three year life span the bugs pass their first winter as II-III-instar nymphs, the second as IV-instar nymphs, and the third winter as adults.

Pine bark bugs are rather sedentary insects. Males are always wingless and unable to fly. Usually only 1-3 % of females have wings capable of flight, but the proportion of macropters may increase when living conditions become worse, e.g. the conduction of pine sap decreases, or the chemical composition of the sap changes. The bugs live through their two- or three-year life cycle in the host tree, in a slowly changing and predictable habitat, and abrupt alterations in their density caused by dispersal seem to be relatively uncommon (Heliövaara 1984a).

3. The biogeography of *Aradus cinnamomeus*

The distribution pattern of *Aradus cinnamomeus* is very unusual: In most of Europe, there seem to be two alternate-year generations which live almost exclusively in different geographical areas. The situation in Finland is fairly precisely known (Heliövaara & Väisänen 1984a, b). In eastern Finland, the bugs reproduce in even years, and in western Finland in odd years (see Fig. 1). The two alternate-year generations border upon each other in a narrow zone of overlap, where both even- and odd-year bugs are found in about equal numbers, even on the same trunks. Due to alternate-year maturity the two populations live in reproductive isolation even in the transition zone (Heliövaara, Väisänen, Hantula, Lokki & Saura, unpubl.). The width of this transition zone, where an adult population gradually turns into a nymphal one, is about 3.5 kilometres in one study locality and certainly no more than 20 kilometres (usually less than 10 kilometres) in all the 16 mainland localities previously studied (Heliövaara & Väisänen 1984a, b).

Among the locally dominating population, there always seems to be a very small proportion of bugs which reproduce asynchronously with the larger populations, i.e. in the alternate years. The proportion of these asynchronic bugs among both even- and odd-year populations is usually fewer than one per thousand. They deviate genetically from both of the dominating generations. We have suggested that the differentiation in enzymatic variation between the local minority and majority populations cannot be explained by retarded or accelerated growth nor by dispersal (Heliövaara, Väisänen, Hantula, Saura & Lokki, unpubl.). We have also suggested that intraspecific interference competition between the two co-existing age-classes, reinforced by the impact of parasitoids and intraspecific exploitation competition, is a key factor in the regulation of this principally parapatric distribution of the even- and odd-year populations (Heliövaara & Väisänen 1986b).

No other species in northern Europe is known to show a similar complex geographical distribution pattern, or even a range resembling that of the pine bark bug. Seasonal isolation in closely related sympatric species of insects is not an uncommon phenomenon (see Harrison 1978), but examples of sympatric conspecific populations reproducing in alternate years seem to be relatively scarce (e.g. certain satyrid Lepidoptera; for the alternate-year flight of certain Lepidoptera, see Valle 1933, Suomalainen 1937, Mikkola 1976, Imby & Palmqvist 1978, Linnaluoto & Koponen 1980, and Douwes 1981). In the areas of assumed three-year life span of the pine bark bug, almost nothing is known about the possible spatial dominance relationships of different cohorts. Moreover, the location and sharpness of this type of transition zone, where bugs with a 2-year life cycle turn into bugs with a 3-year cycle, has not been documented.

4. Material and methods

The total material of this study consists of about one million pine bark bugs examined in 1982–1985. We have previously published parts of the results on the proportions of the different cohorts in different areas in other connections (Heliövaara & Väisänen 1984a, b). We summarize here all our published and unpublished records on these proportions and the life history traits in different geographical areas. The bugs have been sampled in different parts of Finland, including Åland, and on the eastern coast of Sweden.

The maximum density method was used to obtain information on the absolute bug densities: The bark of a studied pine was removed at a point on the trunk where tests suggested that the bug density would be highest. All bugs were counted, and their developmental stage and sex were determined according to Vásárhelyi (1983). The bug density was usually counted per 100 × 100 mm^2 of bark. The height of pines studied varied from one to five metres. Most sample plots were situated in dry upland forests, usually along roads. The main body of data for the present study was collected in five substudies described below.

4.1. General pattern

In previous studies we have presented the parapatric pattern of the alternate-year populations in Finland (Heliövaara & Väisänen 1984 a, b). In these studies, several hundred samples of at least ten individuals have been taken at intervals of 10 kilometres along several roads in the western parts of southern and central Finland. Since the biogeographical pattern of the alternate-year populations was coarsely known, it was possible to examine both absolute and relative bug densities in the areas of different life cycle rhythms.

Ten sample plots were chosen in different parts of Finland in August and September, 1984 (Fig. 1 and Table 1). All study sites were pine monocultures in dry upland forests of *Calluna* site type (e.g. Cajander 1926, 1949). At each plot, 25 pines were sampled by removing 100 × 500 mm^2 of bark. Such large samples were preferred in this substudy in order to obtain a representative picture of the occurrence of different age-classes along the latitudinal gradient. The abundance relationships of bark invertebrates in these samples are examined in another paper (Heliövaara & Väisänen 1986c).

4.2. Densities in archipelagoes

The Åland and Turku archipelagoes between Sweden and continental Finland are spatially very heteregeneous, consisting of thousands of islands and islets where Scots pine often abounds (although there is also a zone without conifers in the outer archipelago, see e.g. Kalliola 1973: 181). In previous studies we observed, with a small sample, that in the Åland archipelago neither of the alternate-year generations clearly predominates. We concluded that the overlap zone bends northwards in the archipelago and is there much wider than on the mainland (Heliövaara & Väisänen 1984a).

To obtain more detailed information about the situation in the archipelagoes and in spatially heterogeneous areas in general, 12 sample localities, each of which consisted of 20 pines, were studied in September and October, 1985 (Fig. 1 and Table 1). The densities of bugs and the occurrence of different age-classes were studied using 100 × 100 mm^2 bark samples. The sample plots were chosen to represent the highest densities we could find in the archipelago (about one hundred sites were tested). For comparative purposes an additional sample (B13) was taken from Pargas (Parainen), on the coast of the Finnish mainland.

Table 1. The study localities and their coordinates in the Finnish uniform grid system (Grid 27°E). A. General pattern in Finland. B. The Åland and Turku archipelago. C. Northern Finland. D. Eastern Sweden.

Code	Locality	Coordinates	Date
A1	Hanko Tvärminne	664:28	4.IX.1984
A2	Salo	670:28	4.IX.1984
A3	Humppila	676:30	4.IX.1984
A4	Harjavalta	680:24	4.IX.1984
A5	Muurame	689:43	23.VIII.1984
A6	Jyväskylä mlk.	691:43	23.VIII.1984
A7	Karstula	697:39	24.VIII.1984
A8	Kaustinen	705:33	24.VIII.1984
A9	Pulkkila	713:44	24.VIII.1984
A10	Temmes	717:43	24.VIII.1984
B1	Jomala Gottby	668:10	30.IX.1985
B2	Hammarland Näfsby	669:10	1.X.1985
B3	Hammarland Frebbenby	670:09	1.X.1985
B4	Eckerö Storby	670:08	1.X.1985
B5	Geta Getabergen	671:10	1.X.1985
B6	Finström Västanträsk	670:10	1.X.1985
B7	Sund Tosarby	669:11	1.X.1985
B8	Sund Prästö	669:12	1.X.1985
B9	Finström Godby	670:11	1.X.1985
B10	Lemland Rörstorp	668:11	1.X.1985
B11	Korpo (Korppoo)	668:20	3.X.1985
B12	Nagu (Nauvo)	668:21	3.X.1985
B13	Pargas (Parainen)	669:23	3.X.1985
C1	Pihtipudas	703:43	23.VIII.1985
C2	Pulkkila	713:44	23.VIII.1985
C3	Rantsila	715:43	23.VIII.1985
C4	Temmes	717:43	23.VIII.1985
C5	Oulu	721:42	23.VIII.1985
C6	Kuivaniemi	728:41	23.VIII.1985
C7	Ylitornio	736:35	22.VIII.1985
C8	Pello	741:36	22.VIII.1985
D1	Kapelskär		2.X.1985
D2	Norrtälje		2.X.1985
D3	W of Rimbo		2.X.1985
D4	Hallstavik		2.X.1985
D5	Alunda		2.X.1985
D6	NW of Östhammar		2.X.1985

4.3. Densities in the north

In the north where the life cycle, according to Brammanis (1975), takes three years, adults and two nymphal instars are

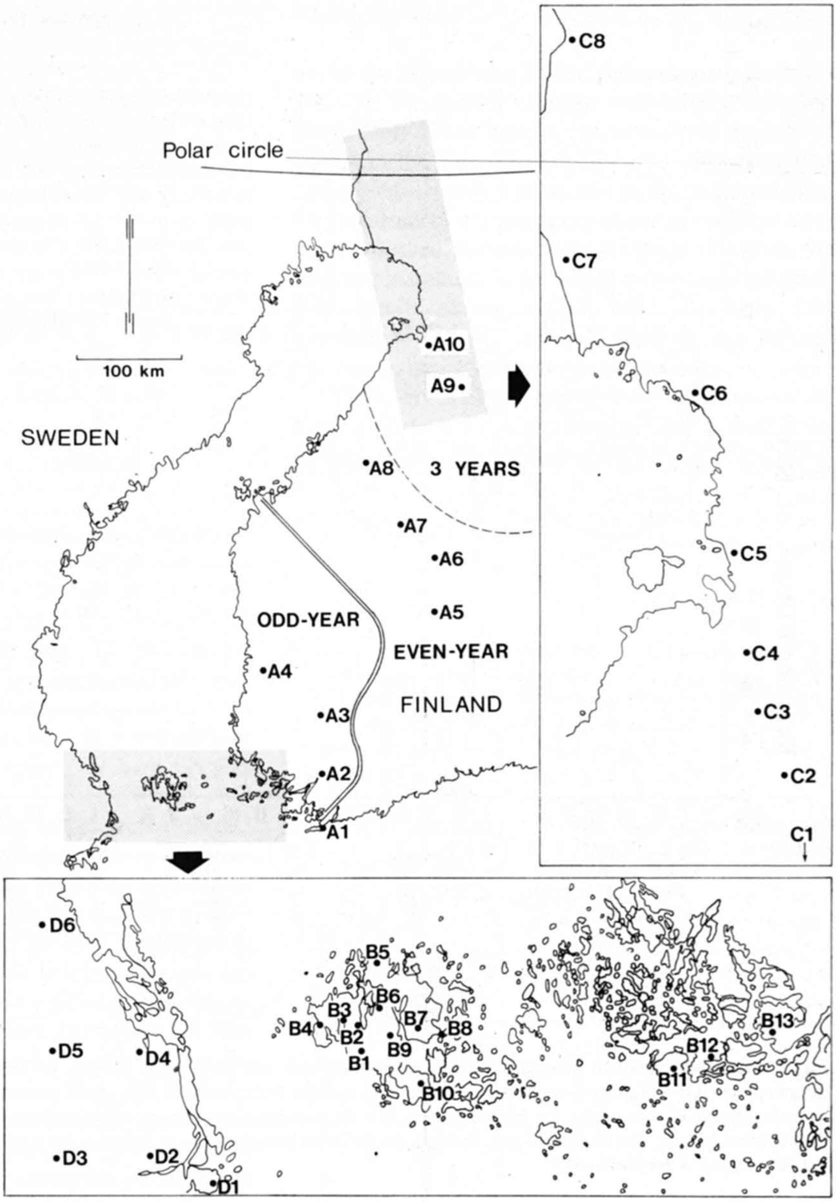

Fig. 1. Sampling localities A1–10, B1–13, C1–8, and D1–6. The transition zone between western odd-year and eastern even-year populations of the pine bark bug is indicated by a double line and the approximate northern limit of the eastern even-year population by a broken line.

found simultaneously. In order to obtain more accurate information about the absolute and relative densities of the bugs in extreme northern conditions, eight sample localities were investigated in late August, 1985 (Fig. 1 and Table 1). Each locality consisted of 20 pines. A 100 × 100 mm^2 area of bark was sampled on every trunk.

4.4. Eastern Sweden — another mainland area

Since the origin of the western odd-year reproducing bugs was one of the main subjects of the study, it was essential to obtain information on the life cycle from eastern Sweden. There was a possibility that the odd-year population in Finland could be only an invaded extension of the Swedish population, if in the same rhythm. It was also necessary to investigate another mainland area, separated by the sea, in order to obtain independent data on the life history strategies in general.

Six sample plots were chosen in different parts of Stockholm and Uppsala provinces, eastern Sweden, in October, 1985 (Fig. 1 and Table 1). At each plot densities of bugs were studied using 20 100 × 100 mm^2 bark samples. In contrast to the Finnish sample localities the landscape was dominated by deciduous trees and the few pine sites were edaphically distinctly better than those on the Finnish mainland.

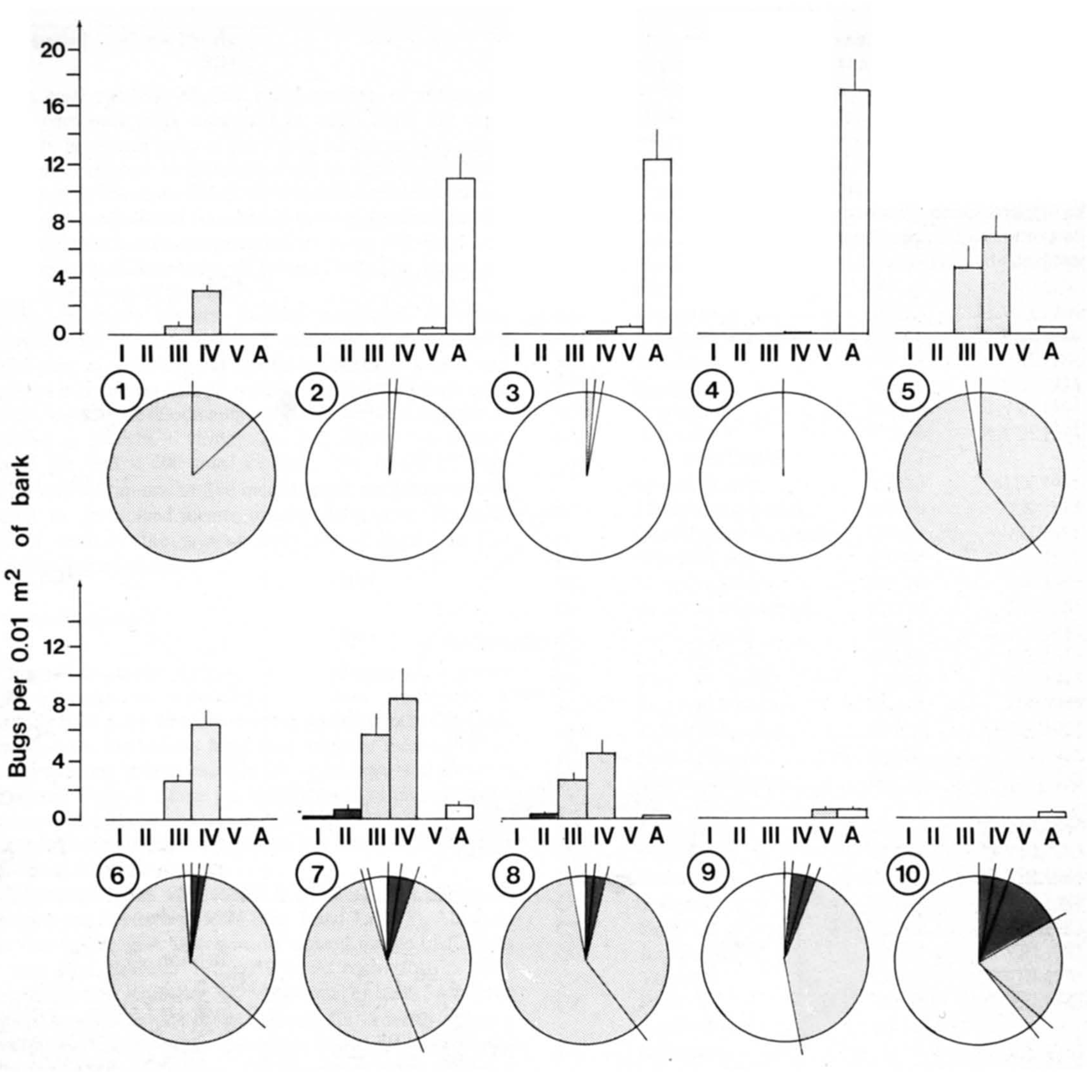

Fig. 2. Mean bug densities (diagram, individuals per 0.01 m2) and proportions (circles) of different developmental stages in ten sample plots (A1–10) along S-N gradient in Finland in autumn 1984. Vertical lines above the bars indicate the standard error of the mean in Figs. 2–6. A = adults, I = instar nymphs, II = second instar nymphs, etc. Sectors of the circles indicate the proportions of the different instars. The shades of grey indicate the different cohorts (the same shades are used for these cohorts in all Figs.). See Table 1 section A for localities.

4.5. Transition zone of the alternate-year populations

In a previous investigation (Heliövaara & Väisänen 1984b) we have presented a map showing the accurate location of the transition zone between the alternate-year populations of *A. cinnamomeus* near the town of Forssa in southern Finland. In the present study we have broadened the approach in order to obtain quantitative information on the densities of the two coexisting populations in the transition zone.

In May, 1984, 70 samples of pine bark bugs were taken in the area of the transition zone at intervals of 100 metres over a distance of 7 kilometres using the highway from Helsinki (60°13'N) to Pori (61°28'N). Each sample plot consisting of ten pines at the roadside were studied by removing 100 × 100 mm2 of bark from every trunk. A smaller sample size was used to avoid habitat changes due to sampling in this permanent study locality, which is not very rich in pines.

Furthermore, the coverage of pines in every 100-metre plot on the roadside was estimated using the scale 1–10. The given coefficient indicates the number of 10-metre slices of the plot where pines were recorded. In 1985, the forest on the roadside was drastically thinned and the study locality was mainly lost.

4.6. Transition zones of the 2-year and 3-year populations

The transition zone between 2-year and 3-year populations was studied in August, 1985, using the highway from Helsinki to Oulu (65°10'). The bug samples were taken at intervals of one kilometre over a distance of 200 kilometres astride the approximate location of the transition zone. The location of the study area is presented in the map in Fig. 6. Twenty pines were sampled using the sample size of a 100 × 100 mm^2 area of bark surface. In about 50 plots out of 200, suitable habitats allowed the bug densities to be counted. In other plots no pine bark bugs were recorded due to unfavourable habitats.

5. Results: Density and life history of the bug

5.1. Mainland areas

Aradus cinnamomeus was very abundant in all the ten sample localities (A1–10) where the large overall samples were taken. The bug density as a mean of 25 sampled pines varied from 0.4 to 18.6 bugs per 0.01 m^2 of bark (Fig. 2). The lowest densities were observed in the northernmost plots, and the highest in the area dominated by the western odd-year population. There was also remarkable variation in the bug density among the bark samples within localities.

At least two developmental stages were recorded at every plot. Individuals belonging to two different cohorts were observed in two plots out of ten, and apparently belonging to three different cohorts in the five northernmost plots. In the two southernmost plots, all individuals recorded belonged to one cohort. As a whole, one cohort predominated clearly over the other(s) in nine plots out of ten. Adults predominated in plots 2, 3 and 4 in the area of the western odd-year population, and III-IV-instar nymphs in plots 1, 5, 6, 7 and 8 in the area of the eastern even-year population. The proportion of individuals belonging to the dominating cohort was more than 90 % in these cases. Adults predominated slightly over nymphs in plots 9 and 10, where the life cycle seems to take three years.

In Sweden, the bugs represented the even-year reproducing generation in contrast to the western part of the Finnish mainland. Among the approx. 400 bugs there was only one individual out of phase indicating, however, the possible presence of an asynchronous population there too. The mean densities varied between 1.1 and 4.9 bugs per 0.01 m^2 of bark. These can be considered as relatively high densities in view of the edaphic quality of the sites.

5.2. Archipelagoes

In the Åland and Turku archipelagoes (samples B1–12), the density of bugs was usually low, and remarkably lower than in the vicinity of the city of Turku in the Finnish mainland, the only exception being Nagu, which lies nearest to the mainland (Fig. 3). Densities of the same magnitude as on Nagu have been observed, for example, at Pargas (B13), on the adjacent mainland. In the Åland archipelago the mean bug density of ten sample plots was only 1.04 individuals per 0.01 m^2, in spite of the habitats seeming externally favourable for the bugs.

Three coexisting cohorts were recorded in all sample plots in the Åland archipelago, as well as on Korpo. Adults predominated slightly in seven plots,

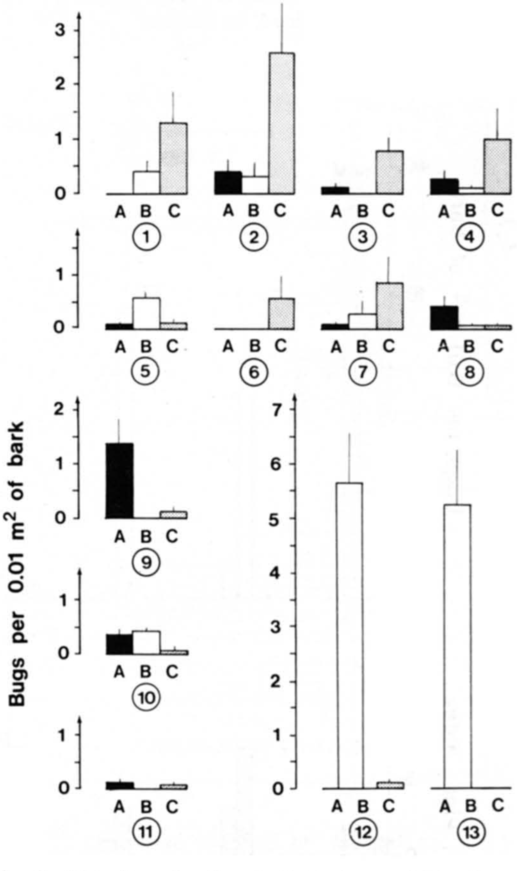

Fig. 3. Mean bug densities (individuals per 0.01 m^2) of different cohorts in 13 localities in the Åland and Turku archipelagoes in autumn 1985. A = small nymphs (I–III), B = large nymphs (IV–V), C = adults. Note the medium-sized nymphs on Nagu and Pargas (loc. 12–13). See Table 1 section B for localities. Note that Fig. 2 shows the situation one year before.

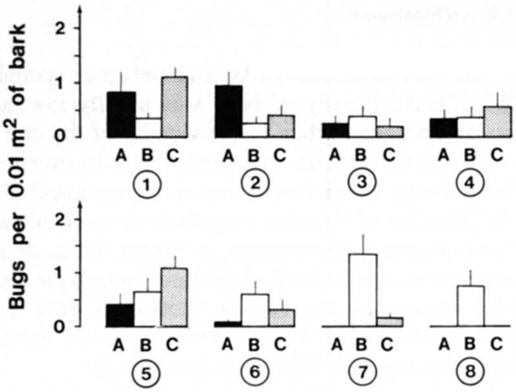

Fig. 4. Mean bug densities (individuals per 0.01 m²) of different cohorts in 8 localities in northern Finland in autumn 1985. A = small nymphs (I–III), B = large nymphs (IV–V), C = adults. See Table 1 section C for localities.

large nymphs in two plots, and small nymphs in two plots on Åland and Korpo. The three simultaneous developmental stages indicate that the life cycle of *A. cinnamomeus* in the archipelago is three years. It is also possible that there is a mixture of two- and three-year bugs, at least in some localities. In the easternmost sample locality (Nagu, B12) which lies closest to the mainland, almost all individuals (99 %) recorded belonged to the western odd-year generation indicating a life cycle of two years.

5.3. Northernmost localities

In the north (samples C1-8), three coexisting cohorts were recorded in all but the two northernmost sample plots (Fig. 4). This supports the idea of the three-year life cycle in the north. It remains possible too that at least in some areas there could be a mixture

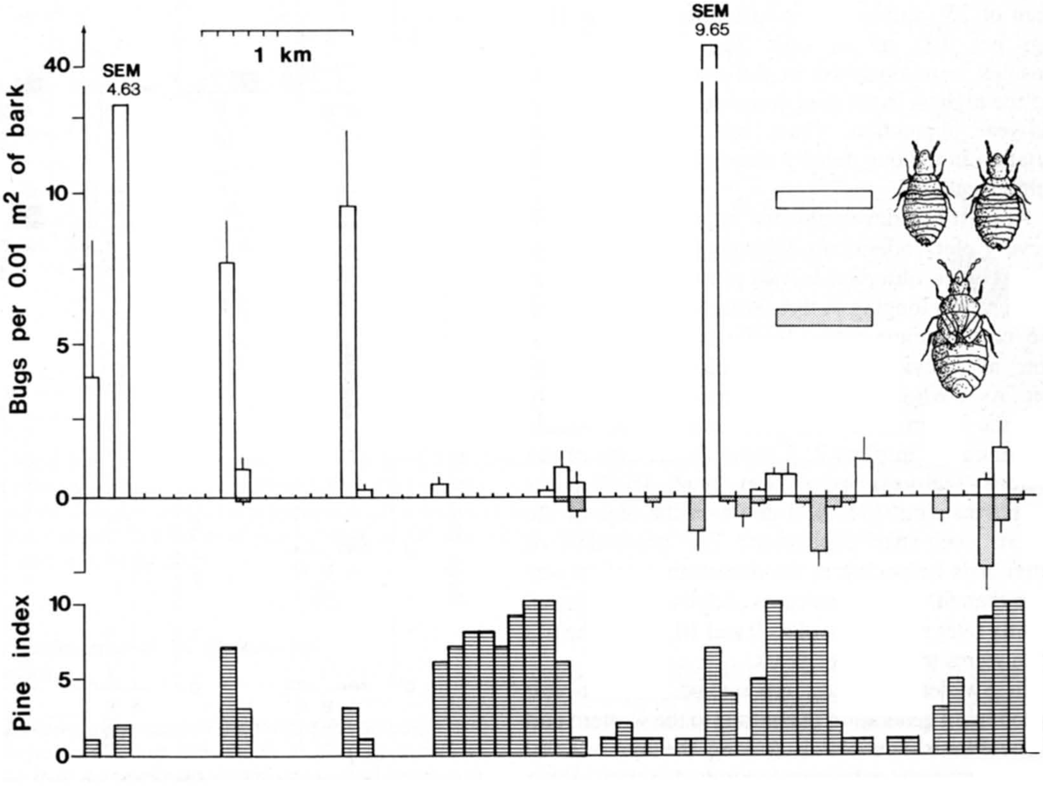

Fig. 5. Mean bug densities (individuals per 0.01 m²) of different cohorts across the transition zone between the alternate-year populations in spring 1984. The whole cross-section of the transition zone (see Heliövaara & Väisänen 1984b) is shown here, but the areas on both sides distinctly dominated by even- or odd-year populations have been omitted. The study site is shown by an asterisk in Fig. 7. White = medium-sized nymphs, grey = adults. The relative coverage of pines is given below in the scale 1...10 (see the text for explanations). SEM = standard error of mean.

of three- and two-year bugs. The cohorts were less distinct than in the area of two cohorts, possibly due to decreased growth rate in some individuals. Dominance relationships among age-classes seem to be fortuitous: adults predominated in one plot, large (or medium-sized) nymphs in four, and small nymphs in three plots. Bug densities were low compared with the densities in the area of the two-year life cycle.

5.4. Transition between the alternate-year populations

The thorough investigation of the bug densities in the transition zone between the alternate-year populations showed that even very high densities exist in the boundary (Fig. 5). The eastern even-year population gradually turns into the western odd-year population. In the transition zone both populations occur in approximately equal densities even on the same pine trunks.

In a small area in the midst of the transition zone, no bugs were recorded in spite of a dense young pine stand. Judged by the yearly growth level of the planted and carefully cultivated saplings, the site is edaphically very good, which serves to increase resistance against pests. This small "point" in the area can be considered very unfavourable for the bugs, which explains their total absence there (see also Heliövaara & Väisänen 1986b). In other parts of the transition zone relatively low densities can partially be explained as the result of repeated investigations which gradually enfeeble the habitat (cf. Heliövaara & Väisänen 1984b).

5.5. Transition between 2-year and 3-year populations

The samples taken over a distance of 200 kilometres astride the approximate transition zone between 2-year and 3-year populations showed no abrupt changes in the total bug density. The bug density only gradually decreased from south to north. The transect across the boundary can be classified into four subzones according to the observed relative density of the bugs of different age-classes (A–D in the right column in Fig. 6).

A: In the southernmost part of the present transect, over a distance of 31 kilometres all the bugs proved to belong to the eastern even-year population. This agrees with our previous studies

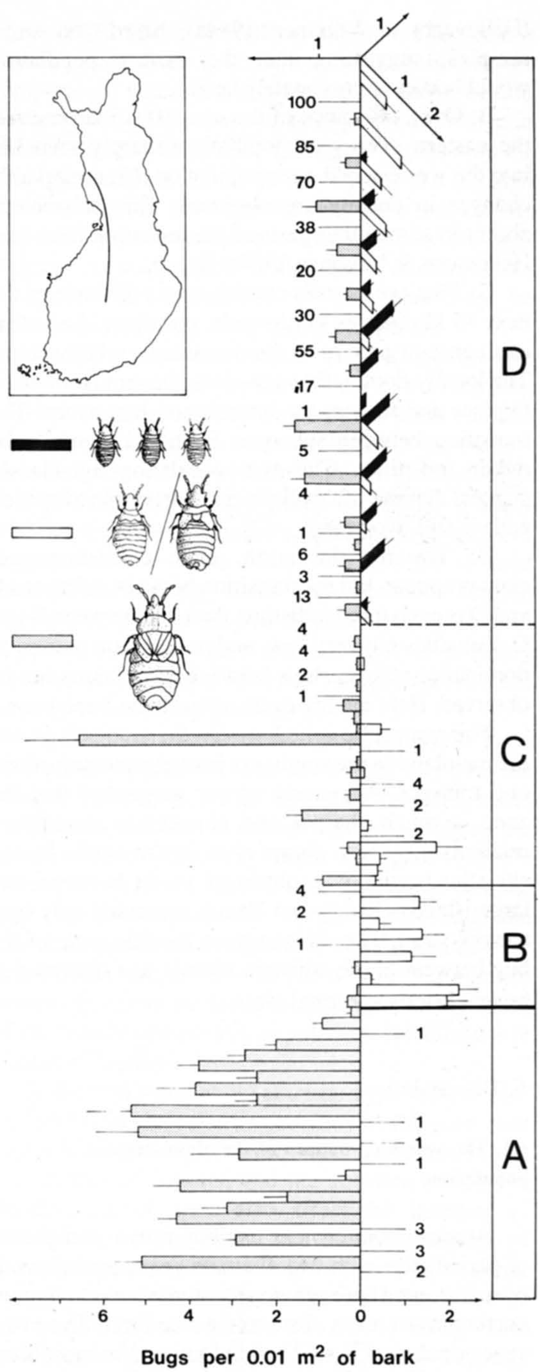

Fig. 6. Mean bug densities (individuals per 0.01 m^2) of different cohorts across the transition zone between the 2-year and 3-year populations in autumn 1985. Black = small nymphs, white = medium-sized (in the south) or large (in the north) nymphs, grey = adults. Numbers between bars indicate kilometres devoid of favourable habitats. For explanations of letters A–D in the right-hand column, see text.

(Heliövaara & Väisänen 1984a), based on small samples, suggesting that the eastern population would border approximately here.

B: Over a distance of the next 10–15 kilometres, the eastern even-year population sharply switches into the western odd-year population. No remarkable changes in density are observed. This subzone is absent in some other parts of the transition zone (see Heliövaara & Väisänen 1984a: fig. 1).

C: Two age-classes coexist over a distance of the next 35 kilometres northwards, but there is no clear and constant pattern in the dominance relationships. The locally dominating age-class changes from place to place and so does the intensity of dominance. The transition between subzones B and C seems to be rather indistinct. The two coexisting age-classes suggest that the life cycle in this part of the transition zone is still two years.

D: Towards the north, three coexisting age-classes appear, but the transition between subzones C and D is even more indistinct than that between B and C. Densities are very low, and no constant pattern of dominance relationships between age-classes can be observed. Here the life cycle seems to be three years.

The respective zone between the archipelago and the mainland in the south was investigated only along one transect. A general survey suggested that the zone is much sharper and changes in dominance relationships more abrupt than in the north. In one site, the border was observed to lie between two large islands (Korpo and Nagu), separated only by a narrow strait. The difference in the life cycle of the bug between these adjacent islands was observed in several briefly surveyed plots.

6. Discussion

6.1. The switching pattern of the alternate-year populations

Aradus cinnamomeus exhibits a two-year pattern of periodicity with two alternate-year populations all over Europe where previously studied, excluding the northernmost areas close to the tree limit. The even-year population is said to predominate in most areas (Tropin 1949, Turcek 1964, Brammanis 1975, Pettersen 1975, Doom 1976, Heliövaara & Väisänen 1984a, b). However, small areas, where odd-year populations have been observed to predominate, are known in the Kiev region, the Ukrainian SSR (Tropin 1949), in Czechoslovakia (Turcek 1965), in southwestern Sweden (Brammanis 1975), and in western Finland (Heliövaara & Väisänen 1984a). In Sweden and Czechoslovakia there are also areas where two cohorts coexist in almost equal numbers (transition zones ?).

The results of the present study confirm the suggestion of distinct predominance of either of the two alternate-year populations over large geographical areas in Finland. The odd-year population predominates in the western, and the even-year population in the eastern, parts of the study area. However, in the eastern parts of Sweden, the even-year population predominates again. The shifts in dominance seem to be abrupt. The general pattern has been constant during the ten-year period of our studies over large geographical areas in southern Finland.

In the area of the two-year life cycle, the dominating allochronic populations of *A. cinnamomeus* appear to overlap only in a narrow transition zone. There is neither a gap nor a distinct decrease in the density of the bugs in the transition zone but both populations live in subequal densities even in the same pine trunks. In the North American periodical cicadas there are theoretically three reasons why broods one year out of phase should never coexist in the same woods (Simon & Lloyd 1982). Firstly, the climatic aberration by which they supposedly arose would be expected to affect the entire population. Secondly, newly-hatched nymphs of the leading brood will settle underground and have the advantage of being already established by the time young nymphs of the lagging brood appear. Given that the cicadas are very abundant, the leading brood may preempt all the suitable feeding sites, leaving nothing for the lagging brood. Thirdly, the numerical response of predators should fall heavily on the brood lagging one year behind another, probably eliminating the lagging brood. However, it should be noted that these arguments are not necessarily applicable in this case because they are applied to animals with very long life cycles (Hoppenstaedt & Keller 1976).

Previously we have shown (Heliövaara & Väisänen 1984b) that the hypothesis of a density-dependent host-parasitoid regulation system in the pine bark bug is not supported by our empirical results. If there was a gap or even a decrease in bug density, it could be imagined that both of the alternate-year populations would have been kept apart by the strong impact of parasitoids or predators, which would make such coexistence impossible in the transition zone, analogously with the periodical cicadas. Similarly, the same mechanisms as in the cicadas may explain the parapatric geographical pattern of the May beetles observed at least in some areas in Central Europe (see Hurpin 1962: Fig. 62).

6.2. Life-history in extreme areas

Several authors have recently produced data to support the theory that insect species occurring over a wide geographical range modify their life histories to suit the local conditions (e.g. Masaki 1978, Tauber & Tauber 1981, Bradshaw & Holzapfel 1983, Hodek 1983). For instance, some species that are usually univoltine appear to have a longer life cycle at high latitudes or altitudes. Thus it does not come as a big surprise that three coexisting cohorts of *A. cinnamomeus*, indicating a life cycle of three years instead of two, were observed in the north. What is entirely unexpected is that the same phenomenon was now observed in the southwestern part of the study area in the Åland archipelago. It is difficult to find any common environmental factors which could explain the similarity of these very different areas: the Åland archipelago belongs to the hemiboreal and the northern area to the mid- and northern boreal vegetation zones (the whole southern boreal zone lying between them; Ahti et al. 1968). However, there are "northern" features in the vegetation of the Baltic islands (e.g. Häyrén 1914, Kalliola 1973: 153, Ahti 1980). Among insects, e.g. the proportion of brachypterous forms of Heteroptera and Coleoptera is high both in the archipelagoes and in the north (Lindberg 1929, Gillerfors 1966).

The areas are situated at quite different latitudes so that day-length cannot regulate the pattern observed in the pine bark bug. Neither can the time of low autumn temperatures affecting the beginning of over-wintering (mainly in soil around the pine) explain the pattern: the autumns are long and warm in the archipelago. Thus, it is possible that different climatic factors are involved in the north and in the archipelago, if the life-history of the bug is essentially regulated by the climate.

However, there may be certain climatic factors in common with the archipelago and the northern areas. These include the low daily maximum temperatures in mid-summer. In fact, the shift in the life-cycle period from two to three years coincides with the long term mean values of the warmest months, for instance, roughly with the 21°C isotherm of the mean maximum daily temperatures of July (Kolkki 1966, Heino 1976, Heino & Hellsten 1983). We consider it possible that these low maximum temperatures (or temperature sums counted for values above certain critical limit temperature) may explain the change in the life cycle strategy. The biological explanation for this correlation is not clear. We suggest that the high daily maximum temperatures may be a prerequisite for the 2-year development. For instance, the high degree of evaporation under such circumstances increases the conduction of sap and may be advantageous for the sap sucking behaviour.

Both in the north and in the archipelago the absolute densities of bugs with very few exceptions were remarkably low. In the north the harsh climatic conditions may be the main explanation for the low densities, since the northern limit of the species is close. In the archipelago better resistance of pines and the spatial heterogeneity (note the two scales of fragmentation: islands themselves and the isolated pine patches among fields and deciduous forests) may partially cause the low densities of bugs, but we suppose that even here climatic factors probably causing the prolonged life cycle may also prevent the bugs from increasing in numbers.

In these extreme areas of 3-year life cycle, none of the cohorts predominates unambiguously over the others. Sometimes, as in the study of Brammanis (1975: two localities in northern Sweden), one of the cohorts can be distinctly more abundant than the others, but the dominance is never as drastic as in the area of the 2-year life cycle. Concerning the principally parapatric occurrence of the alternate-year populations we have concluded that interference competition may explain the biogeographical pattern of the locally dominating populations (Heliövaara & Väisänen 1986b).

In the environmentally extreme areas at least three factors affect the relative densities of the pine bark bug cohorts, namely climatic and edaphic conditions, the number of cohorts, and the absolute population density. All of these also affect the intensity of intraspecific competition. The interrelationships of these factors are more or less obscure, and several interpretations can be given. For instance, it can be assumed that bad climatic conditions make these localities unfavourable for the bugs, which naturally leads to a decrease in bug density. When the bug density is low, the possible intraspecific competition breaks down, which renders the coexistence of three age-classes possible at low numbers.

An alternative explanation suggests that the harsh climate causes the change in the life cycle period, and this change in the number of coexisting cohorts as such leads to the decrease in dominance and the fortuitous dominance pattern of the cohorts. The latter explanation was tested by a simple computer simulation.

An attempt has been made to describe the life history characteristics of periodical insects by means of several mathematical models. We used the model, with an exponential competition coefficient, proposed by Bulmer (1977). The mathematical model is briefly described in the Appendix. In the case of the two alternate-year cohorts, the following assumptions were made: the competition coefficient within a cohort $\beta_i=0.01$, the competition coefficient indicating the inhibitory effect of young nymphs on old nymphs $\beta_0=0$, and the coefficient signifying the inhibition of young nymphs by old (β_2) varies from 0.021 to 0.035 (Table 2a). At the beginning both cohorts have the same density (10). The coefficient of population growth is the same (2) for both age-classes. The coefficients were obtained by random testing of some biologically relevant parameter values. Highly deviating coefficients would have lead to the accelerated exclusion of one of the cohorts. The values are not based on empirically calculated results on the pine bark bug (see, however, Heliövaara & Väisänen 1986b). The simulation gave the following results: one cohort disappears in about 40 years when the intensity of competition $\beta_2=0.035$, in 50 years when $\beta_2=0.030$, in 100 years when $\beta_2=0.025$, in 150 years when $\beta_2=0.023$, and only after several hundred years when $\beta_2=0.021$.

In the case of three sympatric cohorts with a three-year life cycle, the following assumptions were made: the competition coefficient within any cohort $\beta_i=0.01$, and the competition coefficient indicating the inhibitory effect of younger nymphs on older ones $\beta_0=0$. The coefficient of medium-sized nymphs on the youngest and respectively that of the oldest nymphs on the medium-sized ones β_1 varies from 0.014 to 0.017, and that of the oldest nymphs on the youngest nymphs β_2 from 0.021 to 0.035 (Table 2b). The densities of all the cohorts are the same (10) at the beginning. The coefficient of population growth is the same (2) for all the cohorts. The simulation gave the following results: the system is approximately stable when $\beta_1=0.014$ and $\beta_2=0.025$, one cohort disappears in about 540 years and two cohorts in 810 years when $\beta_1=0.016$ and $\beta_2=0.03$, and two cohorts disappear in 200 years when $\beta_1=0.014$ and $\beta_2=0.025$.

Table 2. Competition coefficients for (a) two and (b) three allochronic competitive cohorts used in the computer simulation.

2-year life cycle		
	Nymphs	Adults
Nymphs	0.01	0.021–0.035
Adults	0	0.01

3-year life cycle			
	Small nymphs	Large nymphs	Adults
Small nymphs	0.01	0.01 –0.017	0.021–0.035
Large nymphs	0	0.01	0.014–0.017
Adults	0	0	0.01

The above simulations lead to a conclusion that the rate of disappearance of a cohort is remarkably lower in the system of three cohorts than that of two cohorts, even when the intensity of competition is the same. However, it must be emphasized that the mechanism of the possible competition is not known (Heliövaara & Väisänen 1986b). Moreover, the above deterministic model does not take into account spatial heterogeneity and inter-year climatic variation affecting the system.

6.3. The origin of the alternate-year pattern

We have previously discussed the possible explanations for the origin of the present highly exceptional biogeographical pattern (Heliövaara & Väisänen 1984a). The following three explanations have been offered for the alternate-year pattern: 1. the two populations have invaded Finland from different directions, 2. a meteorological catastrophe has destroyed the dominance of a chief population, and 3. one population or the other has originated in the north and spread southwards into an area where neither population occurred originally.

According to the present results either of the locally dominating populations in the mainland may also have originated in the archipelago, where three age-classes are found simultaneously. It can be assumed that successful dispersal in one year could cast sporadic individuals on any island devoid of bugs leading to spatial dominance of its offspring. In fact, this seems to us to be the most probable mechanism for the origin of the parapatry of the alternate-year populations. For instance, if the bug has invaded Finland from Sweden through the Åland archipelago, it may have resulted in different dominant cohorts on the Finnish mainland due to this "random dominance generator" (Fig. 7). It is also

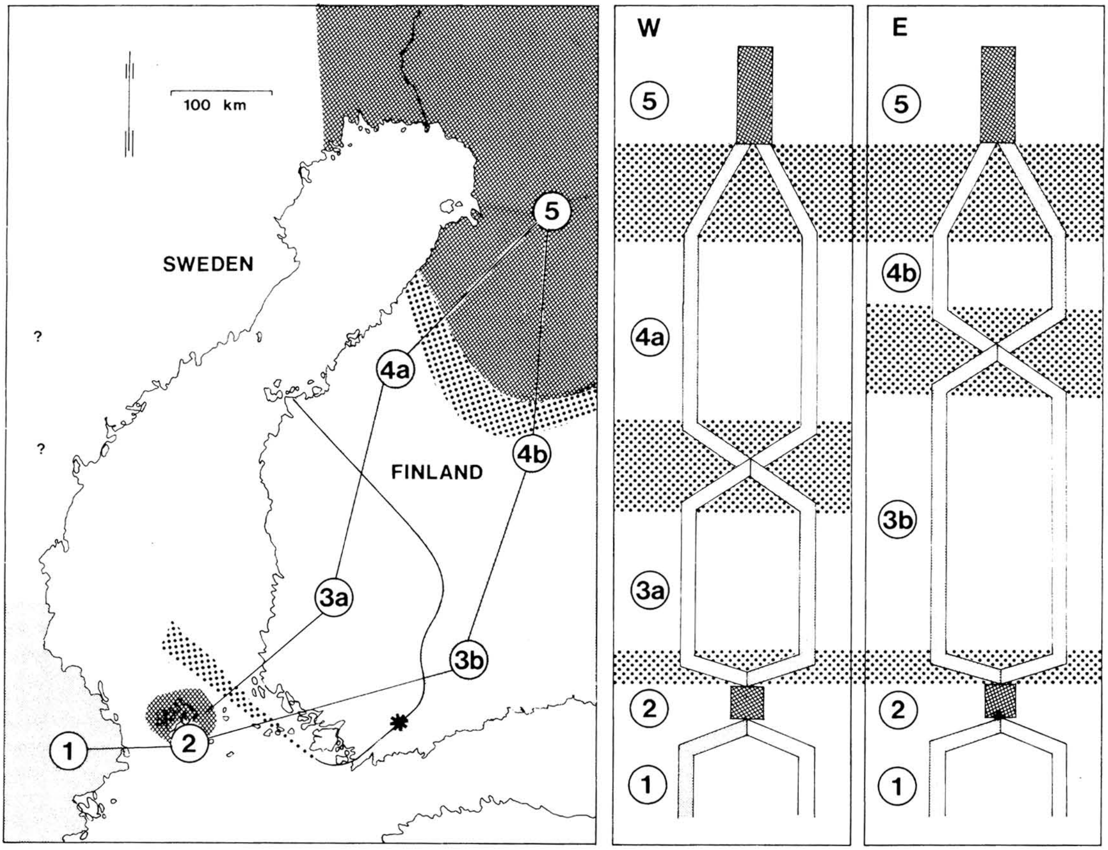

Fig. 7. Distribution and dominance of bugs with different life-cycles in Finland and eastern Sweden, and the proportions of alternate-year populations in the 2-year area along two transects (a and b, diagrams below the map). The local relative proportions of the allochronic even- (=grey) and odd-year (=white) populations along these transects are either near 0 or 100 %, except in the transition zones (=dotted). In the 3-year areas (=cross-lining) there is not such a distinct numerical dominance of one cohort over another. The asterisk on the transition zone refers to Fig. 5.

possible that the bug has invaded Finland from the southeast as an even-year predominated population and from the southwest as another even-year population which, however, has become odd-year dominant when the 3-year life-cycle area has been used as a stepping stone for dispersal.

The subzone B between the 2- and 3-year areas (see Fig. 6) may have originated from the action of the other, northern area of the 3-year life cycle: By chance, due to annual differences in the duration of the life cycle near the 2- and 3-year limit, the odd-year population has gained dominance within the normal area of the even-year population. The whole cohort may have been retarded in its growth in one year due to unfavourable weather conditions, resulting in these deviating dominance relationships. Even the changing pattern of local dominance in the subzone C may have resulted from minor annual variation in the development time.

Roff (1980) has explored the problem of adapting development time to changes in the length of time conditions that are favourable for growth and reproduction. Systematic changes in this "season length" along some gradient such as latitude can generate either simple clines in development time or "saw-tooth"clines (requiring no sharp environmental changes). He concludes that fitness is maximized, in general, when the whole season is utilized for growth and reproduction. The observation that the transition zone between the 2- and 3-year life-cycle areas of the bug is relatively sharp, especially in the archipelago, may partially result from genetic adaptation of the bugs to their local environments. There could be canalized 2-year and 3-year bugs which would differ genetically from each other in the length of their life-cycle. If there were environmentally induced mechanisms to choose between the two life-cycle strategies, one could expect the transition zone to be wider due to inter-year variation (which on the other hand increases the difficulty of determining the optimal phenology in a particular environment), individual differences in the responses, and especially spatial differences due to microclimatic (and edaphic) conditions. However, the observed relatively sharp pattern is possible, even if the change in life cycle were only due to developmental plasticity, i.e. either developmental conversion or phenotypic modulation (Smith-Gill 1983). When the phenotype is altered due to input of the environment, it is commonly referred to that process of alteration known as developmental plasticity. In developmental conversion, organisms use specific environmental cues to activate alternative genetic programmes controlling development. This conversion may be considered adaptive. In phenotypic modulation, non-specific phenotypic variation results from environmental influences on rates or degrees of expression of the developmental programme, but genetic programmes controlling development are not altered. Thus, the organism is simply passively responding to a variable environment. Smith-Gill (1983) concludes that modulation, which is not necessarily adaptive, is probably the common form of environmentally induced phenotypic variation, especially in higher organisms. Also intraspecific competition between cohorts which are too similar in their age and size may affect the width of the transition zone between the 2- and 3-year life-cycle areas (at least in the case of modulation this may be the main factor). According to the above computer simulations, high values of competitive coefficients indicating the inhibitory effect of one cohort on another would lead to the rapid disappearance of one cohort through competitive exclusion.

6.4. Gene exchange between allochronic bugs

The geographical variation in the life history traits of the pine bark bug observed in the present study clearly shows that there exists a possibility for gene exchange between the allochronic sympatric bugs, although they are reproductively isolated from each other in the area of the same length of the life cycle (Fig. 7). The mechanism of supposed gene exchange between allochronic odd/even-year populations via mutual contact with the 3-year life cycle is illustrated in Fig. 8. It should be pointed out that the presence of the 3-year life-cycle would promote gene exchange between the allochronic cohorts only in places where it could come in contact with both even- and odd-year cohorts. For example, the 3-year population in northern Finland would not necessarily promote gene exchange between even- and odd-year populations, while the 3-year population in the archipelago could do so.

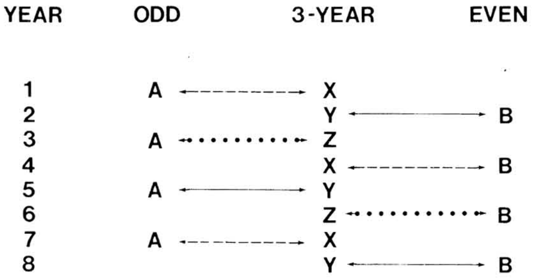

Fig. 8. Gene exchange among allochronic even/odd-year populations could be achieved via mutual contact with the 3-year life-cycle. In this example, cohorts are lettered. Cohort A could mate with cohort X every 6 years. Cohort A could mate with cohort X and 3 years later cohort X could mate with cohort B, with the possibility of gene transfer from A, and so on with Y and Z such that A and B could receive each other's genes every generation. The arrows indicate possible gene exchange.

This phenomenon is related to the well-known cases of "ring species" (Cain 1954, Mayr 1963, Wake & Yanev 1986, Wake & al. 1986) in which the distal populations of a species with a circular geographical distribution are reproductively isolated due to the accumulated genetic differences reflecting the ecology and behaviour of these distal ends. In the present case, however, the genetic isolation mechanisms have probably not yet developed (Heliövaara, Väisänen, Hantula, Saura & Lokki, unpubl.). Moreover, the reproductively isolated bug populations have, in fact, the same distribution (in spite of the strong dominance of one cohort over another), in contrast to the relatively small areas of sympatric but reproductively isolated populations in the case of ring species. The fact that the genetic isolation is not total has a different basis in the two cases. In the ring species the gene exchange between the distal ends happens more or less continuously through a series of geographically adjacent populations. In the pine bark bug there are, in addition to the series of synchronic geographically adjacent populations, also distinct zones where the gene change between allochronic populations is possible. In the resulting pattern the sympatric but allochronic bugs of the "central" area of the species may be more isolated from each other than are synchronic widely allopatric populations, although the actual degree of isolation is, of course, also related to the rate of gene flow.

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Appendix. Bulmer's (1977) mathematical model for competition in periodical insects

An insect population is said to be periodical if the life cycle has a fixed length of k years ($k > 1$) and if the adults do not appear every year but only every kth year. Periodical behaviour might result from competitive exclusion between year-classes if competition is stronger between insects of different ages than between insects of the same age. Bulmer (1977) has represented this idea by a mathemathical model:

$$N_{j+1}(t+1) = S_j N_j(t) \exp\,[-\sum_i \alpha_{ij} N_i(t)], \quad 0 \le j \le k-2,$$

$$N_0(t+1) = B\, S_{k-1} N_{k-1}(t) \exp\,[-\sum_i \alpha_{i,\,k-1} N_i(t)].$$

In these equations $N_j(t)$ is the number of insects of age j in year t ($j = 0, 1, \ldots, k-1$) counted just after the eggs have been laid and the adults have died, S_j is the probability that an individual of age j will survive for one year in the absence of competition, B is the average number of eggs laid per adult, and a_{ij} is a coefficient of competition which specifies the relative amount by which an individual of age i decreases the survival rate of an individual of age j.

The subsequent analysis is easier to interpret if we work with the transformed variables

$$n_j(t) = c_j N_j(t)$$

$$\beta_{ij} = \alpha_{ij} / c_i,$$

where

$$c_j = F^{j/k} / S_0 S_1 \ldots S_{j-1}$$

$$F = S_0 S_1 \ldots S_{k-1} B$$

F is the power of increase per generation in the absence of competition. In terms of these variables the equations (1) become

$$n_{j+1}(t+1) = F^{1/k} n_j(t) \exp\,[-\sum_i \beta_{ij} n_i(t)], \quad 0 \le j \le k-2,$$

$$n_0(t+1) = F^{1/k} n_{k-1}(t) \exp\,[-\sum_i \beta_{i,\,k-1} n_i(t)].$$

The transformation defined in (2) and (3) was chosen so as to make the ratio $n_{j+1}(t+1) / n_j(t)$ a constant in the absence of competition. The justification for this transformation is that the competition coefficients α_{ij} are not directly comparable with one another for different values of i, since they take no account of the number of individuals of age i which are competing with an individual of age j. The transformation ensures that at equilibrium the values of n_j are at least approximately the same at all ages, so that the competition coefficients β_{ij} are comparable.

Information about stability can be obtained by numerical simulations (see the text). For further details on the model and its interpretation, see the original paper by Bulmer (1977).

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